



**HAL**  
open science

# The biodiversity of the Palaeozoic phytoplankton

David Kroeck

► **To cite this version:**

David Kroeck. The biodiversity of the Palaeozoic phytoplankton. Paleontology. Université de Lille, 2019. English. NNT : 2019LILUR077 . tel-03647907

**HAL Id: tel-03647907**

**<https://theses.hal.science/tel-03647907>**

Submitted on 21 Apr 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Université de Lille

UMR 8198 – Evo-Eco-Paléo – CNRS

Ecole Doctorale – 104

Sciences de la Matière, du Rayonnement et de l'Environnement

Thèse en vue de l'obtention du titre de Docteur de l'Université de Lille

Spécialité: Géosciences, Ecologie, Paléontologie et Océanographie

par

**David M. KROECK**

---

**La biodiversité du phytoplancton du Paléozoïque**

---

Thèse dirigée par

Thomas SERVAIS

et

Claude MONNET

Date de soutenance prévue le 06 décembre 2019

Membres du jury:

Catherine CRÔNIER	Université de Lille, France, <i>Examineur</i>
Frédérique EYNAUD	Université de Bordeaux, France, <i>Rapporteur</i>
Thomas H. P. HARVEY	University of Leicester, Royaume-Uni, <i>Examineur</i>
Jun LI	Nanjing Institute of Geology and Palaeontology, Chine, <i>Examineur</i>
Claude MONNET	Université de Lille, France, <i>Co-directeur de thèse</i>
Thomas SERVAIS	Université de Lille, France, <i>Directeur de thèse</i>
Gerard VERSTEEGH	Universität Bremen, Allemagne, <i>Examineur</i>
Karin ZONNEVELD	Universität Bremen, Allemagne, <i>Rapporteur</i>





University of Lille

UMR 8198 – Evo-Eco-Paléo – CNRS

Doctoral School – 104

Sciences of Matter, Radiation and the Environment

Thesis for obtaining the title of Doctor of the University of Lille

Specialisation: Geosciences, Ecology, Palaeontology and Oceanography

by

**David M. KROECK**

---

**The biodiversity of the Palaeozoic phytoplankton**

---

Thesis directed by

Thomas SERVAIS

and

Claude MONNET

Public defense scheduled for the 06<sup>th</sup> December 2019

Members of the jury:

Catherine CRÔNIER	Université de Lille, France, <i>Examiner</i>
Frédérique EYNAUD	Université de Bordeaux, France, <i>Reviewer</i>
Thomas, H. P. HARVEY	University of Leicester, United Kingdom, <i>Examiner</i>
Jun LI	Nanjing Institute of Geology and Palaeontology, China, <i>Examiner</i>
Claude MONNET	Université de Lille, France, <i>Co-Director</i>
Thomas SERVAIS	Université de Lille, France, <i>Director</i>
Gerard VERSTEEGH	Universität Bremen, Germany, <i>Examiner</i>
Karin ZONNEVELD	Universität Bremen, Germany, <i>Reviewer</i>



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

## Abstract

The phytoplankton play a major part in Earth's ecosystems. They constitute a large part of the base of marine foodchains and therefore represent the starting point for most biological activity in the oceans. Moreover, phytoplanktic organisms are responsible for most photosynthetic activity on Earth, producing at least half the amount of oxygen, and they are responsible for a major part of the carbon transfer from the atmosphere to the ocean. Changes in ancient phytoplankton composition probably had impacts on both the climate and the marine ecosystems.

The major aim of my study concerns diversity trends of the phytoplankton during the Palaeozoic. Palaeobiodiversity trajectories are computed from an exhaustive database of occurrences described in literature, and by means of different diversity metrics to account for various facets and biases.

The results show generally high diversity values in the early and middle parts of the Palaeozoic followed by very low diversity in the late Palaeozoic. Major radiations are recorded from the Lower to Middle Ordovician, in the lower Silurian, and in the Upper Devonian, and major extinctions in the latest Ordovician, in the late Silurian–Lower Devonian interval, and from the Upper Devonian to the Carboniferous. Several palaeoenvironmental factors are found to be probably related to the recorded diversity trends, such as palaeogeography, sea-level changes, terrestrial sediment influx, and atmospheric CO<sub>2</sub> concentrations.

A major problem concerning the study of acritarchs in general, and the study of their biodiversity in particular, is their questionable taxonomy. With many previous studies done in a stratigraphic context, a high number of taxa was described, without considering intrageneric and intraspecific morphological variability. Therefore, taxonomic revisions are needed. Within the present work, three studies were done to assess this issue:

A first study concerns the genus *Vulcanisphaera*. A revision of the literature and the use of statistical methods based on morphometric measurements on populations from Algeria, Iran and England, shows that only three of 32 species described in literature can be maintained within the genus *Vulcanisphaera*: *V. africana*, *V. mougnoana*, and *V. simplex*.

A second study is focusing on *Orthosphaeridium*. After a comprehensive review of the literature and new investigations on material from Iran and China, only four of 20 species described in literature are maintained: *O. bispinosum*, *O. ternatum*, *O. rectangulare*, *O. octospinosum*.

A third investigation concerns the peteinoid acritarchs. In my new palynological investigation of samples from Öland, large populations of peteinoid acritarchs (*Peteinosphaeridium*, *Liliosphaeridium*) were recovered. The results of statistical methods indicate that the currently used taxonomy is not applicable.

In addition to temporal biodiversity trends, the database is also used to detect palaeogeographic signals. Within the present work, the latitudinal diversity gradient (LDG) of the microphytoplankton of the early Palaeozoic is reconstructed. The results show an unimodal LDG, with highest diversity in mid latitudes of the Southern Hemisphere. Changes in the amplitude of the LDG during the Cambrian–Ordovician interval are interpreted as being related to long-term cooling.

A last part of the study represents an investigation related to biostratigraphy and palaeobiogeography. During the Lower and Middle Ordovician, marked provincialism is known for the phytoplankton, with two major distinguishable microfloras. A new study on samples from Colombia was performed in order to investigate the provincial affinities of the microphytoplankton associations of northwestern South America. In addition, the samples allowed a precise stratigraphic assignment based on the palynoflora. The sample material can be assigned to the Floian (Lower Ordovician) and belongs clearly to the peri-Gondwanan acritarch province.

**Keywords:** palaeopalynology, micropalaeontology, phytoplankton, acritarchs, prasinophytes, Palaeozoic, biodiversity, palaeogeography, palaeoecology, taxonomy, biostratigraphy

## Résumé

Le phytoplancton joue un rôle majeur dans les écosystèmes de la Terre. Ils constituent une grande partie des chaînes alimentaires marines et représentent donc le point de départ de la plupart des activités biologiques dans les océans. De plus, les organismes phytoplanctiques sont responsables de la plupart des activités photosynthétiques sur Terre, produisant au moins la moitié de la quantité d'oxygène, et sont responsables de la majeure partie du transfert de carbone de l'atmosphère à l'océan. Les modifications du phytoplancton ancien ont probablement eu des effets à la fois sur le climat et les écosystèmes marins.

L'objectif de mon étude est l'analyse de la diversité du phytoplancton au Paléozoïque. Les trajectoires de paléobiodiversité sont calculées à partir d'une base de données exhaustive d'occurrences décrites dans la littérature et à l'aide de différentes métriques de diversité afin de prendre en compte diverses facettes et biais.

Les principales radiations du phytoplancton sont enregistrées dans l'Ordovicien inférieur et moyen, dans le Silurien inférieur et dans le Dévonien supérieur, et les extinctions majeures dans l'Ordovicien Supérieur, dans l'intervalle du Silurien supérieur au Dévonien inférieur, et du Dévonien supérieur au Carbonifère. Plusieurs facteurs, tels que la paléogéographie, les variations du niveau de la mer, l'afflux de sédiments terrestres et les concentrations de CO<sub>2</sub> dans l'atmosphère ont été relevés comme influençant ces fluctuations de diversité.

Un problème majeur concernant l'étude des acritarches, et l'étude de leur biodiversité en particulier, est leur taxonomie discutable. De nombreuses études antérieures ayant été réalisées dans un contexte stratigraphique, et un grand nombre de taxons a été décrit, sans tenir compte de la variabilité morphologique. Par conséquent, des révisions taxonomiques sont nécessaires. Dans le cadre du présent travail, trois études ont été réalisées pour évaluer cette question.

Une première étude concerne le genre *Vulcanisphaera*. Une révision de la littérature et l'utilisation de méthodes statistiques basées sur des mesures morphométriques sur des populations d'Algérie, d'Iran et d'Angleterre montrent que seules trois des 32 espèces décrites dans la littérature peuvent être conservées dans le genre.

Une deuxième étude porte sur *Orthosphaeridium*. Après une revue complète de la littérature et de nouvelles recherches sur du matériel provenant d'Iran et de Chine, seules quatre des 20 espèces décrites dans la littérature sont conservées.

Une troisième enquête concerne les acritarches péteinoïdes. Dans ma nouvelle analyse palynologique des échantillons d'Öland les méthodes statistiques indiquent que la classification actuellement appliquée se révèle inutilisable.

La base de données est également utilisée pour détecter les signaux paléogéographiques. Dans le présent travail, le gradient de diversité latitudinale (LDG) du microphytoplancton du Paléozoïque inférieur est reconstruit. Les résultats montrent un LDG unimodal, avec la diversité la plus élevée dans les latitudes moyennes de l'hémisphère Sud.

Une dernière partie de l'étude consiste en une analyse palynologique appliquée à la biostratigraphie et la paléobiogéographie. Au cours de l'Ordovicien inférieur et moyen, le phytoplancton se caractérise par un provincialisme marqué, avec deux grandes microflores distinguées. Notre étude sur des échantillons provenant de Colombie a permis de préciser les affinités provinciales des associations de microphytoplancton du nord-ouest de l'Amérique du Sud. En outre, les échantillons ont permis une datation stratigraphique précise basée sur la palynoflore. L'intervalle d'échantillonnage peut être attribué à l'Ordovicien Inférieur (Floian) et fait définitivement partie de la province péri-gondwanienne.

**Mots-clés:** paléopalynologie, micropaléontologie, phytoplancton, acritarches, prasinophytes, Paléozoïque, biodiversité, paléogéographie, paléoécologie, taxonomie, biostratigraphie

## **Acknowledgements / Remerciements / Danksagung**

First of all I want to express my gratitude for the opportunity to work on this project under the supervision of Thomas Servais and Claude Monnet. I want to thank both of them for their great support, their advice, and their proofreading. I am deeply grateful to Claude for all the calculations, which constitute a great part of the basis of this work. Also, I want to thank very much Axelle Zacaï for her precious contribution to the database and her advice in so many things. I thank Gary Mullins for providing me with the data in the first place, for his support and advice, and the discussions we had helping me to advance.

I thank my dear friends and colleagues Navid Navidi-Izad, Houcine Benachour, Zhen Shen, Shucan Zheng, Valentin Bault and Vahram Serobyan for their advice, the many scientific discussions that helped my work to move forward.

Many thanks to the team of Evo-Eco-Paléo for three nice years, welcoming me so warmly, and the many laughs during the obligatory coffee breaks. I thank Sylvie Régner for the preparation of my samples. A special thank also to Elisabeth Locatelli and Jessie Cuvelier for providing me with literature when the internet could not.

I thank also Lorena Tessitore, Chloé Amberg, Ninon Allaire and Noemi Sevêque for their valuable support in the first months of my PhD studies, especially in all the problems a foreigner faces when settling in France.

I want to express my gratitude to Martin Langer, who called my attention to the project in the first place.

I thank Mathilde Blanchon for her initial work on *Vulcanisphaera*.

Many thanks to Andrés Pardo-Trujillo, Angelo Plata Torres, Millerlandy Romero-Baéz, Elena Raevskaya, Zbigniew Szczepanik, Anders Lindskog, Mats Eriksson and Michel Dubois, who co-author my papers and contributed with their valuable suggestions and advices greatly to this work.

I am grateful to Laurence Debeauvais and François Holvoete for managing with all the paperwork I burdened them with.

I would like to thank Cathérine Cronier, Frédérique Eynaud, Tom Harvey, Li Jun, Gerard Versteegh and Karin Zonneveld, who agreed to review my work as members of the jury.

I want to thank also Lucie Legros and Marion Joly, without whom I would have lost my will early on, for their great support and making me feel home.

Und vielen Dank an meinen liebsten Schatz. Ohne Dich hätte ich es nicht geschafft.

## Table of contents

Abstract .....	2
Résumé.....	3
Acknowledgements / Remerciements / Danksagung.....	4
List of enclosed articles.....	6
Introduction.....	7
1 <i>Phytoplankton</i> .....	7
1.1 <i>Phytoplankton and climate</i> .....	7
1.2 <i>Phytoplankton and the trophic chain</i> .....	9
1.3 <i>Primary production vs. diversity</i> .....	9
1.4 <i>Early history of phytoplankton</i> .....	9
1.5 <i>Phytoplankton in the Palaeozoic</i> .....	10
1.6 <i>Acritarchs – affinities and biology</i> .....	11
1.7 <i>Application of acritarchs</i> .....	12
2 <i>The Palaeozoic Era</i> .....	13
2.1 <i>Geochronology</i> .....	13
2.2 <i>Bioevents</i> .....	13
2.2.1 <i>Diversification Events</i> .....	13
2.2.2 <i>Extinction events</i> .....	14
2.3 <i>Palaeozoic palaeogeography</i> .....	14
2.4 <i>Palaeozoic sea level changes</i> .....	15
2.5 <i>Palaeozoic climate history</i> .....	15
3 <i>Objectives</i> .....	16
3.1 <i>Biodiversity of the phytoplankton of the Palaeozoic</i> .....	16
3.2 <i>Classification of Palaeozoic organic-walled microphytoplankton</i> .....	16
3.3 <i>Biostratigraphy</i> .....	19
3.4 <i>Palaeoecology</i> .....	20
3.4.1 <i>Abiotic factors</i> .....	20
3.4.2 <i>Biotic factors</i> .....	21
3.5 <i>Palaeobiogeography of Palaeozoic microphytoplankton</i> .....	21
3.5.1 <i>Latitudinal diversity gradients</i> .....	21
3.5.2 <i>Provincialism</i> .....	22
References.....	23



## **List of enclosed articles**

**Article I** – The Biodiversity of the Palaeozoic phytoplankton

**Article II** – Revision of the Cambrian–Ordovician acritarch genus *Vulcanisphaera* Deunff 1961

**Article III** – Revision of the Middle and Upper Ordovician acritarch genus *Orthosphaeridium* Eisenack 1968

**Article IV** – Morphological variability of peteinoid acritarchs from the Middle Ordovician of Öland, Sweden and implications for acritarch classification

**Article V** – Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia

**Article VI** – Truncated bimodal latitudinal diversity gradient in early Palaeozoic phytoplankton

## Introduction

### *1 Phytoplankton*

The term phytoplankton describes the part of the plankton composed of photoautotrophic organisms. Thus, the term stands for a diverse, polyphyletic group of aquatic photosynthetic organisms floating in the water column and drifting with currents (Falkowski & Raven, 1997). The phytoplankton appears to comprise taxa from 14 phyla of bacterial and eukaryotic protist domains (Reynolds, 2006). Within Earth's ecosystems, the phytoplankton plays a major role in regulating ocean-atmosphere interactions, and in constituting the base of marine foodchains.

#### *1.1 Phytoplankton and climate*

The modeling of climate history was previously focused on ecosystems on land, with data for terrestrial vegetation included in most climate models, while the oceanic realm, and the role of the phytoplankton in particular, was neglected. But in recent years it became clear that the phytoplankton is a significant part of the regulation of climatic processes. However, our understanding of the impact of the marine plankton is still very limited.

Phytoplankton are an important part of the global carbon cycle. While they constitute less than 1 % of Earth's photosynthetic biomass, they account for half of all photosynthetic activity on Earth and are responsible for at least 45 % of net primary production (e.g., Field et al., 1998; Behrenfeld et al., 2001). Phytoplankton removes high amounts of CO<sub>2</sub> from the atmosphere, and when dying, subsequently transfers large parts of organic carbon to deep sea sediments, where it is sequestered for centuries or longer (Falkowski, 2012). By lowering the partial pressure of CO<sub>2</sub> in the upper ocean layers, the absorption of CO<sub>2</sub> from the atmosphere is facilitated by the generation of a steeper CO<sub>2</sub> gradient (Falkowski et al., 2000). Therefore, phytoplankton is attributed a strong influence on climatic processes (e.g., Murtugudde et al., 2002) and on biogeochemical cycles (e.g., Sabine et al., 2004; Roemmich & McGowan, 1995). Indeed, Tappan (1968) and Tappan & Loeblich (1970) argued that oceanic phytoplankton was the main control for atmospheric CO<sub>2</sub>/O<sub>2</sub> balance since the early Precambrian, with decreasing CO<sub>2</sub> and increasing O<sub>2</sub> as a result of higher phytoplankton productivity. On the basis of these assumptions they produced an atmospheric composition curve. However, this curve does not stand comparison to more recent models, which partly even showed inverse relationships.

Phytoplankton not only play a crucial role within the Earth's carbon cycle but are also an important part of the global sulfur cycle. Dimethylsulfide (DMS), the most abundant biological sulfur compound emitted to the atmosphere, originates primarily from the decomposition of dimethylsulfoniopropionate (DMSP), which is a major secondary metabolite in phytoplankton. 95 % of the DMS flux to the atmosphere is derived from the oceans (Kettle & Andreae, 2000). DMS is involved in the biological regulation of global climate (Bates et al., 1987; Charlson et al., 1987). In the atmosphere the gas oxidises to dimethyl sulfoxide (DMSO), dimethyl sulfone, methanesulfonic acid and SO<sub>2</sub>, and ultimately to sulfuric acid. Sulfuric acid condensates and forms aerosols. These aerosols represent as cloud condensation nuclei the dominant source for cloud formation over the oceans (Charlson et al., 1987). Therefore, DMS shall be assumed to have a significant impact on the climate. Two contrasting hypotheses suggest feedback mechanisms between the ocean ecosystem and the climate mediated by DMS. The CLAW hypothesis describes a negative feedback in the climate system, with cloud formation due to ocean-produced DMS reducing sunlight reaching the photic zone. This in turn would decrease phytoplankton growth and related DMS production (Charlson et al., 1987). The anti-CLAW hypothesis, however, proposes that increasing temperatures would lead to higher ocean stratification, causing a declining primary production by a decrease in nutrient supply from the deep ocean to the photic zone. The consequence would be a decrease in

DMS production and, therefore, cloud formation, leading to further climate warming (Lovelock, 2006).

Awareness of climate change as a major global crisis has significantly increased in the last decades. Its effects are already perceptible in many of the Earth's ecosystems. It has become an important task to estimate future consequences of the rapidly changing climate. Considering the forementioned role of the phytoplankton within the biosphere it is of great significance to predict the impact of changes of the ecosystems on the phytoplankton, such as rising temperatures and atmospheric CO<sub>2</sub> levels. It is estimated that marine ecosystems account for nearly one third of the anthropogenic CO<sub>2</sub> emissions being removed from the atmosphere (Hader et al., 2014). Increases of atmospheric CO<sub>2</sub> concentration through human activity is known to influence organisms and delivery of oceanic ecosystem services at a global scale (Doney et al., 2009; Sampaio et al., 2018).

One of the impacts of increasing atmospheric CO<sub>2</sub> concentrations is ocean acidification. This may result in shifts in the distribution of inorganic carbon species in seawater (Caldeira & Wickett, 2003). Phytoplankton may raise pH values by photosynthetic fixation of CO<sub>2</sub>, which is also observed during algal blooms, leading to significantly lower CO<sub>2</sub> concentrations in the aquatic milieu than in the atmosphere (e.g., Seitzinger, 1991; Pinckney et al., 1997; Jacoby et al., 2000). Several studies concern the effects of ocean acidification on diatoms, coccolithophorids and cyanobacteria (Dutkiewicz et al., 2015). While some studies concern the effects of elevated CO<sub>2</sub> concentrations on phytoplankton growth rates and photosynthesis, the conclusions are divergent: While Hein & Sand-Jensen (1997), Riebesell et al. (2007), Iglesias-Rodriguez et al. (2008) and Huang et al. (2018) find a positive response in phytoplankton primary production, Tortell & Morel (2002), Beardall et al. (2009), Feng et al. (2009) and Trimborn et al. (2009) observe no significant effect of higher CO<sub>2</sub> availability, and Gao & Zheng (2010) and Rokitta & Rost (2012) determined negative effects.

Further consequences of warming climate include increasing ocean stratification, reduced mixed layer depth and slowed ocean circulation. Several models predict a declining primary production as a result, as these factors would lead to a decrease in nutrient supply from deep ocean to the photic zone (Sarmiento et al., 1998; Cox et al., 2000; Steinacher et al., 2010). This in turn may accelerate global climate warming. Already, long-term declines in phytoplankton biomass related to increasing ocean temperatures are recorded in the recent past (Gregg & Conkright, 2002; Gregg et al., 2003; Boyce et al., 2010). Additionally, climate change may lead to changes in phytoplankton composition. Bopp et al. (2005) predict a floral shift in favor of small phytoplanktonic organisms at the expense of diatoms due to more nutrient-depleted conditions in the upper ocean layers.

Palaeontological investigations provide another tool to predict processes in changing environments by reconstructing past intercorrelations. Inversing the famous quote of the Scottish geologist Sir Charles Lyell, "The present is the key to the past", our understanding of processes in Earth history may help us to estimate future developments. Changes of phytoplankton composition in context of past environmental changes are a key to predict the impact of future developments on aquatic ecosystems, and the feedbacks on the environment. Thus, it is important to reconstruct phytoplankton biodiversity trends during times of major changes in atmospheric composition, climate and ocean chemistry. The Palaeozoic represents an Era of significant climate shifts, several important biotic events and, major extinctions. The early Palaeozoic atmosphere had much higher concentrations of CO<sub>2</sub>, while in the Carboniferous the lowest concentrations were reached. Several shifts from greenhouse to icehouse climates and vice versa are recorded. With the phytoplankton representing a key factor within the carbon cycle and the marine ecosystems, it is vital to investigate its responses to these developments.

### *1.2 Phytoplankton and the trophic chain*

As primary producers phytoplankton comprise a large part of the marine food web, representing the primary energy source for ecosystems in the oceans (Field et al., 1998). The quantity and quality of the food represented by the phytoplankton is crucial for maintenance, growth and reproduction of zooplankton and organisms higher up in the trophic chain (Sterner, 2002; Martin & Quigg, 2012). Several authors suggest a large role of the phytoplankton in diversification events of the marine biosphere, e.g., as a ‘trigger’ or ‘fuel’, especially during major bioevents (e.g., Martin & Quigg, 2012; Martin & Servais, 2019).

This study concerns diversity trends of the phytoplankton during the Palaeozoic, i.a., in order to assess the role these organisms had during major events. Diversity trajectories are calculated from a vast database comprising occurrences described in literature. Different diversity metrics are used to account for various facets and biases.

### *1.3 Primary production vs. diversity*

With rare information on abundance available, most data derived from literature does not give information about primary production or biomass. Therefore, the results of the biodiversity analyses do not directly account for these factors, whether it would be the most important information to assess the influence the marine phytoplankton had on marine geochemistry, climate and marine ecosystems during the course of the Palaeozoic in general and during major biotic events in particular. Notwithstanding, the diversity alone does provide valuable data, not only to show important shifts in taxonomic composition that can be interpreted for example in context of changes in palaeoenvironmental conditions, but also to estimate the forementioned role of the phytoplankton for major developments in the biosphere. The relationship between phytoplankton biodiversity and primary production is subject to current research. Several studies based on marine ecosystem models and sampling data on a local (Li, 2002, Goebel et al., 2013) and global scale (Irigoien et al., 2004; Vallina et al., 2014) suggest a curvilinear/unimodal relationship between productivity and diversity, with diversity peaking at intermediate levels of productivity. Vallina et al. (2014) interpret these patterns as mainly controlled by resource supply and competition: At low nutrient levels, low productivity and low diversity prevail, since only slow-growing specialists with high nutrient affinity can survive. With increasing nutrient availability, assemblages become more diverse with slow-growing specialists and fast-growing opportunists, leading to higher productivity. In high nutrient conditions, few fast-growing specialists outcompete less competitive species, thus the communities become less diverse, often with only one dominant single species, but with highest productivity (phytoplankton blooms). However, it is difficult to determine a consistent relationship model, since many factors contribute to diversity variations and therefore to the relationships of diversity and productivity (Adler et al., 2011).

### *1.4 Early history of phytoplankton*

The origins of photosynthesis/photoautotrophy are uncertain. Anaerob bacteria represent the first cells. Green and purple sulfur bacteria and green and purple nonsulfur bacteria used special pigments (bacteriochlorophylls) that allowed them, with carbon and anorganic compounds, such as iron and sulfur, to convert light energy into chemical energy. This biochemical process is called photosynthesis. While the first photosynthetic processes were anoxygen, a new group, the cyanobacteria, developed the oxygenic photosynthesis, which is based on a new pigment molecule: chlorophyll (Fischer et al, 2016).

Carbon isotope measurements indicate a widespread autotrophy as early as 3.8 Ga (Rosing, 1999). Fossil lipid biomarker records indicate the existence of cyanobacteria and oxygenic photoautotrophy in 2.7–2.8 Ga old successions (Brocks et al., 1999, 2003; Summons et al., 1999;

Brocks & Summons, 2003), but an older origin is suggested by several authors (Schopf, 1993, 2002; Knoll, 2003; Rosing & Frei, 2004). Sedimentary microstructures that have been questionably interpreted as cyanobacterial were found in 3.5 Ba rocks (Schopf, 1993, 2002). According to Rosing & Frei (2004), oxygenic photosynthesis might have evolved even before 3.7 Ga, as indicated by carbon and Pb isotope geochemistry.

A waste product of oxygenic photosynthesis is oxygen. With the presence of reducing minerals, especially iron, most of the oxygen produced was initially used up, and only very small quantities persisted in the atmosphere. But after these minerals were mostly oxidised, oxygen concentrations began to rise, which caused a shift from a reducing to an oxidising atmosphere. The oxidation of the atmosphere started around 2.4–2.0 Ga (Bekker et al., 2004; Lyons et al., 2014). As a result, almost all life on Earth went extinct in the so called Great Oxidation Event.

The first abundant organic-walled fossils of probable eukaryotic origin are found in 1.9–1.7 Ba sediments (Tappan, 1980; Han & Runnegar, 1992; Knoll, 1994; Javaux et al., 2001). The incorporation of ancestral cyanobacteria as plastids by early eukaryote protists in endosymbiotic associations lead to the first eukaryotic phytoplankton (Margulis, 1970; 1981; Delwiche, 1999; Palmer, 2003). Around 1.6–1.2 Ba, an evolutionary schism in eukaryotic photoautotrophs occurred, leading to the “green” and “red” plastid groups. The “green” plastid line contains chlorophyll *b*, the “red” line chlorophyll *c*. Three major extant phytoplankton phyla, the Chlorophyta, the Rhodophyta, and the Glaucophyta, descended from the primary endosymbiosis. In the marine realm, “red” line eukaryotes became ecologically dominant in the Mesozoic, with three major groups radiating: The dinoflagellates, the coccolithophorids, and the diatoms. In the Neoproterozoic and Palaeozoic, however, the “green” line was as the major constituent of the phytoplankton (Vidal & Knoll, 1983; Butterfield et al., 1994; Arouri et al., 1999; Talyzina & Moczyłowska, 2000). During this era, one branch of this clade settled on land. Thus, all terrestrial algae and plants contain “green” plastids (e.g., Falkowski et al., 2004).

### *1.5 Phytoplankton in the Palaeozoic*

While in today’s oceans the calcareous coccolithophores, the siliceous diatoms, and the organic-walled dinoflagellate constitute major parts of the phytoplankton, none of these groups is present in the Palaeozoic fossil record. During the Palaeozoic, the marine eukaryotic phytoplankton were dominantly represented by organic-walled microfossils attributed to the acritarchs and the prasinophytes, which are considered to belong to the “green” algal lineage. However, Munnecke & Servais (2008) argue that calcareous plankton probably existed already in the early Palaeozoic, as microfossils from the Silurian indicate (Munnecke & Servais, 2008; cf., Servais et al., 2009; Versteegh et al., 2009).

The oldest known unequivocal eukaryotic acritarchs are sphaeromorph and acanthomorph forms from the Early Proterozoic strata, c. 1.95–2.2 Ga (e.g., Pflug & Reitz, 1985, 1992; Yin et al., 2020). A first radiation is known to have occurred in the late Precambrian, c. 900–600 Ma. During this time, large sphaeromorphs, acanthomorphs and polygonomorphs appeared. Many of these forms became extinct during the Vendian (e.g., Vidal, 1981; Vidal & Knoll, 1983; Knoll & Butterfield, 1989). The first prismatomorph and melanocyrrillid (vase-shaped) forms appear during this time (Vidal, 1984). A second major radiation is known from the early Cambrian (e.g., Moczyłowska & Zang, 2005; Moczyłowska, 2011). This time is characterised by the appearance of small, spinose acanthomorphs, herkomorphs, netromorphs and diacromorphs. Acritarchs represent the dominant palynomorphs in many lower Palaeozoic sediments.

### 1.6 Acritarchs – affinities and biology

The term ‘acritarch’ is derived from the greek words ἀκριτος, which means ‘uncertain’, and αρχη, which stands for ‘origin’. Per definition, the biological affinities of organisms assigned to this group are unknown. Therefore the group is most probably polyphyletic. Acritarchs comprise hollow, organic-walled microfossils, essentially eukaryotic unicells. Evitt, who created the group Acritarcha (Evitt, 1963), defines them as

*“Small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed by a wall of multiple layers and of chiefly organic composition; symmetry shape, structure and ornamentation varied; central cavity closed or communicating with the exterior by varied means, for example pores, a slitlike or irregular rupture, a circular opening (the pylome)”* (Evitt, 1963, p. 300)

Evitt (1963) already considered acritarchs as a polyphyletic group, and suggested to treat Acritarcha as a form-group *incertae sedis* according to the International Code of Botanical Nomenclature. An emendation of the group was provided by Downie et al. (1963, p.7):

*“Unicellular or apparently unicellular microfossils consisting of a test composed of organic substances and enclosing a central cavity. Shape of the test spherical, ellipsoidal, discoidal, elongate, or polygonal; test surface smooth, granular, punctate, or perforate. Spines or other processes, raised ridges (crests), flanges, wings or other outgrowth present or absent; where present, connected to the test by varied means or lacking such connection. Shell opens by rupture, splitting, or formation of a simple circular pylome. Rarely, a number of tests loosely associated in a chain”* (Downie et al., 1963, p.7).

Most acritarchs are interpreted to represent cysts, i.e., the resting stages, of marine phytoplanktic algae. Microfossils grouped under the term acritarchs exist from the Mid-Precambrian to Recent. Acritarchs had their acme in the Palaeozoic. Since they are interpreted to be the remains of phytoplanktic organisms, they represent the marine primary producers of the Proterozoic and Palaeozoic. With the forementioned problems regarding the group Acritarcha, some workers avoid the term and refer to these microfossils as “organic-walled microphytoplankton”.

The resistant wall of acritarchs is composed of sporopollenin-like high polymere organic compounds, similar to vascular plant spores and dinoflagellate cysts (Martin, 1993). Even though the wall chemistry might have potential for taxonomy, few comparative studies were done, since it is difficult to obtain monospecific samples in sufficient quantities for chemical analyses, and because diagenesis might have obscured original differences. The wall may be single or double layered, or made of complex wall ultrastructures. Wall thickness ranges between < 0.5 and 7 µm. The exterior surface may be smooth, granulate, or ornamented with spinose or reticulate features, indentations, or microspores. The group comprises microfossils mostly in between 20 and 150 µm. Acritarchs usually consist of a vesicle, i.e., a central body, enclosing a general cavity. Sometimes the vesicle is ornamented with processes or crests.

Various proposals as to what acritarchs were made over time, from fossil eggs to cysts to tests of unicellular or multicellular animals or plants. Most were interpreted to be unicellular algae. Eisenack (1963) argued that hystrichospheres were a homogenous group comprising shelled and naked stages of ancestors of dinoflagellates. Lister (1970) interpreted acritarchs as being unicellular phytoplankton. Subsequently, many authors proposed algal affinities (Cramer & Díez, 1972).

Similarities with cyst stages of modern prasinophytes and dinoflagellates are evident, as pointed out by numerous authors (Rasul, 1974; Tappan, 1980; Margulis & Schwartz, 1982; Martin, 1993; Mendelson, 1993; Cobalth & Grenfell, 1995; Servais, 1996; Strother, 1996; Butterfield & Rainbird, 1998). They have a comparable size and vesicle shape, and a similar chemical composition. Several taxa of acanthomorph acritarchs are known to have, as dinoflagellate cysts, double-walled features. However, morphological evidence is not sufficient to establish a relation to dinoflagellates, as

acritarchs lack characteristic features, such as a thecal tabulation, and have different excystment openings than the archeopyles of Mesozoic and Cenozoic dinocysts. However, several living dinoflagellates from the order Gymnodiniales also produce cysts that show no clearly defined archeopyles or tabulation (e.g., Wall & Dale, 1968). Indeed, the extant genus *Gymnodinium* is known to produce spinose cysts without paratabulation and clearly defined archeopyles, thus resembling certain acritarchs. While reliable fossil evidence of dinoflagellates is not known from strata older than the Triassic, biomarkers, such as dinosteranes and 4 $\alpha$ -methyl-24-ethylcholestane, are recorded in Neoproterozoic and Cambrian sediments (Summons et al., 1992; Moldowan et al., 1996; Moldowan & Talyzina, 1998; Talyzina et al., 2000), and with RNA-sequence data indicating an origin of dinoflagellates in the Neoproterozoic (Lipps, 1993), it is likely that many acritarchs represent ancestors of dinoflagellates.

Several forms, especially herkomorph, pteromorph and prismatomorph acritarchs, are considered to be chlorophyceans, particular the phycmata, i.e. the non-motile stages, of prasinophytes. Prasinophytes are mostly marine non-cellulosic, green, flagellate algae (e.g., Armstrong & Brasier, 2005). They are known from the Ordovician to Recent. Fossil prasinophytes are characterised by a perforate wall and a cyclopyle or median-split as an excystment opening. Prasinophytes had a larger role in the Palaeozoic than in recent oceans (Colbath & Grenfell, 1995; Talyzina & Moczydlowska, 2000). Important forms of prasinophytes during the Palaeozoic, which were formerly described as acritarchs, are *Tasmanites*, *Cymatiosphaera*, *Leiosphaeridia*, *Pterospermopsis*. Other forms are compared to zygneatacean green algae (e.g., Tappan, 1980; Brenner & Foster, 1994; van Geel & Grenfell, 1996). Some sphaeromorphs resemble alete spores of multicellular algae (see also discussion in Navidi-Izad et al., 2019). Additionally, various other algal phyla produce cysts similar to acritarchs. Other sphaeromorph acritarchs are compared to eggs of planktic organisms, such as copepods.

### 1.7 Application of acritarchs

Acritarchs are very useful for biostratigraphic correlation and dating in the upper Precambrian (e.g., Vidal & Knoll, 1983; Martin, 1993) and the Palaeozoic (e.g., Molyneux et al., 1996), particularly the early Palaeozoic. The high quantity of acritarchs in many lower Palaeozoic sediments makes them an important source for palaeobiological information and attractive for quantitative biostratigraphy and palaeobiological studies. They are also used as a tool in palaeoenvironmental analyses. For example, they are used to reconstruct ancient ocean currents and climate belts. However, generalised interpretations have proven to be not very robust. Acritarchs have been used in studies of climate change, e.g., concerning the Northern Hemisphere glaciation 2.9–2.2 Ma (Versteegh, 1997). Reworked acritarchs provide information about uplift and erosion of basin margins, and are useful for sedimentary provenance studies (e.g., McCaffrey et al., 1992). The acritarch alteration index (AAI) is used to reconstruct the burial and thermal history of sedimentary rocks based on the colour alteration of specimens (e.g., Dorning, 1996). Within this work, several uses of acritarchs are applied. one publication concerns, among other issues, this more traditional use of acritarchs. In our study published in *Article V*, an acritarch assemblage recovered from samples of the Palaeozoic in a well in the Llanos Orientales Basin in Colombia allowed to establish a precise age determination of the study interval. The samples were dated based on the presence of several diagnostic taxa with known first appearance data (FAD), as well as the absence of easily recognisable taxa characteristic for younger strata.

## 2 The Palaeozoic Era

### 2.1 Geochronology

The Palaeozoic is the first era of the Phanerozoic, comprising c. 289 Myr, from the Ediacaran/Cambrian boundary at  $541.0 \pm 1.0$  Ma to the Permian/Triassic boundary at  $251.902 \pm 0.024$  Ma). The era is divided into six periods: The Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian.

Period boundaries are defined by conodonts (Ordovician, Carboniferous, Permian) and graptolites (Silurian, Devonian). The base of the Palaeozoic era ( $541.0 \pm 1.0$  Ma) is defined by a GSSP at the Fortune Head section in Newfoundland, Canada based on the FAD of the ichnofossil *Trichophycus* (= *Treptichnus*, *Mannykodes*, *Phycodes*) *pedum* (Brasier et al., 1994; Landing, 1994, 1996; 2004). The Cambrian/Ordovician boundary ( $485.4 \pm 1.9$  Ma) is defined by a GSSP at the Green Point section in Newfoundland, coinciding with the appearance of *Iapetognathus fluctivagus* (Cooper & Nowlan, 1999; Cooper et al., 2001). A GSSP at the Linn Branch Trench section in Scotland defines the base of the Silurian ( $443.8 \pm 1.5$  Ma), coinciding with the base of the *Akidograptus ascensus* Zone, marked by the FAD's of *A. ascensus* and *Parakidograptus praematurus* (= *P. acuminatus sensu lato*) (Melchin & Williams, 2000). The GSSP for the Silurian/Devonian boundary ( $419.2 \pm 3.2$  Ma) is in the Klonk section in the Czech Republic, marked by the FAD of *Monograptus uniformis* (Martinsson, 1977). The base of the Carboniferous ( $358.9 \pm 0.4$  Ma) has been defined by a GSSP in the La Serre section in France, at the FAD of *Siphonodella sulcata* (Paproth et al., 1991). The FAD of *Streptograthodus isolatus* at the Aidaralash section marks the GSSP at the Carboniferous/Permian boundary ( $298.9 \pm 0.15$  Ma) (Davydov et al., 1998). The GSSP for the Palaeozoic/Mesozoic boundary ( $251,902 \pm 0.024$  Ma) is defined at a section near Meishan, China, coinciding with the FAD of *Hindeodus parvus* (Yin et al., 2001, 2005).

### 2.2 Bioevents

The Palaeozoic is characterised by significant geological, palaeoclimatological, and evolutionary changes, with the appearance and diversification of most modern phyla in the Cambrian. At the beginning of the Palaeozoic life only existed in the oceans, but subsequently it began to conquer land in the process of terrestrialisation. In the late Palaeozoic, vast terrestrial floras, including large forests, and faunas were established. In the marine realm, considerable changes of the ecosystems are evident. While first reefs build up by stromatolites existed already in the Precambrian, larger and more complex reef systems developed in the Ordovician. In the Silurian diverse reef communities with stromatopores, corals and bryozoans established, and reef communities developed further during the Devonian. During the Palaeozoic, three evolutionary faunas as defined by Sepkoski (1981) coexisted, with the 'Cambrian fauna' declining in the upper Cambrian, while the Palaeozoic fauna was radiating. The Modern fauna was also part of the ecosystems since the early Palaeozoic and gradually gained importance.

#### 2.2.1 Diversification Events

The Palaeozoic represents an era of major biotic and ecologic changes. The term 'Cambrian Explosion' or 'Cambrian Radiation' describes the seemingly sudden appearance and radiation of almost all animal phyla and classes within a short period of time in the early Cambrian. However, molecular data and fossil records suggest the divergence of several lineages already in the Neoproterozoic (e.g. Xiao & Knoll, 2000; Erwin et al., 2011; Xiao et al., 2012). During the middle Cambrian, the 'Cambrian Substrate Revolution' or 'agronomic revolution' (e.g., Seilacher & Pflüger, 1994; Bottjer et al., 2000) marks the start of bioturbation of the expanding benthos, creating a mixed layer in the sediment, leading to the disappearance of the biomats, which dominated the sea floor during the Ediacaran.



The late Cambrian to Ordovician interval is characterised by the most important radiations of life in the Phanerozoic, the ‘Great Ordovician Biodiversification Event’ (GOBE) with the rapid increase in the number of taxa in most groups (Webby et al., 2004). A debate exists, if the Cambrian Explosion and the GOBE represent separate events or if the latter is a continuation of the former (e.g., Droser & Finnegan; 2003; Na & Kießling; 2015). During the Ordovician, more complex ecosystems, and modern trophic chains established (Signor & Verneij, 1994).

A major shift in marine ecosystems is recorded from the Silurian to the Carboniferous, with the diversification of nektic organisms (Klug et al., 2010; Whalen & Briggs, 2018). While Klug et al. (2010) described a rather rapid event (‘Devonian Nekton Revolution’), Whalen & Briggs (2018) suggested a longer, gradual diversification.

### *2.2.2 Extinction events*

In the Palaeozoic, mass extinction events of various orders are recognised for many marine groups, including two of the ‘Big Five’ events. During the Cambrian, several faunal crises are recorded (‘end-Botomian extinction event’, ‘Dresbachian extinction event’, ‘Cambrian–Ordovician extinction’; e.g., Zhuravlev & Wood, 1996; Saltzman et al., 2000; Shergold & Cooper, 2004; Hough et al., 2006; Pagès et al., 2016). The latest Ordovician is marked by the second-largest mass extinction of the Phanerozoic, with the extinction of 49–60 % of marine genera and 85 % of marine species (e.g., Jablonski & Chaloner, 1994; Christie et al., 2013). The Silurian is a period of major marine turnovers related to perturbations in the global carbon cycle and climate (‘Ireviken’, ‘Mulde’, ‘Lau’ events; Talent et al., 1993; Samtleben et al., 1996; 2000; Kaljo et al., 1997; 2003; 2006; Saltzman, 2001; Munnecke et al., 2003; Cramer & Saltzman, 2005; Calner et al., 2006; Cramer et al., 2006; Lenz et al., 2006). During the Late Devonian, several events (‘Kellwasser’, ‘Hangenberg’ events) summarised as the ‘Late Devonian extinction’ represent the second of the ‘Big Five’ events occurring during the Palaeozoic, with the disappearance of estimated 50% of genera and 70% of species (Briggs et al., 2008).

### *2.3 Palaeozoic palaeogeography*

The Palaeozoic is characterised by significant palaeogeographic changes, with continental breakups and assemblies, and openings and closures of different seas. Many global palaeogeographical reconstructions for the Palaeozoic were published since the 1960s (Wilson, 1966; Smith et al., 1973; Cocks & McKerrow, 1973; Ziegler et al., 1977, 1989; McKerrow & Scotese, 1990; Torsvik et al., 1990; Cocks & Torsvik, 2002, 2006; Torsvik & Cocks, 2005, 2013; Basset, 2009; Domeier & Torsvik, 2014). While the position and movements of certain land-masses, such as South China, is still discussed in literature, there is broad consensus in this regard about the major palaeocontinents, Gondwana, Laurentia, Baltica, and Siberia. In the following the most important palaeogeographical developments during the Palaeozoic are summarised, based on McKerrow & Scotese (1990) and Torsvik & Cocks (2013).

The dominating supercontinent during the early and middle Palaeozoic was Gondwana, which covered much of the Southern Hemisphere until the Carboniferous. During this time, most of the Northern Hemisphere was covered by the Panthalassa Ocean. Laurentia was in equatorial position during the Cambrian, separated from Gondwana by the Iapetus Ocean. To its east, separated by the Ægir Ocean, Siberia was positioned. Baltica was located in a southeastern position of Laurentia and in the South-West of Siberia, with the Ran Ocean between Baltica and Gondwana. The Iapetus Ocean was constantly widening throughout the Cambrian, and reached its maximum width during the Early Ordovician. During the Cambrian–Ordovician boundary interval, several terranes (e.g., Canderia, Avalonia, Carolina, Meguma) separated from Gondwana, and the Rheic Ocean opened between Gondwana and Avalonia. With Avalonia approaching Baltica, the Tornquist Sea became narrower, until it closed during the latest Ordovician–earliest Silurian, with the merger of the two

land masses. The Iapetus Ocean also became narrower during the Ordovician and Silurian, and was closed in the late Silurian to Early Devonian, when Avalonia-Baltica merged with Laurentia, leading to the assembly of Laurussia in the Caledonian and Acadian orogenies. With the Rheic Ocean closing, Gondwana drifted northward during the Devonian and collided with Laurussia in the Carboniferous, creating Pangaea during the Variscan Orogeny. This supercontinent persisted until the Mesozoic.

#### *2.4 Palaeozoic sea-level changes*

Important changes in sea-level are recorded during the Palaeozoic. One of the first attempts to reconstruct Palaeozoic sea-level changes was published by Vail et al. (1977). A review of data regarding Palaeozoic sea level was provided by Hallam (1992). The Exxon corporation produced 1988 a sea-level curve for the Phanerozoic (unpublished) based on reconstructions by Haq et al. (1987), Ross & Ross (1987, 1988) and Posamentier & Vail (1988). Regional sea-level trends during the Phanerozoic in the Arabian Platform are described in Haq & Al-Qahtani (2005). Miller et al. (2005) gave a review of Phanerozoic sea-level changes including data for the Palaeozoic of Vail et al. (1977) and Haq & Al-Qahtani (2005). A comprehensive study on Palaeozoic sea level was provided by Haq & Schutter (2008). The following history of sea level is based on the latter authors. Long-term sea level gradually rises during the Cambrian and the Ordovician, with highest levels reached in the Late Ordovician. Related to the Hirnantian glaciation, a distinct short-term fall is noticed. Sea level increased subsequently, reaching high stands in the mid-Silurian. A decrease is recorded from the Silurian to Lower Devonian. The Middle Devonian is characterised by another sea-level rise, peaking in the Middle–Late Devonian boundary interval. Subsequently, sea level is decreasing up until near the Mississippian–Pennsylvanian boundary. A short increase is recorded during the Pennsylvanian. During the earliest Permian, sea level is decreasing, followed by relative constant levels until the Middle Permian. A further increase characterises the Middle and early Late Permian, followed by a rise in the latest Permian.

#### *2.5 Palaeozoic climate history*

The climate history of the Palaeozoic is not well understood and under permanent revision. Most models for ancient climate reconstructions are based on the examination of sedimentary rocks and climate sensitive fossils (e.g., Cocks, 2007), or oxygen isotopes from the shells of marine organisms as a temperature proxy (e.g., Veizer et al., 2000; Royer et al., 2004; Veizer & Prokoph, 2015). However, uncertainties arise from differences in spatial and temporal distribution of sediments and fossils used as proxies for past climates, as well as diagenetic and burial-metamorphic overprinting distorting oxygen isotope values. Trends in oxygen isotope composition might not always reflect climate changes but variations in the isotope composition of the ocean, or post-depositional alterations. Therefore, independent estimates of sea-water isotopic composition are needed to assess this issue. More recent studies using the ‘carbonate clumped isotope’ or  $\delta^{47}$  technique (Eiler, 2007, 2011), which does not require independent estimates of the isotopic composition of the Palaeozoic oceans, show promising results (Came et al., 2007, 2008; Finnegan et al., 2011; Wacker et al., 2012; Cummins et al., 2014; Henkes et al., 2014, 2018).

Boucot et al. (2013) provide an atlas showing climatic zones plotted on palaeogeographical reconstructions, highlighting climate changes throughout the Phanerozoic. The Palaeozoic climate history is characterised by changes between icehouse and greenhouse climatic regimes. Atmospheric CO<sub>2</sub> concentrations were possibly the main control of climate changes (e.g., Frakes et al., 1992; Royer et al., 2004). The lower and mid Palaeozoic (Cambrian to Late Devonian) atmosphere and oceans was mostly hot (e.g., Cocks, 2007; Veizer & Prokoph, 2015). An interval of global cooling during the Ordovician lead to an icehouse climate in the Late Ordovician and early Silurian (e.g., Veizer et al., 2000; Royer et al., 2004; Cocks, 2007), accompanied by glaciations and

sea-ice formations in the Gondwanan realm (e.g., Caputo & Crowell, 1985; Frakes & Francis, 1988). Global temperatures rose again until the Late Devonian, followed by another climate cooling, leading to a longer ice-house phase in the Carboniferous and Early Permian (e.g., Veizer et al., 2000; Royer et al., 2004; Cocks, 2007), with records of long-term glaciation (e.g., Montañez & Poulsen, 2013). The final stages of the Palaeozoic are characterised by hot climates (Veizer et al., 2000; Royer et al., 2004).

### 3 Objectives

#### 3.1 Biodiversity of the phytoplankton of the Palaeozoic

The reconstruction of past biodiversity changes are a valuable tool to assess the evolutionary history of life, and help to understand intercorrelations of organisms and ecosystems. While the diversity trends of Mesozoic and Cenozoic phytoplankton groups (dinoflagellates, diatoms, coccolithophores) are well researched (e.g., Stover et al., 1996; Spencer-Cervato, 1999; Bown et al., 2004), the biodiversity of the Palaeozoic phytoplankton is poorly understood. Global diversity curves for the whole Palaeozoic (Tappan & Loeblich, 1972; 1973; Tappan, 1980; Strother, 1996; Martin, 2003; Katz et al., 2004, Cruz, 2011) are mostly based on outdated data, often imprecise, and do not sufficiently account for the various biases that studies on palaeodiversity are facing, as new metrics have been developed since.

The major aim of this work is to produce biodiversity trajectories for the organic-walled microphytoplankton throughout the whole Palaeozoic in order to assess the role these organisms had during major macroecological events. The diversity curves are computed from a new exhaustive database of occurrences described in literature by means of different diversity metrics to account for various facets and biases. The production of biodiversity trajectories is strongly depending on the quality of palaeontological data. The completeness of the fossil record, the accuracy of taxonomy, and the precision of stratigraphic correlations and chronometric dating have to be considered (e.g., Sepkoski, 1997). Differences in the amount of studies in a certain region or a certain time interval, the quantity of sediment, and the quality of preservation lead to biases, that need to be accounted for (e.g., Sepkoski, 1997; Aberhan & Kiessling, 2012; Alroy et al., 2008). Thus, several biodiversity metrics are used in order to produce the most representative diversity trajectories.

Considering the forementioned role the phytoplankton have in the climate system of Earth, it is important to interpret diversity trends in the context of established models of past climate. In order to identify the main drivers for long-term phytoplankton diversity changes, our study attempts to determine interrelations with certain palaeoenvironmental parameters. Palaeozoic phytoplankton diversity is probably influenced by various environmental factors, including palaeogeography, sea-level changes, terrestrial sediment influx, and atmospheric CO<sub>2</sub> concentrations. Therefore, the results of the diversity analysis is compared to global trends of these parameters during the Palaeozoic. The results of this investigation are presented in *Article I*.

#### 3.2 Classification of Palaeozoic organic-walled microphytoplankton

A fundamental problem with the taxonomy of organic-walled microphytoplankton from the Palaeozoic is the phenetic classification. (Morpho-)genus and (morpho-)species represent the only taxonomic ranks. Informal groupings exist, which are based on overall morphology, wall structure, excystment opening, but are not reflecting biological affinity or evolution. The identification of species and genera is based on morphological differences, e.g., in the shape of the vesicle, the presence/absence, and shape of processes, surface ornamentation. The original shape is often modified by compression, pyrite growth or other diagenetic processes. Various authors proposed a classification system based on major morphological subgroups (Downie et al., 1963; Châteauneuf &

Reyre, 1974; Tappan, 1980): The Sphaeromorphytae comprise forms without processes or crests. These are usually spherical or ellipsoidal with smooth or ornamented vesicle walls. Acritarchs from the Herkomophytae subgroup display crests, which divide the vesicle surface into polygonal fields. The subgroup Acanthomorphytae includes acritarchs with a more or less spherical vesicle that shows processes, which may be simple or branching. Forms with a bipolar build, e.g., having a smooth equatorial zone and two ornamented polar areas are summarised in the subgroup Diacromorphytae. The Netromorphytae subgroup comprises fusiform acritarchs, which are mostly long, elongate, with one or both poles often extended as processes. Egg-shaped, polarised forms, with one smooth and one ornamented end, are belong to the Oomorphytae. Acritarchs of the Polygonomorphytae subgroup show a polygonal vesicle and mostly simple processes. The Prismatomorphytae include prismatic or polygonal forms. This classification is still phenetic, therefore arbitrary and artificial. Many attempts to create more natural classification systems (e.g., Downie, 1973; Tappan, 1980; Mendelson, 1993) were not successful. In more recent times, several studies prove the potential of biometrical investigations (e.g., Servais et al., 1996; Stricanne & Servais, 2002; Yan et al., 2017) as well as the chemistry of the vesicle wall (e.g., Colbath & Grenfell, 1995) for a more natural classification.

Since most studies on acritarchs until the late 1980s were primarily focused on biostratigraphic usability (Brocke et al., 1995), with a purely descriptive approach, and only few works including palaeobiological and palaeoecological aspects, the number of described species and genera is very high. It is difficult to affirm if morphological evolution is primarily controlled biologically rather than chronologically. With a classification only based on the description of certain morphologies, biological affinities might very well be distorted. The definition of a species or a genus depends on the morphological variability, which is often not known, due to the fact that samples generally represent a narrow window in respect to stratigraphic age or palaeogeographical location. The whole spectrum of morphologies may not be present in single samples. Even with numerous samples, only certain morphotypes might be present in each of them, developed for each respective depositional conditions. Intermediate morphotypes might be present, but not sampled. Given this reality, morphological variability is most often defined subjectively by the respective taxonomist. With most studies of acritarchs neglecting palaeoecological aspects, the mechanisms influencing acritarch morphology are not well understood and morphological variability underestimated. Therefore, it can be inferred that many taxa may not represent separate biological entities, but rather phenotypes of a single taxon.

Similar to acritarchs, the classification of dinoflagellate cysts is largely based on the interpretation of morphology, and therefore might distort biological affinities. In this respect to recent and subrecent dinoflagellate cysts, the genus *Lingulodinium* is well studied in regard of morphological variability. In view of great variations in process number, distribution, and morphology observed in cultures of *L. polyedrum* (*L. machaerophorum* and *Gonyaulax baltica* in cyst-based taxonomy), Islam (1983) proposes synonymisations of several species of the genus. Three formerly separate species were defined as junior synonyms of *L. machaerophorum* by Kokinos & Anderson (1995). This species is known to develop different morphotypes, including large variations of process length and shape, in response to changing temperatures and salinities (Wall et al., 1973; Turon, 1984; Nehring, 1994, 1997; Dale, 1996; Matthiessen and Brenner, 1996; Hallett, 1999; Ellegaard, 2000; Mudie et al., 2001; Brenner, 2005; Sorrel et al., 2006; Marret et al., 2007; Mertens et al., 2009). For this single species alone, up to 15 different process types are found (Wall et al., 1973; Harland, 1977; Kokinos & Anderson, 1995; Lewis & Hallett, 1997; Hallett, 1999), from very short, columnar, pointed or bulbous, to very long tapering processes, with or without irregular spinules (Wall et al., 1973; Sorrel et al., 2006). The cyst morphology is found to be essentially depending on the level of development before rupture of the expanding outer membrane (Kokinos & Anderson, 1995). Premature ruptures might result in a wide variation of morphologies, particularly with respect to size, number and distribution of processes. Changes in environmental conditions, such as temperature, salinity, or pH value, are observed to result in premature ruptures.

Considerable variations in cyst morphology in response to changes in salinity are observed in many recent and subrecent dinoflagellate taxa, e.g., *Lingulodinium machaerophorum*, *Protoceratium reticulatum* (= *Operculodinium centrocarpum*), *Pyxidiniopsis psilatum*, *Spiniferites cruciformis*, *Spiniferites* spp., *Homotryblium* spp. (Zonneveld & Susek, 2006; Mertens et al., 2011). In several cases, e.g., in *L. machaerophorum*, *Spiniferites bulloideus*, *Spiniferites* spp., and *Protoceratium reticulatum* (= *Operculodinium centrocarpum*), shorter and thicker processes are observed in low salinity environments (Wall et al., 1973; Turon, 1984; Dale, 1988, Nehring, 1994; Lewis & Hallett, 1997; Hallett, 1999; Ellegaard, 2000; Brenner, 2001). The species *Spiniferites cruciformis* shows extreme morphological variations probably linked to salinity fluctuations, i.e., in regard of sutural septa, ridges and processes (Wall et al., 1973; Ellegaard, 2000; Mudie et al., 2001; Sorrel et al., 2006; Ferguson et al., 2018). Here, a full range of intermediate morphotypes between no development of flanges and septa to well-developed and perforate-fenestrate flanges and septa exist (Sorrel et al., 2006).

Cultural experiments document that the morphology of *Tuberculodinium vancampoeae*, the resting cyst of the dinoflagellate *Pyrophacus steinii*, is related to temperature, but not to salinity. *S. baltica* shows variations in body size in response to changing salinity and temperature, but with no effects observed with changes in each of the variables alone (Ellegaard et al., 2002). A high morphological variability is also known from resting cysts of other phytoplanktic organisms. Based on cultural experiments, Sandgren (1983) describes variations of cyst morphology in large populations of the chrysophycean species *Dinobryon cylindricum*. According to the author, genetic differences among vegetative clones as well as water temperature during the encystment process have strong influence on the density, shape and length of processes. These observations indicate that single biological species can produce a wide range of morphologies, which possibly would be attributed to different (morpho-)species in the fossil record.

With acritarchs interpreted to represent resting cysts of phytoplanktic organisms, and with many forms probably related to dinoflagellates, it can be inferred that many species and genera possess a large morphological variability. In order to examine the amount of morphological variability, taxonomic revisions and studies on large populations of taxa, including morphometric measurements and statistical methods, such as principal component and linear discriminant analyses, are needed. Furthermore, sedimentological investigations may help to determine depositional settings in order to correlate specific morphologies to environmental conditions. This would greatly enhance palaeoenvironmental applications of Palaeozoic organic-walled microphytoplankton. Indeed, since the introduction of population analyses in acritarch research, high amounts of morphological variability have been revealed for many taxa, and an increasing value for palaeoecological applications has been recognized (e.g., Le Hérissé, 1989). Several acritarch taxa have been investigated in detail, including taxonomical revisions, as well as biostratigraphical and palaeogeographical analyses. Among the early Palaeozoic taxa that have been revised in detail, are, in alphabetical order: *Acanthodiacrodium* Timofeev 1958 emend. Deflandre & Deflandre-Rigaud 1962 restrict. Moczydlowska & Stockfors 2004 (Paalits & Heuse, 2000; Moczydlowska & Stockfors, 2004), *Ampullula* Righi 1991 (Yan et al., 2010), *Arbusculidium* Deunff 1968 (Fatka & Brocke, 1999), *Arkonía–Striatotheca* Burmann 1970 emend. Sarjeant & Stancliffe 1994 (Servais, 1997), *Aureotesta* Vavrdová 1972 (Brocke et al., 1997), *Barakella* Cramer & Díez 1977 (Yan et al., 2017), *Coryphidium* Vavrdová 1972 emend. Servais, Molyneux & Vecoli 2008 (Servais et al., 2008), *Crassianguilina* Jardiné, Combaz, Magloire & Peniguel 1974 (Wauthoz et al., 2003), *Cristallinium randomense* Martin in Martin & Dean 1981 emend. Martin in Martin & Dean 1988 (Vanguestaine 2002), *Cycloposphaeridium* Uutela & Tynni 1991 emend. Playford, Ribecai & Tongiorgi 1995 (Playford et al., 1995), *Dactylofusa velifera* Cocchio 1982 (Wang et al., 2015) *Dicrodiacrodium* Burmann 1968 (Servais et al., 1996), *Diornatosphaera* Downie 1958 (Paalits & Heuse, 2000), *Domasia* Downie 1960 emend. Hill 1974 (Wauthoz & Gérard 1999), *Eliasum* Fombella 1977 (Tonarová & Fatka 2006) *Frankea* Burmann 1970 emend. Servais 1993 (Servais, 1993; Fatka et al., 1997; Vecoli et al. 1999; Wang et al., 2017), *Ferromia pellita* Martin 1977

(Martin, 1996) *Liliosphaeridium* Uutela & Tynni 1991 emend. Playford, Ribecai & Tongiorgi 1995 (Playford et al., 1995), *Lusatia* Burmann 1970 emend. Sarjeant & Vavrdová 1997 (Albani et al., 2007), *Marrocanium* Cramer et al. 1974 (Brocke et al., 1997), *Nellia* Golub & Volkova in Volkova & Golub 1985 (Stricanne et al., 2005) *Pachysphaeridium* Burmann 1970 (Ribecai & Tongiorgi, 1999), *Peteinosphaeridium* Staplin, Jansonius & Pocock 1965 emend. Eisenack 1969 (Playford et al., 1995), *Rhopaliophora* Tappan & Loeblich 1971 (Li et al., 2014), *Sacculidium* (Ribecai et al., 2002), *Skiagia* Downie 1982 emend. Moczydłowska 1991 (Moczydłowska & Zang 2006), *Veryhachium* Deunff 1954 emend. Downie & Sarjeant 1963 emend. Turner 1984 emend. Sarjeant & Stancliffe 1994 (Servais et al., 2007) "*Veryhachium*" *dumontii* Vanguetaine 1973 (and "*Dasydiacrodium*" *caudatum* Vanguetaine 1973) (Raevskaya & Servais, 2009). While no direct correlations of acritarch morphologies to environmental conditions has been proven yet, several studies indicate that such relations exist. Servais et al. (2004) observed morphological trends in a shallow to deeper water setting, with variations ranging from smooth specimens without ornamentation to forms with a polygonal pattern of processes, forms with randomly distributed processes, and forms with membranes between the processes.

In order to illustrate the problems of acritarch classification and to document morphological variability in Palaeozoic microphytoplankton, several taxonomic revisions are included in this thesis. These studies help to highlight the problematic definition of taxonomic ranks in acritarchs. Can the intraspecific and -generic morphological variation be assessed in order to reevaluate the current classification? The forementioned works on acritarchs highlight the existing problems concerning the taxonomy of this group. We argue on this basis that the number of species is probably exaggerated. It is important, particularly for biodiversity studies, to have a proper classification in order to gain representative results. Therefore, more taxonomic revisions, especially of important genera, are needed. Within this work, we re-examined three important taxa in detail, including comprehensive literature revisions and statistical analyses based on morphometric measurements of large populations from material from different locations.

A first study (*Article II*) concerns *Vulcanisphaera*, an important palaeogeographically widespread late Cambrian to Middle Ordovician genus, with in total 32 species described. A second study (*Article III*) focuses on *Orthosphaeridium*, which occurs very frequently in Ordovician sediments, with 20 species assigned to the genus. A third investigation (*Article IV*) concerns the peteinoid acritarchs that constitute a common component of global palynofloras of the Lower and Middle Ordovician. In literature, a high number of species were assigned to this group. Additionally, a fourth revision is presently carried out on the important Palaeozoic palynomorph *Saharidia*.

The investigation of morphological variations allows a better understanding of the biology and the ecological role of acritarchs. Furthermore, by determining the dependence of the morphology on different environments, certain morphological characteristics can be used in future environmental studies. The proportion of certain forms within a given microphytoplankton assemblage can therefore help in determining the palaeoenvironmental context of the depositional area.

### 3.3 Biostratigraphy

As beforementioned, one of the main applications of lower Palaeozoic palynology in the past has been biostratigraphic correlation. Several acritarch assemblage biozonations have been proposed for the Palaeozoic (e.g., Martin & Dean 1981, 1988; Volkova et al., 1979; 1983; Molyneux et al., 1996). This work includes a study (*Article V*), in which one of the objectives is to precisely date a sample interval based on the recovered microphytoplankton assemblage. The study material is derived from a borehole in the Llanos Orientales Basin in Colombia. This Andean foreland basin represents an important structure for hydrocarbon exploration. However, most work has been done on the late Mesozoic and Cenozoic sediments, while the Palaeozoic deposits have been widely neglected. This study represents the first detailed investigation on lower Palaeozoic palynomorphs in the subsurface, and one of few works in this respect in northwest South America. The study attempts to

provide useful biostratigraphic data for future correlation efforts in the Palaeozoic strata of this basin.

### 3.4 Palaeoecology

Acritarchs are mainly found in marine sediments, especially in shales and mudstones, but also in sandstones and limestones. Most forms are found in marine or brackish environments. Non-marine forms are known from the Recent. Palaeoecological interpretations of acritarchs are rather difficult, since the taxonomy and the biological affinities are poorly understood. Moreover, acritarchs are rare in modern environments. However, several models were proposed for the reconstruction of depositional environments based on variations in diversity and composition of microphytoplankton assemblages (e.g. Staplin 1961; Smith and Saunders 1970; Jacobson 1979; Dorning 1981; Al-Ameri 1983; Wicander and Wood 1997; Vecoli 2000, 2004; Tongiorgi et al. 2003; Li et al. 2004; Stricanne et al. 2004; Molyneux 2009; Lei et al. 2012; Yan et al. 2013). These generalised patterns of facial acritarch distribution show similarities to Mesozoic and recent phytoplankton (Tyson, 1995), with processes becoming longer and more complex with increasing distance to the shoreline, and diversity being highest in distal shelf facies, and low in both, shallow water and deep basin facies. Therefore, based on investigations on the organic-walled microphytoplankton content, statements on the palaeoenvironment can be made. One aim of *Article V* included in this work is the reconstruction of the depositional environment based on the recovered palynoflora.

#### 3.4.1 Abiotic factors

Acritarch biodiversity is probably controlled by various environmental factors, such as water depth, temperature, light, salinity, space, nutrient supply. To identify the major factors influencing long-term diversity trends, it is important to test for correlations with data of a variety of palaeoenvironmental parameters. Therefore, the results of the biodiversity analyses (*Article I*) are compared with different trajectories representing palaeoenvironmental changes throughout the Palaeozoic. Much emphasis is therein given to (eco)space, which, in the case of marine organisms, is crucially dependent on sea level and continental configuration, and nutrient supply.

Ecospace represents a major control on global biodiversity, with radiations related to expansion of suitable habitat area and vice versa (e.g., Sepkoski, 1984; Sepkoski & Miller, 1985; Rosenweig, 1995). One factor controlling marine ecospace on a long-term scale is plate tectonics, in relation with sea-level changes. A high degree of continental fragmentation, i.e., many smaller land masses exist instead of few large continents, the amount of coastline and therefore shelf region is higher. Moreover, larger distances between continents might produce barriers between assemblages, fostering provincialism. Marine ecospace is crucially related to sea-level changes flooding, for example the continental platforms during a transgression. With increasing sea levels the continental area covered by sea, and therefore habitable area, is expanding. Diversity curves for Mesozoic and Cenozoic phytoplankton groups are known to correlate well with sea-level changes (e.g., Stover et al., 1996; Falkowski et al., 2004; Katz et al., 2004).

Since nutrients, such as nitrate, phosphate and iron, are essential for the growth of phytoplanktic organisms, nutrient availability represents a major control on phytoplankton distribution in time and space (e.g., Strother, 2008; Martin & Quigg 2012; Martin & Servais, 2019). It is therefore essential to compare Palaeozoic phytoplankton biodiversity to the nutrient evolution of Palaeozoic oceans. The main sources for the formentioned nutrients are terrestrial sediments and oceanic upwelling. In order to assess the influence of nutrient availability on phytoplankton diversity, the results of the diversity analyses will be compared to the strontium isotope curve (e.g., Prokoph et al., 2008), which represents a proxy for continental runoff (e.g., Faure, 1986; Taylor & Lasaga, 1999; Martin, 2003), and corrected Palaeozoic trends of sediment flux (Flögel et al., 2000).

### 3.4.2 Biotic factors

Not much is known yet about biotic parameters controlling phytoplankton growth and diversity, except predation by zooplankton. Several studies highlight the impact of parasites and viruses, as well as symbiotic interactions (Brussaard et al., 2008; Siano et al., 2011). This can have an impact on global biogeochemical cycles (Strom, 2008). However, it is difficult to test for these factors, except for comparisons of diversity changes of phytoplankton and zooplanktic groups, such as radiolaria, which are known to feed on phytoplankton and to form symbioses with phytoplanktic organisms, chitinozoans and graptolites.

## 3.5 Palaeobiogeography of Palaeozoic microphytoplankton

### 3.5.1 Latitudinal diversity gradients

Biodiversity is not only changing in time but also in space. Therefore, besides the examination of chronological changes in phytoplankton, it is also important to consider a palaeogeographical component by investigating spatial diversity gradients. Many recent terrestrial and marine taxa show a decline in diversity with increasing latitude (e.g., Currie, 1991; Chown & Gaston, 2000; Hillebrand, 2004; Brown, 2014). Studies show that marine planktic organisms, such as bacterioplankton (Pommier et al., 2007; Fuhrman et al., 2008) and coccolithophorids (Honjo & Okada, 1974; Cermeño et al., 2008) might also show latitudinal diversity gradients. Barton et al. (2010) modeled spatial diversity gradients of phytoplankton and show a general pattern of decreasing diversity from the equator to the poles, with sporadic regions of enhanced diversity related energetic ocean circulation.

Acritarchs are found in a wide geographical range, from the poles to the tropics. However, palaeogeographical patterns are widely unknown. While several works on palaeobiogeography were published (e.g., Cramer, 1970a; Cramer & Díez, 1972; Vavrdová, 1974; Colbath, 1990; Le Hérisse & Gourvenec, 1995; Molyneux et al., 2013), most of these concern differences in assemblage composition (s. 1.3.5.2 *Provincialism*), with none focusing on diversity gradients. Additionally, new palaeogeographical reconstructions became available since. Thus, one of the aims of this work is, in addition to temporal biodiversity trends, to also use the database to detect palaeogeographic signals. The respective study (*Article VI*) attempts to investigate, if global early Palaeozoic (Cambrian–Ordovician) phytoplankton distribution is palaeogeographically, for instance, latitudinally controlled, and further, if it is possible to define patterns of diversity changes in palaeogeographical transects. Thus, the investigation aims to reconstruct patterns of latitudinal diversity distribution and their change through time, and to determine the factors controlling this distribution, such as temperature, salinity, and continental area covered by sea.

### 3.5.2 Provincialism

Plate tectonics may create barriers preventing floral interchanges, fostering the formation of distinct provinces. However, no distinct provinciality is known until the Cambrian/Ordovician boundary. While the Cambrian and the Late Ordovician are characterised by a high degree of cosmopolitanism (Molyneux et al., 2013), distinct biogeographic provinces have been established for the Lower–Middle Ordovician. The Baltic Province represents a more warm water, tropical acritarch flora, and the peri-Gondwanan Province comprises forms adapted to a colder, boreal environment (Cramer & Díez, 1974a, b; Vavrdová, 1974; Servais et al., 2003; Molyneux et al., 2013). Several factors probably played a role in the formation and maintenance of this provincialism, such as water temperature and ocean currents (Playford et al., 1995; Tongiorgi et al., 1995; Molyneux et al., 2013; Servais et al., 2014). Similarly, in many of their works, Cramer & Díez described latitudinal dependent acritarch associations in the Silurian (Cramer, 1968, 1969, 1970a, b, Cramer & Díez, 1972, 1974a, b). Cramer (1968, 1969) discovered that acritarch floras differ in composition from



warm carbonate rich to cold siliciclastic areas. In total, six provinces were defined by the authors (Cramer, 1970a; Cramer & Díez, 1972, 1974a, b). However, their latitude parallel models proved to be incompatible with more recent palaeogeographical reconstructions, and were subsequently superseded (e.g., Le Hérisse & Gourvenec, 1995; Le Hérisse et al., 1997). The different biofacies were controlled by depositional environment rather than biogeography (Le Hérisse & Gourvenec, 1995). Le Hérisse & Gourvenec (1995) showed that acritarch distribution was not merely controlled by latitudes, as suggested by Cramer (1971) and Cramer & Díez (1972, 1974a, b), but the combined effects of continental configuration, latitude, environment and oceanic circulation. While provincialism is recognised to some degree for the Early Devonian (Le Hérisse et al., 1997), acritarch assemblages contained a higher amount of cosmopolitan taxa (Le Hérisse et al., 2009). Colbath (1990) investigated the biogeographical distribution of Late Devonian microfloras. Provincialism broke down with the continuing closure of the Rheic Ocean, leading to a higher degree of cosmopolitanism in the Middle and Late Devonian (Molyneux et al. 2013).

Phytoplankton provinces provide a useful tool, e.g., in reconstructing ancient climate belts and ocean currents. However, due to uneven geographic sampling coverage, the extent of palaeoprovinces is poorly known. Herein, a study (*Article V*) is included attempting to investigate the distribution of the Ordovician peri-Gondwanan province. While the North African margin of Gondwana is well researched, many other regions are not. In some more northern parts of Gondwana, as well as adjacent regions, mixed assemblages, including both typical peri-Gondwanan and typical Baltic taxa, are found (Molyneux et al., 2013), e.g., in Argentina (e.g., Achab et al., 2006; Rubinstein et al., 2011), Australia (Playford & Martin, 1984; Quintavalle & Playford, 2006a, b), and South China (e.g., Tongiorgi et al., 1995; 1998). But the extent to where Baltic taxa are found is unknown, since many regions between these mixed provinces and the classic peri-Gondwanan province are not yet studied in terms of palynological assemblages. Particularly the South American margin has a very limited number of locations well researched in this matter. Indeed, most studies are done in a region in northwestern Argentina (Jujuy and Salta provinces). As beforementioned, acritarch communities from this region include taxa with affinities to the Baltic Province. Studies on Lower Palaeozoic palynology from northwestern South America, however, are very rare, while the late Mesozoic and Cenozoic in this region is well researched due to hydrocarbon exploration. Therefore, more studies are needed to examine lower Palaeozoic phytoplankton assemblages from this part of Gondwana in order to evaluate the extent of the peri-Gondwanan Province. Moreover, this data permits to assess floral exchanges between the provinces, which gives important information about lower Palaeozoic palaeogeography and palaeoceanography. As each of the different provinces comprise taxa with certain palaeoenvironmental preferences, assemblages can give information for the prevailing palaeoecological conditions. In this sense, we studied sub-surface samples from the Llanos Orientales Basin in Colombia on their palynological composition, to determine, if this locality belongs to the peri-Gondwanan acritarch province or if it also includes, as NW Argentina, taxa with Baltic affinities, therefore represents a mixed province. This study therefore enhances the knowledge about the composition of the peri-Gondwanan province, the palaeogeographical distribution of certain acritarch taxa, and allows reassessing palaeogeographical information of NW South America.

## References

- Aberhan, M., Kiessling, W., 2012. Phanerozoic Marine Biodiversity: A Fresh Look at Data, Methods, Patterns and Processes. In: Talent, J.A. (ed.), *Earth and Life, International Year of Planet Earth*. Springer, Dordrecht.
- Achab, A., Rubinstein, C.V., Astini, R.A., 2006. Chitinozoans and acritarchs from the Ordovician peri-Gondwana volcanic arc of the Famatina System, northwestern Argentina. *Review of Palaeobotany and Palynology* 139(1–4), 129–149.
- Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S., Buckley, Y.M., Calabrese, L.B., Chu, C.-J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N., Hille Ris Lambers, J., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P., Yang, L.H., 2011. Productivity is a poor predictor of plant species richness. *Science* 333, 1750–1753.
- Al-Ameri, T.K., 1983. Acid-resistant microfossils used in the determination of Palaeozoic palaeoenvironments in Libya. *Palaeogeography, Palaeoclimatology, Palaeoecology* 44, 103–116.
- Albani, R., Bagnoli, G., Ribecai, C., Raevskaya, E., 2007. Late Cambrian acritarch Lusatia: Taxonomy, palaeogeography, and biostratigraphic implications. *Acta Palaeontologica Polonica* 52(4), 809–818.
- Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J., Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomašových, A., Visaggi, C.C., 2008. Phanerozoic Trends in the Global Diversity of Marine Invertebrates. *Science* 321, 97–100.
- Armstrong, H.A., Brasier, M.D., 2005. *Microfossils*. Blackwell Publishing, Oxford, U.K., 304 pp.
- Arouri, K., Greenwood, P.F., Walter, M.R., 1999. A possible chlorophycean affinity of some Neoproterozoic acritarchs. *Organic Geochemistry* 30(10), 1323–1337.
- Barton, A.D., Dutkiewicz, S., Flierl, G., Bragg, J., Follows, M.J., 2010. Patterns of diversity in marine phytoplankton. *Science* 327, 1509–1511.
- Basset, M.G. (ed.), 2009. *Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography*. Geological Society, London, Special Publications 325, 287 pp.
- Bates, T.S., Charlson, R.J., Gammon, R.H., 1987. Evidence for the climatic role of marine biogenic sulphur. *Nature* 329, 319–321
- Beardall, J., Stojkovic, S., Larsen, S., 2009. Living in a high CO<sub>2</sub> world: impacts of global climate change on marine phytoplankton. *Plant Ecology and Diversity* 2(2), 191–205.
- Behrenfeld, M.J., Randerson, J.T., McClain, C.R., Feldman, G.C., Los, S.O., Tucker, C.J., Falkowski, P.G., Field, C.B., Frouin, R., Esaias, W.E., Kolber, D.D., Pollack, N.H., 2001. Biospheric primary production during an ENSO transition, *Science* 291, 2594–2597.
- Bekker, A., Holland, H.D., Wang, P.-L., Rumble, D., III, Stein, H.J., Hannah, J.L., Coetzee, L.L., Beukes, N.J., 2004. Dating the rise of atmospheric oxygen: *Nature* 427, 117–120.

- Bopp, L., Aumont, O., Cadule, P., Alvain, S., Gehlen, M., 2005. Response of diatoms distribution to global warming and potential implications: A global model study. *Geophysical Research Letters*, 32, 1–4.
- Bottjer, D.J., Hagadorn, J.W., Dornbos, S.Q., 2000. The Cambrian substrate revolution. *GSA today* 10(9). 1–7.
- Boucot, A.J., Xu, C., Scotese, C.R., Morley, R.J., 2013. Phanerozoic paleoclimate: An atlas of lithologic indicators of climate. SEPM (Society for Sedimentary Geology), Tulsa, OK, U.S.A., 30 pp.
- Bown, P.R., Lees, J.A., Young, J.R., 2004. Calcareous nannoplankton diversity and evolution through time. In: Thierstein, H., Young, J.R. (eds), *Coccolithophores — from Molecular Processes to Global Impact*. Springer-Verlag, Berlin, Germany, pp. 481–507.
- Boyce, D.G., Lewis, M.R., Worm, B., 2010. Global phytoplankton decline over the past century. *Nature* 466, 591–596.
- Brasier, M., Cowie, J., Taylor, M., 1994. Decision on the Precambrian–Cambrian boundary stratotype. *Episodes* 17(1–2), 3–8.
- Brenner, W., 2001. Organic-walled microfossils from the central Baltic Sea, indicators of environmental change and base for ecostratigraphic correlation. *Baltica* 14, 40–51.
- Brenner, W., 2005. Holocene environmental history of the Gotland Basin (Baltic Sea) — a micropalaeontological model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 227–241.
- Brenner, W., Foster, C.B., 1994. Chlorophycean algae from the Triassic of Australia. *Review of Palaeobotany and Palynology* 80, 209–234.
- Briggs, D., Crowther, P.R., 2008. *Palaeobiology II*. John Wiley & Sons, New Jersey, U.S.A., 600 pp.
- Brocke, R., Fatka, O., Molyneux, S.G., Servais, T., 1995. First appearance data of selected Early Ordovician acritarch taxa from Peri-Gondwana. In: Cooper, J.D., Droser, M.L., Finney, S.C. (eds), *Ordovician Odyssey: Short Papers for the 7th International Symposium on the Ordovician System*. Pacific Section – Society for Sedimentary Geology (PS-SEPM), Fullerton (CA), USA, pp. 473–476.
- Brocke, R., Fatka, O., Servais, T., 1997. A review of the Ordovician acritarchs *Aureotesta* and *Marrocanium*. *Annales de la Société Géologique de Belgique* 120(1), 1–21
- Brocks, J.J., Summons, R.E., 2003. Sedimentary hydrocarbons, biomarkers for early life. *Treatise on Geochemistry* 8, 63–115.
- Brocks, J.J., Logan, G.A., Buick, R., Summons, R.E., 1999. Archean molecular fossils and the early rise of eukaryotes. *Science* 285, 1033–1036
- Brocks, J.J., Buick, R., Summons, R.E., Logan, G.A., 2003. A reconstruction of Archean biological diversity based on molecular fossils from the 2.78 to 2.45 billion-year-old Mount Bruce Supergroup, Hamersley Basin, Western Australia. *Geochim. Cosmochim. Acta* 67, 4321–4335.
- Brown, J.H., 2014. Why are there so many species in the tropics? *Journal of Biogeography* 41(1), 8–22.
- Brussaard, C.P.D., Wilhelm, S.W., Thingstad, F., Weinbauer, M.G., Bratbak, G., Haldal, M., Kimmance, S.A., Middelboe, M., Nagasaki, K., Paul, J.H., Schroeder, D.C., Suttle, C.A., Vaqué, D., Wommack, K.E., 2008. Global-scale processes with a nanoscale drive: The role of marine viruses. *ISME Journal* 2, 575–578.
- Butterfield, N.J., Rainbird, R.H., 1998. Diverse organic-walled fossils, including ‘possible

- dinoflagellates', from the early Neoproterozoic of arctic Canada. *Geology* 26(11), 963–966.
- Butterfield, N.J., Knoll, A.H., Swett, K., 1994. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils & Strata* 34, 1–84.
- Caldeira, K., Wickett, M.E., 2003. Oceanography: anthropogenic carbon and ocean pH. *Nature* 425(6956), 365.
- Calner, M., Kozłowska, A., Masiak, M., Schmitz, B., 2006. A shoreline to deep basin correlation chart for the middle Silurian coupled extinction-stable isotopic event. *GFF* 128, 79–84.
- Came, R.E., Eiler, J.M., Veizer, J., Azmy, K., Brand, U., Weidman, C.R., 2007. Coupling of surface temperature and atmospheric CO<sub>2</sub> concentrations during the Paleozoic era. *Nature* 449, 198–201.
- Came, R.E., Brand, U., Guo, W., Veizer, J., Azmy, K., Eiler, J., 2008. Application of carbonate “clumped isotope” thermometry to marine brachiopods from icehouse to greenhouse periods in the Paleozoic era - Preliminary results. *Geol. Soc. Am. Annu. Mtg., Abstr.* 40(6), 402.
- Caputo, M.V. and Crowell, J.C., 1985. Migration of glacial centers across Gondwana during Paleozoic Era. *Bulletin of the Geological Society of America* 96, 1020-1036
- Cermeño, P., Dutkiewicz, S., Harris, R.P., Follows, M., Schofield, O., Falkowski, P.G., 2008. The role of nutricline depth in regulating the ocean carbon cycle. *PNAS* 105, 20344–20349.
- Charlson, R.J., Lovelock, J.E., Andreae, M.O., Warren, S.G., 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326, 655–661
- Châteauneuf, J.J., Reyre, Y., 1974. *Éléments de Palynologie: Applications Géologiques*. Laboratoire de Paléontologie de l'Université de Genève, Genève, 345 pp.
- Chown, S.L., Gaston, K.J., 2000. Areas, cradles and museums: the latitudinal gradient in species richness. *15*(8), 5.
- Christie, M., Holland, S.M., Bush, A.M., 2013. Contrasting the ecological and taxonomic consequences of extinction. *Paleobiology* 39(4), 538–559.
- Colbath, G.K., Grenfell, H.R., 1995. Review of biological affinities of acid-resistant, organic-walled eukaryotic algal microfossils (including ‘acritarchs’). *Review of Palaeobotany and Palynology* 86, 287–314.
- Cocks, L.R.M., 2007. Blowing hot and cold in the Palaeozoic. *Proceedings of the Geologists' Association* 118, 225–237.
- Cocks, L.R.M., McKerrow, W.S., 1973. Brachiopod distributions and faunal provinces in the Silurian and Lower Devonian. *Special Papers in Palaeontology* 12, 291–304.
- Cocks, L.R.M., Torsvik, T.H., 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society, London* 159, 631–644.
- Cocks, L.R.M., Torsvik, T.H., 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. In: Gee, D.G., Stephenson, R.A. (eds), *European Lithosphere Dynamics*. Geological Society, London, *Memoirs* 32, 83–95.
- Colbath, G.K., 1990. Palaeobiogeography of Middle Palaeozoic organic-walled phytoplankton. In: McKerrow, W.S., Scotese, C.R. (eds), *Palaeozoic Palaeogeography and Biogeography*. Geological Society, London, *Memoirs* 12, 207–213.
- Colbath, G.K., Grenfell, H.R., 1995. Review of the biological affinities of Paleozoic acid-resistant, organic walled eukaryotic algal microfossils (including ‘acritarchs’). *Review of Palaeobotany and Palynology* 96, 297–314. Cooper & Nowlan, 1999

- Cooper, R.A., Nowlan, G.S., 1999. Proposed global stratotype section and point for base of the Ordovician System. *Acta Universitatis Carolinae – Geologica* 43(1/2), 61–64.
- Cooper, R.A., Nowlan, G.S., Williams, H.S., 2001. Global stratotype section and point for base of the Ordovician System. *Episodes* 24, 19–28.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408, 184–187.
- Cramer, F.H., 1968. Silurian palynologic microfossils and paleolatitudes. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1968, 591–597.
- Cramer, F.H., 1969. Possible implications for Silurian paleogeography from phytoplankton assemblages of the Rose Hill and Tuscarora Formations of Pennsylvania. *Journal of Paleontology* 43, 485–491.
- Cramer, F.H., 1970a. Distribution of selected Silurian acritarchs: an account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa. *Revista Española de Micropaleontología, Numero Extraordinario* 1, 1–203. [imprinted 1970, issued 1971]
- Cramer, F.H., 1970b. Middle Silurian continental movements estimated from phytoplankton facies transgression. *Earth and Planetary Science Letters* 10, 87–93.
- Cramer, F.H., Díez, M. del C.R., 1972. North American Silurian palynofacies and their spatial arrangement: acritarchs. *Palaeontographica, Abteilung B* 138, 107–180.
- Cramer, F.H., Díez, M. del C.R., 1974a. Early Paleozoic palynomorph provinces and paleoclimate. In: Ross, C.A. (ed.), *Paleogeographic Provinces and Provinciality*. Society of Economic Paleontologists and Mineralogists, Tulsa, OK, Special Publications 21, 177–188.
- Cramer, F.H., Díez, M. del C.R., 1974b. Silurian acritarchs: distribution and trends. *Review of Palaeobotany and Palynology* 18, 137–154.
- Cramer, B.D., Saltzman, M.R., 2005. Sequestration of  $^{12}\text{C}$  in the deep ocean during the early Wenlock (Silurian) positive carbon isotope excursion. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219, 333–349.
- Cramer, B.D., Kleffner, M.A., Saltzman, M.R., 2006. The Late Wenlock Mulde positive carbon isotope ( $\delta^{13}\text{C}_{\text{carb}}$ ) excursion in North America. *GFF* 128, 85–90
- Cruz, N.M., 2011. Acritarcos. In: Carvalho, I.S. (ed.), *Paleontologia – Microfósseis, Paleoinvertebrados*. Editora Interciência, Rio de Janeiro, 2, 221–228.
- Cummins, R.C., Finnegan, S., Fike, D.A., Eiler, J.M., Fischer, W.W., 2014. Carbonate clumped isotope constraints on Silurian ocean temperature and seawater  $\delta^{18}\text{O}$ . *Geochimica et Cosmochimica Acta* 140, 241–258.
- Currie, D.J., 1991. Energy and Large-Scale Patterns of Animal- and Plant-Species Richness. *The American Naturalist* 137(1), 27–49.
- Dale, B., 1988. Low salinity dinoflagellate cyst assemblages from recent sediments of the Baltic region. Abstracts of the 7<sup>th</sup> International Palynological Congress, Brisbane, Australia, 33.
- Dale, B., 1996. Dinoflagellate cyst ecology: modelling and geological applications. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*, vol. 3. AASP Foundation, Dallas, TX, pp. 1249–1275.
- Davydov, V.I., Glenister, B.F., Spinosa, C., Ritter, S.M., Chernykh, V.V., Wardlaw, B.R., Snyder,

- W.S., 1998. Proposal of Aidaralash as GSSP for base of the Permian System. *Episodes* 21, 11–18.
- Delwiche, C.F., 1999. Tracing the thread of plastid diversity through the tapestry of life. *The American Naturalist* 154, S164–S177.
- Domeier, M., Torsvik, T.H., 2014. Plate tectonics in the late Paleozoic. *Geoscience Frontiers* 5, 303–350.
- Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean acidification: the other CO<sub>2</sub> problem. *Annual Review of Marine Science* 1, 169–192.
- Dorning, K.J., 1981. Silurian acritarch distribution in the Ludlovian Shelf Sea of South Wales and the Welsh Borderland. In: Neale, R.G., Brasier, M.D. (eds), *Microfossils from Recent and Fossil Shelf Seas*. Chichester: Ellis Horwood, pp. 31–36.
- Dorning, K.J., 1996. Organic microfossil geothermal alteration and interpretation of regional tectonic provinces. *Journal of the Geological Society, London* 143, 219–220.
- Downie, C., 1973. Observations on the nature of the acritarchs. *Palaeontology* 16, 239–259.
- Downie, C., Evitt, W.R., Sarjeant, W.A.S., 1963. Dinoflagellates, hystrichospheres, and the classification of the acritarchs. *Stanford University Publications in Geological Sciences* 7, 1–16.
- Droser, M.L., Finnegan, S., 2003. The Ordovician Radiation: A follow-up to the Cambrian Explosion? *Integrative and Comparative Biology* 43(1), 178–184.
- Dutkiewicz, S., Morris, J.J., Follows, M.J., Scott, J., Levitan, O., Dyhrman, S.T., Berman-Frank, I., 2015. Impact of ocean acidification on the structure of future phytoplankton communities. *Nature Climate Change* 5 (11), 1002–1006.
- Eiler, J.M., 2007. “Clumped-isotope” geochemistry—the study of naturally-occurring, multi-substituted isotopologues. *Earth and Planetary Science Letters* 262, 309–327.
- Eiler, J.M., 2011. Paleoclimate reconstruction using carbonate-clumped isotope thermometry. *Quaternary Science Reviews* 30, 3575–3588.
- Eisenack, A., 1963. Hystrichospheren. *Biological Reviews* 38, 10–139.
- Ellegaard, 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109, 65–81.
- Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects of temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp. nov. (dinophyceae) from the Baltic Sea area. *Journal of Phycology* 38, 775–789.
- Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., Peterson, K.J., 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* 334, 1091–1097.
- Evitt, W.R., 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs I – *Proceedings of the National Academy of Science of the United States of America* 49, 158–164.
- Falkowski, P., 2012. The power of plankton. *Nature* 483, 17–20.
- Falkowski, P.G., Raven, J.A., 1997. *Aquatic Photosynthesis*. Blackwell Scientific, Oxford, 375 pp.
- Falkowski, P., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Hogberg, P., Linder, S., Mackenzie, F.T., Moore, B., III, Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V., Steffen, W., 2000. The global carbon cycle: A test of our knowledge of earth as a system. *Science* 290, 291–296.

- Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305, 354–360.
- Fatka, O., Brocke, R., 1999. Morphologic variability in two populations of *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972. – *Palynology* 23, 153–180.
- Fatka, O., Molyneux, S.G., Servais, T., 1997. The Ordovician acritarch *Frankea*: some critical remarks. *Geobios* 30 (3), 321–326.
- Faure, G., 1986. Principles of Isotope Geology. John Wiley and Sons, New York, 606 pp.
- Feng, Y.Y., Warner, M.E., Zhang, Y., Sun, J., Fu, F.X., Rose, J.M., Hutchins, D.A., 2009. Interactive effects of increased pCO<sub>2</sub>, temperature and irradiance on the marine coccolithophore *Emiliania huxleyi* (*Prymnesiophyceae*). *Eur. J. Phycol.* 43(1), 87–98.
- Ferguson, S., Warny, S., Escarguel, G., Mudie, P.J., 2018. MIS 5–1 dinoflagellate cyst analyses and morphometric evaluation of *Galeacysta etrusca* and *Spiniferites cruciformis* in southwestern Black Sea. *Quaternary International* 465, 117–129.
- Field, C., Behrenfeld, M., Randerson, J., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–40.
- Finnegan, S., Bergmann, K., Fischer, W.W., Jones, D.S., Fike, D.A., Hughes, N.C., Tripathi, A., Eiler, J.M., 2011. Constraints on the durations and magnitude of Late Ordovician–Early Silurian glaciation. *Science* 331, 903–906.
- Fischer, W.W., Hemp, J., Johnson, J.E., Evolution of oxygenic photosynthesis. *Annual Review of Earth and Planetary Sciences* 44, 647–83.
- Flögel, S., Wold, C., Hay, W., 2000. Evolution of sediments and ocean salinity. Abstracts volume, 31st International Geological Congress, Rio de Janeiro, Brazil, August 6–17, 2000, 4 pp.
- Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. Climate Modes of the Phanerozoic – The history of the Earth’s climate over the past 600 million years. Cambridge University Press, Cambridge, 274 pp.
- Frakes, L.A., Francis, J.E., and Syktus, J.I., 1992, Climate Modes of the Phanerozoic: Cambridge, Cambridge University Press, Cambridge, 274 pp.
- Fuhrman, J.A., Steele, J.A., Hewson, I., Schwalbach, M.S., Brown, M.V., Green, J.L., Brown, J.B., 2008. A latitudinal diversity gradient in planktonic marine bacteria. *PNAS* 105, 7774–7778.
- Gao, K.S., Zheng, Y.Q., 2010. Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). *Glob. Chang. Biol.* 16(8), 2388–2398.
- Goebel, N.L., Edwards, C.A., Zehr, J.P., Follows, M.J., Morgan, S.G., 2013. Modeled phytoplankton diversity and productivity in the California Current System. *Ecological Modelling* 264, 37–47.
- Gregg, W.W., Conkright, M.E., 2002. Decadal changes in global ocean chlorophyll. *Geophysical Research Letters* 29, 1730–1734
- Gregg, W.W., Conkright, M.E., Ginoux, P., O’Reilly, J.E., Casey, N.W., 2003. Ocean primary production and climate: Global decadal changes. *Geophysical Research Letters* 30(15), 3-1–3-4.
- Hader, D.P., Villafane, V.E., Helbling, E.W., 2014. Productivity of aquatic primary producers under global climate change. *Photochemical & Photobiological Sciences* 13, 1370–1392.
- Hallam, A., 1992. Phanerozoic sea-level changes. Columbia University Press, New York, 266 pp.

- Hallett, R.I., 1999. Consequences of environmental change on the growth and morphology of *Lingulodinium polyedrum* (Dinophyceae) in culture. PhD Thesis, University of Westminster, London.
- Han, T.M., Runnegar, B., 1992. Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee iron-formation, Michigan. *Science* 257, 232–35.
- Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic, *Science*, 235, 1156–1187.
- Haq, B.U., Al-Qahtani, A.M., 2005. Phanerozoic cycles of sea-level change on the Arabian Platform. *GeoArabia* 10, 127–160.
- Haq, B.U. Shutter, S.R., 2008. A chronology of Paleozoic sea-level changes. *Science* 322, 64–68.
- Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of fluctuating sea levels since the triassic. *Science* 235, 1156–1167.
- Harland, R., 1977. Recent and Late Quaternary (Flandrian and Devensian) dinoflagellate cysts from marine continental shelf sediments around the British Isles. *Palaeontographica Abteilung B Paläophytologie* 164, 87–126.
- Hein, M., SandJensen, K., 1997. CO<sub>2</sub> increases oceanic primary production. *Nature* 388(6642), 526–527.
- Henkes, G.A., Passey, B.H., Grossman, E.L., Stenton, B.J., Perez-Huerta, A., Yancey, T.E., 2014. Temperature limits for preservation of primary calcite clumped isotope temperatures. *Geochim. Cosmochim. Acta* 139, 362–382.
- Henkes, G.A., Passey, B.H., Grossman, E.L., Stenton, B.J., Yancey, T.E., Perez-Huerta, A., 2018. Temperature evolution and the oxygen isotope composition of Phanerozoic oceans from carbonate clumped isotope thermometry. *Earth and Planetary Science Letters* 490, 40–50.
- Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. *The American Naturalist* 163(2), 192–211.
- Honjo, S., Okada, H., 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. *Micropaleontology* 20, 209–230.
- Hough, M.L., Shields, G.A., Evins, L.Z., Strauss, H., Henderson, R.A., Mackenzie, S., 2006. A major sulphur isotope event at c. 510 Ma: a possible anoxia-extinction-volcanism connection during the Early-Middle Cambrian transition?: Global warming as a major determining factor in biosphere evolution. *Terra Nova* 18(4), 257–263.
- Huang, Y., Liu, X., Laws, E.A., Chen, B., Li, Y., Xie, Y., Wu, Y., Gao, K., Huang, B., 2018. Effects of increasing atmospheric CO<sub>2</sub> on the marine phytoplankton and bacterial metabolism during a bloom: A coastal mesocosm study. *Science of the Total Environment* 633, 618–629.
- Iglesias-Rodriguez, M.D., Halloran, P.R., Rickaby, R.E., Hall, I.R., Colmenero-Hidalgo, E., Gittins, J.R., Green, D.R., Tyrrell, T., Gibbs, S.J., von Dassow, P., Rehm, E., Armbrust, E.V., Boessenkool, K.P., 2008. Phytoplankton calcification in a high-CO<sub>2</sub> world. *Science* 320(5874), 336–340.
- Irigoien, X., Huisman, J., Harris, R.P., 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429, 863–867.
- Islam, M.A., 1983. Dinoflagellate cysts from the Eocene of London and the Hampshire Basins, southern England. *Palynology* 7, 71–92.
- Jablonski, D., Chaloner, W.G., 1994. Extinctions in the Fossil Record [and Discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 344(1307), 11–



- Jacobson, S.R., 1979. Acritarchs as palaeoenvironmental Indicators in Middle and Upper Ordovician Rocks from Kentucky, Ohio and New York. *Journal of Paleontology* 53(5), 1197–1212.
- Jacoby, J.M., Collier, D.C., Welch, E.B., Hardy, F.J., Crayton, M., 2000. Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. *Canadian Journal of Fisheries and Aquatic Sciences* 57(1), 231–240.
- Javaux, E.J., Knoll, A.H., Walter, M.R., 2001. Morphological and ecological complexity in early eukaryotic ecosystems. *Nature* 412, 66–69
- Kaljo, D., Kiipli T., Martma, T., 1997. Correlation of carbon isotope event markers through the Wenlock-Pridoli sequence at Ohesaare (Estonia) and Priekule (Latvia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 132, 211–223
- Kaljo, D., Martma, T., Männik, P., Viira, V., 2003. Implications of Gondwana glaciations in the Baltic late Ordovician and Silurian and a carbon isotopic test of environmental cyclicality. *Bull. Soc. Géol. Fr.* 174, 59–66
- Kaljo, D., Martma, T., 2006. Application of carbon isotope stratigraphy to dating Baltic Silurian rocks. *GFF* 128, 161–168.
- Katz M.E., Finkel, Z.V., Grzebyk, D., Knoll, A.H., Falkowski, P.G., 2004. Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. *Annual Review of Ecology, Evolution, and Systems* 35, 523–556.
- Kettle, A.J., Andreae, M.O., 2000. Flux of dimethylsulfide from the oceans: A comparison of updated data sets and flux models. *Journal of Geophysical Research* 105(D22), 26,793–26,808.
- Klug, C., Kröger, B., Kiessling, W., Mullins, G., Servais, T., Frýda, J., Korn, D., Turner, S., 2010. The Devonian nekton revolution. *Lethaia* 43, 465–477.
- Knoll A.H., 1994. Proterozoic and Early Cambrian protists: evidence for accelerating evolutionary tempo. *PNAS* 91, 6743–50.
- Knoll, A.H. 2003. *Life on a Young Planet: The First Three Billion Years of Evolution on Earth*. Princeton Univ. Press, New Jersey, 277 pp.
- Knoll, A.H., Butterfield, N.J., 1989. Palaeontology: new window on Proterozoic life. *Nature* 337, 602–603.
- Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the marine dinoflagellate *Lingulodinium polyedrum* (= *L. machaerophorum*). *Palynology* 19, 143–166.
- Landing, E., 1994. Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. *Geology* 22, 179–182.
- Landing, E., 1996. Avalon: Insular continent by the latest Precambrian. In: Nance, R.D., Thomlpson, M.D. (eds), *Avalon and Related Peri-Gondwana Terranes of the Circum-North Atlantic*. Geological Society of America, Special Paper 304, pp. 29–63.
- Landing, E., 2004. Precambrian-Cambrian boundary interval deposition and the marginal platform of the Avalon microcontinent. *Journal of Geodynamics* 37, 411–435.
- Le Hérisse, A., 1989. Acritarches et kystes d'algues Prasinophycées du Silurien de Gotland, Suède. *Palaeontographia Italica* 76, 57–302.
- Le Hérisse, A., Gourvenec, R., 1995. Biogeography of upper Llandovery and Wenlock acritarchs. *Review of Palaeobotany and Palynology* 86, 111–113.

- Le Hérissé, A., Al-Tayyar, H. & van der Eem, H. 1995. Stratigraphic and paleogeographical significance of Silurian acritarchs from Saudi Arabia. *Review of Palaeobotany and Palynology* 89, 49–74.
- Le Hérissé, A., Gourvenec, R., Wicander, R. 1997. Biogeography of Late Silurian and Devonian acritarchs and prasinophytes. *Review of Palaeobotany and Palynology* 98, 105–124.
- Le Hérissé, A., Dorning, K.J., Mullins, G.L., Wicander, R., 2009. Global patterns of organic-walled phytoplankton biodiversity during the late Silurian to earliest Devonian. *Palynology* 33(1), 25–75.
- Lei, Y., Servais, T., Feng, Q., He, W., 2012. The spatial (nearshore-offshore) distribution of latest Permian phytoplankton from the Yangtze Block, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 363–364:151–162.
- Lenz, A.C., Noble, P.J., Masiak, M., Poulson, S.R., Kozłowska, A., 2006. The *lundgreni* Extinction Event: integration of paleontological and geochemical data from Arctic Canada. *GFF* 128, 153–158.
- Lewis, J., Hallett, R., 1997. *Lingulodinium polyedrum* (*Gonyaulax polyedra*) a blooming dinoflagellate. *Oceanography and Marine Biology: An Annual Review* 35, 97–161.
- Li, W.K.W., 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419, 154–157.
- Li, J., Servais, T., Yan, K., Zhu, H., 2004. A nearshore–offshore trend in acritarch distribution from the Early–Middle Ordovician of the Yangtze Platform, South China. *Review of Palaeobotany and Palynology* 130(1–4), 141–161.
- Li, J., Servais, T., Yan, K., 2014. The Ordovician acritarch genus *Rhopaliophora*: Biostratigraphy, palaeobiogeography and palaeoecology. *Review of Palaeobotany and Palynology* 208, 1–24.
- Lipps, J.H. (ed.), 1993. *Fossil Prokaryotes and Protists*. Blackwell Scientific, Boston, pp. 342 pp.
- Lister, T.R., 1970. A monograph of the acritarchs and chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope areas, Shropshire. *Palaeontographical Society, London, U.K.*, 100 pp.
- Lovelock, J., 2006. *The Revenge of Gaia*. Penguin Books, London, U.K., 192 pp.
- Lyons, T.W., Reinhard, C.T., Planavsky, N.J., 2014. The rise of oxygen in Earth's early ocean and atmosphere. *Nature* 506(7488), 307–315.
- Margulis, L., 1970. *Origin of Eukaryotic Cells*. Yale University Press, New Haven U.S.A. 371 pp.
- Margulis, L. 1981. *Symbiosis in cell evolution: life and its environment on the early earth*. Freeman, San Francisco, 419 pp.
- Margulis, L., Schwartz, K.V., 1982. *Five Kingdoms. An Illustrated Guide to the Phyla of Life on Earth*. W.H.Freeman, San Francisco, 338 pp.
- Marret, F., Mudie, P., Aksu, A., Hiscott, R.N., 2007. A Holocene dinocyst record of a two-step transformation of the Neoeuxinian brackish water lake into the Black Sea. *Quaternary International* 197(1–2), 72–86.
- Martin, F., 1993. Acritarchs: A review. *Biological Reviews* 68, 475–538.
- Martin, F., 1996. Systematic revision of the acritarch *Ferromia pellita* and its bearing on Lower Ordovician stratigraphy. *Review of Palaeobotany and Palynology* 93, 23–34.
- Martin, R.E., 2003. The fossil record of biodiversity: nutrients, productivity, habitat area and differential preservation. *Lethaia* 36, 179–193.
- Martin, F., Dean, W.T., 1981. Middle and Upper Cambrian and Lower Ordovician acritarchs from

- Random Island, Eastern Newfoundland. Geological Survey of Canada, Bulletin, 43 pp.
- Martin, F., Dean, W.T., 1988. Middle and Upper Cambrian acritarch and Trilobite zonation at Manuels River and Random Island, eastern Newfoundland. Geological Survey of Canada, Bulletin, 91 pp.
- Martin, R., Quigg, A., 2012. Evolving phytoplankton stoichiometry fueled diversification of the marine biosphere. *Geosciences* 2, 130–146.
- Martin, R.E., Servais, T., 2019. Did the evolution of the phytoplankton fuel the diversification of the marine biosphere? *Lethaia*.
- Martinsson, A. (ed.), 1977. The Silurian-Devonian boundary: final report of the Committee of the Siluro-Devonian Boundary within IUGS Commission on Stratigraphy and a state of the art report for Project Ecostratigraphy. International Union of Geological Sciences, Series A, 5, p. 347.
- Matthiessen, J., Brenner, W. 1996. Chlorococcalalgen und Dinoflagellatenzysten in rezenten Sedimenten des Greifswalder Boddens (südliche Ostsee). *Senckenbergiana Maritima* 27, 33–48.
- McCaffrey, W.D., Barron, H.F., Molyneux, S.G. & Kneller, B.C., 1992. Recycled acritarchs as provenance indicatorsimplications for Caledonian Terrane reconstruction. *Geological Magazine* 129, 457–464.
- McKerrow, W.S., Scotese, C.R. (eds), 1990. *Palaeozoic Palaeogeography and Biogeography*. The Geological Society, London, Memoir 12, 435 pp.
- Melchin, M.J., Williams, S.H., 2000. A restudy of the akidograptine graptolites from Dob's Linn and a proposed redefined zonation of the Silurian Stratotype. In: Cockle, P., Wilson, G.A., Brock, G.A., Engerbretsen, M.J., Simpson, A. (eds), *Palaeontology Down-under 2000, 11th–15th July 2000*, Orange, NSW, Geological Society of Australia, Abstracts, pp. 61e63.
- Mendelson, C., 1993. Acritarchs and Prasinophytes. In: Lipps, J.H. (ed.), *Fossil Prokaryotes and Protists*. Blackwell Scientific, Boston, pp. 77–104.
- Mertens K.N., Ribeiro, S., Bouimetarhan, I., Caner, H., Combourieu-Nebout, N., Dale, B., De Vernal, A., Ellegaard, M., Filipova, M., Godhe, A., Goubert, E., Grøsfjeld, K., Holzwarth, U., Kotthoff, U., Leroy, S.A.G., Londeix, L., Marret, F., Matsuoka, K., Mudie, P.J., Naudts, L., Peña-Manjarrez, J.L., Persson, A., Popescu, S.-M., Pospelova, V., Sangiorgi, F., van der Meer M.T.J., Vink, A., Zonneveld, K.A.F., Vercauteren, D., Vlassenbroeck, J., Louwye, S., 2009. Process length variations in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: Investigation its potential as salinity proxy. *Marine Micropalaeontology* 70, 54–69.
- Mertens, K.N., Dale, B., Ellegaard, M., Jansson, I.M., Godhe, A., Kremp, A., Louwye, S., 2011. Process length variation in cysts of the dinoflagellate *Protoceratium reticulatum*, from surface sediments of the Baltic–Kattegat–Skagerrak estuarine system: a regional salinity proxy. *BOREAS* 40, 242–255.
- Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S., 2005. The Phanerozoic record of global sea-level change. *Science* 310, 1293–1298.
- Moczydłowska, M., 2011. The Early Cambrian Phytoplankton Radiation: Acritarch Evidence from the Lükati Formation, Estonia. *Palynology* 35, 103–145.
- Moczydłowska, M., Stockfors, M., 2004. Acritarchs from the Cambrian-Ordovician Boundary Interval on Kolguev Island, Arctic Russia. *Palynology* 28, 15–73.

- Moczydłowska, M., Zang, W.-L., 2005. The plexus of Cambrian acritarch *Skiagia* and its significance for global correlation. *Acta Micropaleontologica Sinica* 22 (supplement), 117–118.
- Moczydłowska, M., Zang, W.-L., 2006. The Early Cambrian acritarch *Skiagia* and its significance for global correlation. *Palaeoworld* 15, 328–347.
- Moldowan, J.M., Talyzina, N.M., 1998. Biogeochemical evidence for dinoflagellate ancestors in the Early Cambrian. *Science* 281, 1168–1170.
- Moldowan, J.M., Dahl, J., Jacobson, S.R., Huizinga, B.J., ago, F.J., Shetty, R., Watt, D.S., Peters, K.E., 1996. Chemostratigraphic reconstruction of biofacies: molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology* 24: 159-162.
- Molyneux, S.G., 2009. Acritarch (marine microphytoplankton) diversity in an Early Ordovician deep-water setting (the Skiddaw Group, northern England): implications for the relationship between sea-level change and phytoplankton diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275(1–4), 59–76.
- Molyneux, S.G., Le Hérisse, A., Wicander, R., 1996. Palaeozoic phytoplankton. In: Jansonius, J., McGregor, D.C. (eds), *Palynology: Principles and Applications*, vol. 2. American Association of Stratigraphic Palynologists Foundation, Dallas, U.S.A., pp. 493–529.
- Molyneux, S.G., Delabroye, A., Wicander, R., Servais, T., 2013. Biogeography of early to mid Palaeozoic (Cambrian – Devonian) marine phytoplankton. In: Harper, D.A.T., Servais, T. (eds), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, *Memoirs* 38, 365–397.
- Montañez, I.P., Poulsen, C.J., 2013. The late Paleozoic ice age: An evolving paradigm. *Annual Review of Earth and Planetary Sciences* 41, 629–656.
- Mudie, P.J., Aksu, A.E., Yasar, D., 2001. Late Quaternary dinoflagellate cysts from the Black, Marmara and Aegean seas: variations in assemblages, morphology and paleosalinity. *Marine Micropaleontology* 43, 155–178.
- Munnecke, A., Servais, T., 2008. Palaeozoic calcareous plankton: evidence from the Silurian of Gotland. *Lethaia* 41, 185–194.
- Munnecke, A., Samtleben, C., Bickert, T., 2003. The Ireviken Event in the lower Silurian of Gotland, Sweden – relation to similar Palaeozoic and Proterozoic events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 99–124.
- Murtugudde, I., Beauchamp, R. J., McClain, C. R., Lewis, M. R., Busalacchi, A., 2002. Effects of penetrative radiation on the upper tropical ocean circulation. *Journal of Climate* 15, 470–486.
- Na, L., Kießling, W., 2015. Diversity partitioning during the Cambrian radiation. *PNAS* 112(15), 4702–4706.
- Navidi-Izad, N., Hashemi, H., Cascales-Miñana, Régnier, S., Wellman, C.H., Servais, T., 2019. Colonial palynomorphs from the Upper Ordovician of north-eastern Iran: ‘thalli’, coenobial Chlorophyceae (Hydrodictyaceae) or cyanobacteria? *Palynology*.
- Nehring, S., 1994. Spatial distribution of dinoflagellate resting cysts in recent sediments of Kiel Bight, Germany (Baltic Sea). *Ophelia* 39(2), 137–158.
- Nehring, S., 1997. Dinoflagellate resting cysts from recent German coastal sediments. *Botanica Marina* 40, 307–324.
- Paalits, I., Heuse, T., 2000. Taxonomic review of the acritarch genera *Acanthodiacrodium* Timofeev, 1958 and *Diornatosphaera* Downie, 1958. *Bollettino della Societa Paleontologica Italiana* 39, 311–317.

- Pagès, A., Schmid, S., Edwards, D., Barnes, S., He, N., Grice, K., 2016. A molecular and isotopic study of palaeoenvironmental conditions through the middle Cambrian in the Georgina Basin, central Australia. *Earth and Planetary Science Letters* 447, 21–32.
- Palmer, J.D., 2003. The symbiotic birth and spread of plastids: How many times and whodunit? *Journal of Phycology* 39, 4–11.
- Paproth, E., Feist, R., Flajs, G., 1991. Decision on the Devonian-Carboniferous boundary stratotype. *Episodes* 14, 331–336.
- Pflug, H.D., Reitz, R., 1985. Earliest Phytoplankton of Eukaryotic Affinity. *Naturwissenschaften* 72, 656–657.
- Pflug, H.D., Reitz, R., 1992. Palynostratigraphy in Phanerozoic and Precambrian Metamorphic Rocks. In: Schidlowski, M., Kimberley, M.M., McKirdy, D.M., Trudinger, P.A. (eds), *Early Organic Evolution: Implications for Mineral and Energy Resources*. Berlin, Springer, pp. 509–518.
- Pinckney, J.L., Millie, D.F., Vinyard, B.T., Paerl, H.W., 1997. Environmental controls of phytoplankton bloom dynamics in the Neuse River Estuary, North Carolina, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 54(11), 2491–2501.
- Playford, G., Martin, F., 1984. Ordovician acritarchs from the Canning Basin, Western Australia. *Alcheringa* 8, 187–223.
- Playford, G., Ribecai, C., Tongiorgi, M., 1995. Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium*: morphology, taxonomy, biostratigraphy, and palaeogeographic significance. *Bollettino Della Società Paleontologica Italiana* 34, 3–54.
- Pommier, T., Canbäck, B., Riemann, L., Boström, K.H., Simu, K., Lundberg, P., Tunlid, A., Hagström, Å., 2007. Global patterns of diversity and community structure in marine bacterioplankton. *Molecular Ecology* 16, 867–880.
- Posamentier, H., Vail, P., 1988. Eustatic controls on clastic deposition II – Sequence and systems tract models. In: Wilgus, C., Hastings, B., Kendall, C., Posamentier, H., Ross, C., Van Wagoner, J. (eds), *Sea-Level Changes: An Integrated Approach*. Society of Economic Paleontologists and Mineralogists (SEPM), Special Publication 42, 125–154.
- Prokoph, A., Shields, G.A., Veizer, J., 2008. Compilation and time-series analysis of a marine carbonate  $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ ,  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{34}\text{S}$  database through Earth history. *Earth-Science Reviews* 87, 113–133.
- Quintavalle, M., Playford, G., 2006a. Palynostratigraphy of Ordovician strata, Canning Basin, Western Australia. Part One: acritarchs and prasinophytes. *Palaeontographica, Abteilung B* 275, 1–88.
- Quintavalle, M., Playford, G., 2006b. Palynostratigraphy of Ordovician strata, Canning Basin, Western Australia. Part Two: chitinozoans and biostratigraphy. *Palaeontographica, Abteilung B* 275, 89–131.
- Raevskaya, E., Servais, T., 2004. *Veryhachium dumontii*: a dicrodiacrodian or a veryhachid acritarch? *Polen 14: Abstracts of the XI International Palynological Congress, Granada, Spain*. Departamento de Biología Vegetal, Universidad de Córdoba, Córdoba, Spain, p. 132.
- Rasul, S.M., 1974. The Lower Palaeozoic acritarchs *Priscogalea* and *Cymatiogalea*. *Palaeontology* 17(1), 41–63.
- Reynolds, C.S., *The Ecology of Phytoplankton*. Cambridge University Press, Cambridge, U.K., 535

pp.

Ribecai, C., Tongiorgi, M., 1999. The Ordovician acritarch genus *Pachysphaeridium* Burmann 1970: new, revised, and reassigned species. *Palaeontographia Italica* 86, 117–153.

Ribecai, C., Raevskaya, E., Tongiorgi, M., 2002. *Sacculidium* gen. nov. (Acritarcha), a new representative of the Ordovician Stelomorpha-Tranvikium plexus. *Review of Palaeobotany and Palynology* 121, 163–203.

Riebesell, U., Schulz, K.G., Bellerby, R.G., Botros, M., Fritsche, P., Meyerhofer, M., Neill, C., Nondal, G., Oeschies, A., Wohlers, J., Zollner, E., 2007. Enhanced biological carbon consumption in a high CO<sub>2</sub> ocean. *Nature* 450(7169), 545–548.

Roemmich, D., McGowan, J., 1995. Climatic warming and the decline of zooplankton in the California current. *Science* 267, 1324–1326.

Rokitta, S.D., Rost, B., 2012. Effects of CO<sub>2</sub> and their modulation by light in the life-cycle stages of the coccolithophore *Emiliana huxleyi*. *Limnol. Oceanogr.* 57(2), 607–618.

Rosenweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, 436 pp.

Rosing MT., 1999. C-13-depleted carbon microparticles in >3700-Ma sea-floor sedimentary rocks from west Greenland. *Science* 283, 674–76

Rosing, M.T., Frei, R., 2004. U-rich Archaean sea-floor sediments from Greenland - indications of >3700 Ma oxygenic photosynthesis. *Earth and Planetary Science Letters* 217(3–4), 237–244.

Ross, C.A., Ross, J.R.P., 1987. Late Paleozoic sea levels and depositional sequences. *Cushman Foundation for Foraminiferal Research Special Publications* 24, 137–149.

Ross, C.A., Ross, J.R.P., 1988. Late Paleozoic transgressive-regressive deposition. In: Wilgus, C.K., Hastings, B.J., Posamentier, H., van Wagoner, J.C., Ross, C.A., Kendall, C.G.St.C. (eds), *Sea-level Change: an Integrated Approach*, SEPM Special Publications 42, 71–108.

Royer, D.L., Berner, R.A., Montañez, I.P., Tabor, N.J., Beerling, D.J., 2004. CO<sub>2</sub> as a primary driver of Phanerozoic climate. *GSA Today* 14(3), 4–10.

Rubinstein, C.V., Vecoli, M., Astini, R.A., 2011. Biostratigraphy and paleoenvironmental characterization of the Middle Ordovician from the Sierras Subandinas (NW Argentina) based on organic-walled microfossils and sequence stratigraphy. *Journal of South American Earth Sciences* 31(1), 124–138.

Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A., Ono, T., Rios, A.F., 2004. The oceanic sink for anthropogenic CO<sub>2</sub>. *Science* 305, 367–371.

Saltzman, M.R., 2001. Silurian  $\delta^{13}\text{C}$  stratigraphy: A view from North America. *Geology* 29, 671–674.

Saltzman, M.R., Ripperdan, R.L., Brasier, M.D., Lohmann, K.C., Robison, R.A., Chang, W.T., Peng, S.C., Ergaliev, G.Kh., Runnegar, B., 2000. Global carbon isotope excursion (SPICE) during the Late Cambrian: Relation to trilobite extinctions, organic-matter burial and sea level. *Palaeogeography, Palaeoclimatology, Palaeoecology* 162, 211–223.

Sampaio, E., Lopes, A.R., Francisco, S., Paula, J.R., Pimentel, M., Maulvault, A.L., Repolho, T., Grilo, T.F., Pousão-Ferreira, P., Marques, A., Rosa, R., 2018. Ocean acidification dampens physiological stress response to warming and contamination in a commercially-important fish (*Argyrosomus regius*). *Science of the Total Environment* 618, 388–398.

- Samtleben, C., Munnecke, A., Bickert, T., Pätzold, J., 1996. The Silurian of Gotland (Sweden): Facies interpretation based on stable isotopes in brachiopod shells. *Geologische Rundschau* 85, 278–292.
- Samtleben, C., Munnecke, A., Bickert, T., 2000. Development of facies and C/O-isotopes in transects through the Ludlow of Gotland: Evidence for global and local influences on a shallow-marine environment. *Facies* 43, 1–38.
- Sandgren, C.D., 1983. Morphological variability in populations of chrysophycean resting cysts. I. Genetic (interclonal) and encystment temperature effects on morphology. *Journal of Phycology* 19(1), 64–70.
- Sarmiento, J., Hughes, T., Stouffer, R., Manabe, S., 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* 393, 245–249.
- Schopf, J.W., 1993. Microfossils of the Early Archean Apex chert: New evidence of the antiquity of life. *Science* 260, 640–46.
- Schopf, J.W., 2002. *Life's Origin: The Beginnings of Biological Organization*. University of California Press, Berkley, 208 pp.
- Seilacher, A., Pflüger, F., 1994. From biomats to benthic agriculture: a biohistoric revolution. *Biostabilization of sediments*, 97–105.
- Seitzinger, S.P., 1991. The effect of pH on the release of phosphorus from Potomac estuary sediments: implications for blue-green algal blooms. *Estuarine, Coastal and Shelf Science* 33(4): 409–418.
- Sepkoski, J.J., Jr, 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7(1), 36 – 53.
- Sepkoski, J.J. Jr., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Sepkoski, J.J., Jr., 1997. Biodiversity: Past, Present, and Future. *Journal of Paleontology* 71(4). 533–539.
- Sepkoski, J.J. Jr., Miller, A.I., 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In: Valentine, J.W. (ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton University Press and Pacific Division, American Association for the Advancement of Science, Princeton, NJ, pp. 393–396.
- Servais, T., 1993. The Ordovician acritarch *Frankea*. In: Molyneux, S.G., Dorning, K. J. (Eds.), *Contributions to acritarch and chitinozoan research*. The Palaeontological Association (Special Papers in Palaeontology 48), Durham, UK, pp. 79–95.
- Servais, T., 1996. Some considerations on acritarch classification. *Review of Palaeobotany and Palynology* 93, 9–22.
- Servais, T., 1997. The Ordovician Arkonia-Striatotheca acritarch plexus. *Review of Palaeobotany and Palynology* 98, 47–79.
- Servais, T., Brocke, R., Fatka, O., 1996. Variability in the Ordovician acritarch *Dicrodiacrodium*. *Palaeontology* 39(2), 389–405.
- Servais, T., Li, J., Molyneux, S., Raevskaya, E., 2003. Ordovician organic-walled microphytoplankton (acritarch) distribution: the global scenario. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195, 149–172.
- Servais, T., Stricanne, L., Montenari, M., 2004. Population dynamics of galeate acritarchs at the Cambrian–Ordovician transition in the Algerian Sahara. *Palaeontology* 47(2), 395–414.

- Servais, T., Vecoli, M., Li, J., Molyneux, S.G., Raevskaya, E.G., Rubinstein, C.V., 2007. The acritarch genus *Veryhachium* Deunff 1954: Taxonomic evaluation and first appearance. *Palynology* 31, 191–203.
- Servais, T., Li, J., Molyneux, S.G., Vecoli, M., 2008. The Ordovician acritarch genus *Coryphidium*. *Revue de micropaléontologie* 51, 97–120.
- Servais, T., Munnecke, A., Versteegh, G., 2009. Silurian calcispheres (Calcitarcha) of Got-land (Sweden): comparisons with calcareous dinoflagellates. *C.R. Palevol* 8, 527–534.
- Servais, T., Danelian, T., Harper, D.A.T., Munnecke A. 2014. Possible ocean circulation patterns, surface water currents and upwelling zones in the Early Palaeozoic. *GFF* 136(1), 229–223.
- Shergold, J.H., Cooper, R.A., 2004. The Cambrian Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (eds), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, UK., pp. 147–164.
- Siano, R., Alves-De-Souza, C., Foulon, E., Bendif, E.M., Simon, N., Guillou, L., Not, F. 2011. Distribution and host diversity of Amoebozoa parasites across oligotrophic waters of the Mediterranean Sea. *Biogeosciences* 8, 267–278.
- Signor & Verneij, 1994
- Smith, N.D., Saunders, R.S., 1970. Paleoenvironments and their control of acritarch distribution: Silurian of east-central Pennsylvania. *Journal of Sedimentary Petrology* 40, 324–333.
- Smith, A.G., Briden, J.C., Drewry, G.E. 1973. Phanerozoic world maps. In: Hughes, N.F. (ed.), *Organisms and Continents through Time*. Special Papers in Palaeontology 12, 1–42.
- Sorrell, P., Popescu, S.-M., Head, M.J., Suc, J.-P., Klotz, S., Oberhänsli, H., 2006. Hydrographic development of the Aral Sea during the last 2000 years based on a quantitative analysis of dinoflagellate cysts. *Palaeography, Palaeoclimatology, Palaeoecology* 234, 304–327.
- Spencer-Cervato, C., 1999. The Cenozoic deep sea microfossil record: explorations of the DSDP/ODP sample set using the Neptune database. *Palaeontologia Electronica* 2, 1–270 .
- Staplin, F.L., 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology* 4, 392–424.
- Steinacher, M., Joos, F., Frölicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S.C., Gehlen, M., Lindsay, K., Moore, J.K., Schneider, B., Segschneider, J., 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7, 979–1005.
- Sterner, R.W., Elser, J.J., 2002. *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, N.J., p. 439.
- Stover, L.E., Brinkhuis, H., Damassa, S.P., de Verteuil, L., Helby, R.J., Monteil, E., Partridge, A.D., Powel, A.J., Riding, J.B., Smelror, M., Williams, G.L., 1996. Mesozoic-Tertiary dinoflagellates, acritarchs & prasinophytes. In: Jansonius, J., McGregor, D.C. (eds), *Palynology: Principles and Applications*, Amer. Assoc. Strat. Palynol Found., pp. 641–750.
- Stricanne, L., Servais, T., 2002. A statistical approach to classification of the Cambro–Ordovician galeate acritarch plexus. *Review of Palaeobotany and Palynology* 118(1–4), 239–259.
- Stricanne, L., Munnecke, A., Pross, J., Servais, T., 2004. Acritarch distribution along an inshore-offshore transect in the Gorstian (lower Ludlow) of Gotland. *Review of Palaeobotany and Palynology* 130(1–4), 195–216.
- Stricanne, L., Servais, T., Talyzina, N., Vanguetstaine, M., 2005. Reevaluation of the late Cambrian–Early Ordovician acritarch *Nellia acifera*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 235, 87–112.



- Strom, S.L., 2008. Microbial ecology of ocean biogeochemistry: A community perspective. *Science* 320, 1043–1045.
- Strother, P.K., 1996. Acritarchs. In: Jansonius, J., McGregor, D.C., (eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Salt Lake City, pp. 81–106.
- Strother, P.K., 2008. A speculative review of factors controlling the evolution of phytoplankton during Paleozoic time. *Revue de micropaléontologie* 51, 9–21.
- Summons, R.E., Thomas, J., Maxwell, J.R., Boreham, C.J., 1992. Secular and environmental constraints on the occurrence of dinosterane in sediments. *Geochimica et Cosmochimica Acta* 56, 2437–2444.
- Summons, R.E., Jahnke, L.L., Hope, J.M., Logan, G.A., 1999. 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis. *Nature* 400(6744), 554–557.
- Talent, J.A., Mawson, R., Andrew, A.S., Hamilton, P.J., Whitford, D.J., 1993. Middle Palaeozoic events: Faunal and isotopic data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 104, 139–152.
- Talyzina, N.M., Moczyłowska, M., 2000. Morphological and ultrastructural studies of some acritarchs from the Lower Cambrian Lükati Formation, Estonia. *Review of Palaeobotany and Palynology* 112, 1–21.
- Talyzina, N.M., Moldowan, J.M., Johannisson, A., Fago, F.J., 2000. Affinities of Early Cambrian acritarchs studied by using microscopy, fluorescence flow cytometry and biomarkers. *Review of Palaeobotany and Palynology* 108, 37–53.
- Tappan, H., 1968. Primary production, isotopes, extinctions and the atmosphere. *Palaeogeography, Palaeoclimatology, Palaeoecology* 4, 187–210.
- Tappan, H.N., 1980. in *The Paleobiology of Plant Protists* (Freeman, San Francisco, 1980), p. 1028.
- Tappan, H., Loeblich Jr., A.R., 1970. Geobiologic implications of fossil phytoplankton evolution and time–space distribution. *Geological Society of America, Special Paper* 127, 247–340.
- Tappan, H., Loeblich Jr., A.R., 1972. Fluctuating rates of protistan evolution, diversification and extinction, in: 24th International Geological Congress, Section 7. pp. 205–213.
- Tappan, H., Loeblich Jr., A.R., 1973. Evolution of the oceanic plankton. *Earth Science Reviews* 9, 207–240.
- Taylor, A.G., Lasaga, A.C., 1999. The role of basalt weathering in the Sr isotope budget of the oceans. *Chemical Geology* 161, 59–88.
- Tonarová, P., Fatka, O., 2006. Morphological variability of the acritarch genus *Eliasum* Fombella 1977. In: Bek, J., Brocke, R., Dašková, J., Fatka, O. (eds.), *Palaeozoic palynology in space and time - Book of Abstracts, CIMP General Meeting 2006, Prague*. Institute of Geology, Academy of Science, Prague, Czech Republic, pp. 55–56.
- Tongiorgi, M., Yin, L.-M., Di Milia, A., 1995. Arenigian acritarchs from the Daping section (Yangtze Gorges area, Hubei Province, Southern China) and their palaeogeographic significance. *Review of Palaeobotany and Palynology* 86, 13–48.
- Tongiorgi, M., Yin, L.-M., Di Milia, A., Ribecai, C., 1998. Changing paleogeographical affinities of the acritarch assemblages throughout the Dawan Formation (Arenig, Yichang Area, South China). *Palynology* 22, 181–196.

- Tongiorgi, M., Yin, L.-M., Di Milia, A., 2003. Lower Yushanian to lower Zhejiangian palynology of the Yangtze Gorges area (Daping and Huanghuachang sections), Hubei Province, South China. *Palaeontographica Abteilung B* 266, 1–160.
- Torsvik, T.H., Cocks, L.R.M., 2005. Norway in space and time: a centennial cavalcade. *Norwegian Journal of Geology*, 85, 73–86.
- Torsvik, T.H., Cocks, L.R.M., 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In: Harper, D.A.T., Servais, T. (eds), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs 38, 5–24.
- Torsvik, T.H., Smethurst, M.A., Briden, J.C., Sturt, B.A., 1990. A review of Palaeozoic palaeomagnetic data from Europe and their palaeogeographical implications. In: McKerrow, W.S., Scotese, C.R. (eds), *Palaeozoic Palaeogeography and Biogeography*. Geological Society, London, Memoirs 12, 25–41.
- Tortell, P.D., Morel, F.M.M., 2002. Sources of inorganic carbon for phytoplankton in the eastern subtropical and equatorial Pacific Ocean. *Limnol. Oceanogr.* 47(4), 1012–1022.
- Trimborn, S., Wolf-Gladrow, D., Richter, K.U., Rost, B., 2009. The effect of pCO<sub>2</sub> on carbon acquisition and intracellular assimilation in four marine diatoms. *J. Exp. Mar. Biol. Ecol.* 376(1), 17–25.
- Turon, J.L., 1984. Le palynoplankton dans l'environnement actuel de l'Atlantique nord-oriental. Evolution climatique et hydrologique depuis le dernier maximum glaciaire. *Mémoires de l'Institut de Géologie du Bassin d'Aquitaine* 17, 1–313.
- Tyson, R.V., 1995. *Sedimentary organic matter. Organic facies and palynofacies*. Chapman & Hall, London, pp. 615.
- Vail, P.R., Mitchum, R.M., Thompson, S., 1977. Seismic Stratigraphy and Global Changes of Sea Level, Part 3: Relative Changes of Sea Level from Coastal Onlap. In: C. E. Payton, Ed., *Seismic Stratigraphy-Applications to Hydrocarbon Exploration*, AAPG Memoir, Vol. 26, 1977, pp. 63–81.
- Vallina, S.M., Follows, M.J., Dutkiewicz, S., Montoya, J.M., Cermeno, P., Loreau, M., 2014. Global relationship between phytoplankton diversity and productivity in the ocean. *Nature Communications* 4299, 1–10.
- van Geel, B., Grenfell, H.R., 1996. Chapter 7A. Spores of zygnemataceae. In: Jansonius, J., McGregor, D.C. (eds), *Palynology: Principles and Applications*, 1. American Association of Stratigraphic Palynologists Foundation, pp. 173–179.
- Vanguetaine, M., 2002. The Late Cambrian acritarch *Cristallinium randomense*: morphology, taxonomy and stratigraphical extension. *Review of Palaeobotany and Palynology* 118, 269–285.
- Vavrdová, M., 1974. Geographical differentiation of Ordovician acritarch assemblages in Europe. *Review of Palaeobotany and Palynology*, 18, 171–175
- Vecoli, M., 2000. Palaeoenvironmental interpretation of microphytoplankton diversity trends in the Cambrian–Ordovician of the northern Sahara Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology* 160, 329–346.
- Vecoli, M., 2004. Stratigraphic and palaeoenvironmental distribution of organic-walled microfossils in Cambrian-Ordovician transitional strata of borehole Bir Ben Tartar-1 (Tt-1; Ghadamis Basin, southern Tunisia). *Memoir of the Association of Australasian Palaeontologists* 29, 13–30.
- Vecoli, M., Tongiorgi, M., Playford, G., The Ordovician acritarchs *Frankrea brevisuscula*, *F. longiuscula*, and *F. sartbernardensis*: A new study. *Bollettino della Società Paleontologica Italiana* 38(2), 343–358.
- Veizer, J., Prokoph, A., 2015. Temperatures and oxygen isotopic composition of Phanerozoic

oceans. *Earth-Science Reviews* 146, 92–104.

Veizer, J., Godderis, Y., François, L.M., 2000. Evidence for decoupling of atmospheric CO<sub>2</sub> and global climate during the Phanerozoic eon. *Nature* 408, 698–701.

Versteegh, G.J.M., 1997. The onset of major Northern Hemisphere glaciations and their impact on dinoflagellate cysts and acritarchs from the Singa section, Calabria (southern Italy) and DSDP Holes 607/607A. *Marine Micropalaeontology* 30, 319–343.

Versteegh, G.J.M., Servais, T., Streng, M., Munnecke, A., Vachard, D., 2009. A discussion and proposal concerning the use of the term calcispheres. *Palaeontology* 52, 343–348.

Vidal, G., 1981. Micropalaeontology and biostratigraphy of the upper Proterozoic and Lower Cambrian sequences in East Finnmark, northern Norway. *Norges Geologiske Undersøkelse Bulletin* 362, 1–53.

Vidal, G., 1984. The oldest plankton. *Scientific American* 250, 48–57.

Vidal, G., Knoll, A.H., 1983. Proterozoic plankton. *Geological Society of America, Memoir* 161, 265–277.

Volkova, N.A., Kirjanov, V.V., Piskun, L.V., Pashkyavichene, L.T., and Jankauskas, T.V., 1979. Microflora. In: Keller, B.M., Rosanov, A.Y., (eds), *Upper Precambrian and Cambrian paleontology of east European Platform*. Academy of Sciences, U.S.S.R., Nauka, pp. 4–38 (in Russian).

Volkova, N.A., Kirjanov, V.V., Piskun, L.V., Paskeviciene, L.T., Jankauskas, T.V., 1983. Plant microfossils. In: Urbanek, A., Rozanov A.Yu. (eds), *Upper Precambrian and Cambrian Palaeontology of the East-European Platform*. Wydawnictwa Geologiczne, Warsaw. pp. 7-46

Wacker, U., Fiebig, J., Munnecke, A., Joachimski, M.M., Schoene, B.R., 2012. Clumped isotopes applied to Silurian brachiopod shells, Gotland/Sweden. *Mineralogical Magazine* 76(6), 2504.

Wang, W., Servais, T., Yan, K., Vecoli, M., Li, J., 2015. The Ordovician acritarch *Dactylofusa velifera* Cocchio 1982: a biostratigraphical and palaeogeographical index species. *Palynology* 39(1), 125–141.

Wang, W., Monnet, C., Servais, T., 2017. Quantitative methods used for understanding the taxonomy of acritarchs: a case study of the Middle Ordovician genus *Frankea* Burmann 1970. *Palynology* 41, 69–79.

Wall, D., Dale, B., 1968. Modern Dinoflagellate Cysts and Evolution of the Peridinales. *Micropalaeontology* 14(3), 265–304.

Wall, D., Dale, B., Harada, K., 1973. Descriptions of new fossil dinoflagellates from the late Quarternary of the Black Sea. *Micropalaeontology* 19(1), 18–31.

Wauthoz, B., Gérard, P., 1999. Biometric study of some *Domasia* species (Acritarcha) from the Silurian of the Brabant Massif, Belgium. In: Tongiorgi, M., Playford, G. (eds), *Studies in Palaeozoic palynology. Selected papers from the CIMP Symposium and Workshops*. Bolletino della Società paleontologica Italiana 38(2–3), 381–395.

Wauthoz, B., Dorning, K.J., Le Hérisse, A., 2003. *Crassianguлина variacornuta* sp. nov. from the late Llandovery and its bearing on Silurian and Devonian acritarch taxonomy. *Bulletin de la Société Géologique de France* 174(1), 67–81.

Webby, B.D., Paris, F., Droser, M.L., Percival, I.G., (eds), 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, U.S.A., 484 pp.

Whalen, C.D., Briggs, D.E.G., 2018. The Palaeozoic colonization of the water column and the rise of global nekton. *Proceedings of the Royal Society B* 285, 1–9.

- Wicander, R., Wood, G.D., 1997. The use of microphytoplankton and chitinozoans for interpreting transgressive/regressive cycles in the Rapid Member of the Cedar Valley Formation (Middle Devonian), Iowa. *Review of Palaeobotany and Palynology* 98(1–2), 125–152.
- Wilson, J.T., 1966. Did the Atlantic close and then reopen? *Nature* 211, 676–681.
- Xiao, S., Knoll, A.H., 2000. Phosphatized animal embryos from the Neoproterozoic Doushantuo Formation at Weng'an, Guizhou, South China. *Journal of Paleontology* 74(5), 767–788.
- Xiao, S., Knoll, A.H., Schiffbauer, J.D., Zhou, C., Yuan, X., 2012. Comment on ‘Fossilized Nuclei and Germination Structures Identify Ediacaran “Animal Embryos” as Encysting Protists’. *Science* 335(6073), 1169.
- Yan, K., Servais, T., Li, J., 2010. Revision of the Ordovician acritarch genus *Ampullula* Righi 1991. *Review of Palaeobotany and Palynology* 163, 11–25.
- Yan, K., Li, J., Servais, T., 2013. An Early–Middle Ordovician acritarch and prasinophyte assemblage from Houping, Chongqing city, South China: Biostratigraphical and palaeoenvironmental implications. *Review of Palaeobotany and Palynology* 198, 110–133.
- Yan, K., Li, J., Molyneux, S.G., Raevskaya, E.G., Servais, T., 2017. A review of the Ordovician acritarch genus *Barakella* Cramer & Díez 1977. *Palynology* 41, 80–94.
- Yin, H., Zhang, K., Tong, J., Yang, Z., Wu, S., 2001. The Global Stratotype Section and Point (GSSP) of the Permian-Triassic boundary. *Episodes* 24, 102–114.
- Yin, H., Tong, J., Zhang, K., 2005. A review of the global stratotype section and point of the Permian-Triassic boundary. *Acta Geologica Sinica* 79, 715–728.
- Yin, L., Meng, F., Kong, F., Niu, C., 2020. Microfossils from the Paleoproterozoic Hutuo Group, Shanxi, North China: Early evidence for eukaryotic metabolism. *Precambrian Research*, 342.
- Zhuravlev, A.Y. & Wood, R.A., 1996. Anoxia as the cause of the mid-Early Cambrian (Botoman) extinction event. *Geology* 24(4), 311–314.
- Ziegler, A.M., Hansen, K.S., Johnson, M.E., Kelly, M.A., Scotese, C.R., Van der Voo, R. 1977. Silurian continental distribution, paleogeography, climatology, and biogeography. *Tectonophysics* 40, 13–51.
- Ziegler, P.A., 1989. *Evolution of Laurussia – A study in late Palaeozoic plate tectonics*. Kluwer Academic Publishers, Royal Geological and Mining Society of the Netherlands (K.N.G.M.G.), Dordrecht, NL, 102 pp.
- Zonneveld, K.A.F., Susek, E., 2006. Effects of temperature, light and salinity on cyst production and morphology of *Tuberculodinium vancampoae* (the resting cyst of *Pyrophacus steinii*). *Review of Palaeobotany and Palynology* 145, 77–88.



## **Article I**

### **Biodiversity of Palaeozoic phytoplankton**

David M. Kroeck, Gary Mullins, Axelle Zacaï, Claude Monnet, Thomas Servais

in preparation; to be submitted to *Earth-Science Reviews*.

## **Biodiversity of Palaeozoic phytoplankton**

David M. Kroeck<sup>a</sup>, Gary Mullins<sup>b</sup>, Axelle Zacaï<sup>a</sup>, Claude Monnet<sup>a</sup>, Thomas Servais<sup>a</sup>

<sup>a</sup> Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

<sup>b</sup> Robertson, a CGG Company, Llandudno, LL30 1SA, United Kingdom

### **ABSTRACT**

The study of ancient phytoplankton diversity on a regional and global scale is of great interest as it can provide valuable insights into the evolution of marine ecosystems and on climate history. Phytoplankton constitute a large part of the base of the marine trophic chain. Using a new database of more than 4,000 species, a comprehensive investigation of the taxonomic diversity of Palaeozoic microphytoplankton, including a variety of diversity metrics, is conducted. This database comprises data from published literature, including taxonomic, geographic and stratigraphic information. The main goal of this study is the construction of biodiversity trajectories for marine phytoplankton throughout the Palaeozoic, with taking account for potential bias. Additionally, indices for taxonomic change and a poly-cohort analysis are calculated to display shifts in global phytoplankton composition. Based on the available data, stratigraphic stages are used as bins. The results indicate potential sampling bias, as a correlation between diversity indices and references per stage is found. The diversity curves show generally high values during the lower Palaeozoic (Cambrian–Devonian) and low values in the upper Palaeozoic (Carboniferous–Permian). Values are highest in the Ordovician and Silurian. The Lower Devonian is characterized by relatively low diversity, whereas the Upper Devonian shows a peak. Distinct diversity declines are visible in the latest Ordovician, from the late Silurian to Lower Devonian, and from the Upper Devonian to the Carboniferous. The low diversity during the late Palaeozoic represents most probably an artifact, as is indicated in literature. The role of the phytoplankton during major biotic events is discussed. By comparing the results with palaeoecological parameters, several factors are found to be possibly related to the long-term diversity trends, such as palaeogeography, sea-level changes, sediment influx, and CO<sub>2</sub>.

**Keywords:** phytoplankton, acritarchs, Palaeozoic, biodiversity, palaeoecology

## 1. Introduction

Biodiversity trends can reveal important insights into the ecological history and intercorrelations within the ecosystems. The phytoplankton play a major role in marine ecosystems. They constitute a major part of the base of marine food chains and therefore represent the starting point for a large fraction of the biological activity in the marine realm. It can be inferred that they are possibly related to major evolutionary events and had an impact on diversifications of marine metazoans (e.g., 'Cambrian Explosion', 'Great Ordovician Biodiversification Event'). Furthermore, the phytoplankton are responsible for at least 50 % of photosynthetic activity (Behrenfeld & Falkowski, 1997; Field et al., 1998) on Earth and responsible for most of the transfer of carbon dioxide from the atmosphere to the oceans. This important carbon sink constitutes a major component in the global carbon cycle. Therefore, changes in ancient phytoplankton populations may had considerable effects on both, the palaeoclimates and the palaeoecosystems. Taxonomic diversity trajectories provide a useful tool to test these hypotheses.

While direct fossil evidence of today's most important phytoplankton groups, i.e., dinoflagellates, diatoms, coccolithophors, is missing before the Mesozoic, the Palaeozoic phytoplankton is mainly represented by acritarchs. This polyphyletic group comprises organic-walled microfossils of unknown biological affinities (Evitt, 1963). Most acritarchs are interpreted to be fossil cysts of unicellular phytoplanktic organisms (e.g., Evitt, 1963; Downie et al., 1963; Tappan, 1980; Mendelson, 1993; Martin, 1993; Colbath & Grenfell, 1995; Servais, 1996; Strother, 1996; 2008). While occurring today only to a very limited extend, acritarchs were abundant in the Palaeozoic, occurring globally in a wide variety of sediments. With many forms showing morphological similarity with modern dinoflagellate cysts (e.g., Rasul, 1974; Tappan, 1980; Martin, 1993; Cobalth & Grenfell, 1995; Servais, 1996; Strother, 1996; Butterfield & Rainbird, 1998), and with records of dinoflagellate biomarkers in the Proterozoic and Palaeozoic (e.g., Summons et al., 1992; Moldowan et al., 1996; Moldowan & Talyzina, 1998; Talyzina et al., 2000), a relation to dinoflagellates is assumed for numerous taxa. Several morphotypes that were assigned to acritarchs have been provisionally transferred to green algal classes (Chlorophyceae, Prasinophyceae, Zygnematophyceae; e.g., Wall, 1962, Tappan, 1980; Le Hérissé, 1984; Guy-Ohlson, 1996; Martin et al., 2008; Kaźmierczak & Kremer, 2009; Moczyłowska, 2010). Prasinophytes, the reproductive phycmata of green algae, are known from the Precambrian to recent, and played, similar to acritarchs, a larger role in the Palaeozoic than in recent times (Colbath & Grenfell, 1995; Talyzina & Moczyłowska, 2000).

The present work aims to provide biodiversity trajectories of the Palaeozoic phytoplankton using different diversity measures to account for different potential biases. While phytoplankton biodiversity is certainly controlled by numerous factors, this paper attempts to investigate the most crucial causes explaining the changes recorded, pointing out the factors controlling abundance, distribution and diversity of the Palaeozoic phytoplankton.

## 2 Previous works

Diversity curves for the microphytoplankton of the Palaeozoic are far from complete. Intensive research of acritarchs did not start before the 1960s, and several palaeocontinents are poorly covered so far (Servais & Paris, 2000; Servais et al., 2004). Several previous studies concern the biodiversity of phytoplankton during the entire Phanerozoic. Tappan & Loeblich (1972, 1973) presented the diversity of Precambrian and Phanerozoic acritarchs as total number of species per period. Based on data of Downie (1984) and Fensome et al. (1990), Strother (1996) published an acritarch diversity curve for the Precambrian and Phanerozoic. Martin (2003) included a diagram showing diversity of acritarchs as appoximate number of species per period for the Phanerozoic, based on a personal



communication by P. Strother. In a comprehensive account about the evolutionary history of phytoplankton in general, Katz et al. (2004) provided biodiversity curves for different groups of phytoplankton, including acritarchs, for the Proterozoic and Phanerozoic using the Palynodata database (see Fensome et al., 1996; Palynodata Inc. and White, 2008). These acritarch data were derived from Knoll (1994) for the Proterozoic and Early Cambrian and from MacRae (unpublished, personal communication) for the Phanerozoic. Strother (2008) showed a genus-level biodiversity curve of acritarchs for the Phanerozoic. Additionally, diversity curves for the Palaeozoic were produced by Tappan (1980), and Cruz (2011).

The diversity of acritarchs of the Neoproterozoic and early Palaeozoic was investigated in several studies. Vidal & Knoll (1982) and Knoll (1994) presented species-level diversity curves of Proterozoic to lower Cambrian acritarchs. A species-level diversity curve of the acritarchs of the Neoproterozoic and Cambrian was published by Vidal & Moczyłowska-Vidal (1997). Moczyłowska (1998) documented Cambrian species diversity in Upper Silesia. Zhuravlev (2001) produced genus-level diversity curves for acritarchs of the Cambrian to earliest Tremadocian. A species diversity curve for acritarchs of the British Isles based on data from Downie (1984) is shown by Servais et al. (2004). Trajectories of taxonomic diversity as well as morphological disparity of Proterozoic to Cambrian acritarchs on genus level were presented by Huntley et al. (2006a, b). Servais et al. (2008) showed diversity changes of acritarchs from the middle Cambrian to Llandovery as numbers of species per stage, based on the PhytoPal database (see Mullins et al., 2005; 2006). Moczyłowska (2011) provided curves of biodiversity of the phytoplankton from the Neoproterozoic to the earliest Ordovician on a global and regional (Baltica) level, also including data from the PhytoPal project. The to date most comprehensive analysis of the Cambrian biodiversity was presented by Nowak et al. (2015), based on an extensive literature investigation. Therein, diversity curves on a global and regional scale were presented on both, genus and species level, using different diversity metrics.

Biodiversity curves for Ordovician phytoplankton exist for different palaeocontinents. Vecoli (2000) documented diversity trends of Late Cambrian to uppermost Ordovician microphytoplankton, including curves for separate morphological classes, in North Africa (Gondwana). Servais et al. (2004) and Vecoli & Le Hérissé (2004) discussed the diversity at the northern peri-Gondwana margin (North Africa and other regions). Servais et al. (2004), Li et al. (2007) and Yan et al. (2011) presented trajectories for the Early to Middle Ordovician of South China (Yangtze Platform). Species-level diversity trajectories and curves for taxonomic change of Lower Ordovician acritarchs of Avalonia are produced by Molyneux (2009), using different diversity metrics. Hints et al. (2010) published species-level total and normalised diversity curves, including taxonomic changes, for Baltica based on an extensive literature investigation and stratigraphical data from boreholes.

Not many studies concern the interval from the Silurian to Permian. Le Hérissé et al. (2009) presented diversity trends for acritarchs, prasinophytes, chlorophytes and total phytoplankton for the late Silurian to Early Devonian based on data from different palaeocontinents and terranes, i.e., Laurentia, Avalonia, Baltica, Perunica and Gondwana. In their work about the Devonian Nekton Revolution, Klug et al. (2010) included biodiversity curves of different groups of marine organisms, amongst them the phytoplankton. The underlying data were derived from the PhytoPal database. The biodiversity of the Carboniferous phytoplankton was described by Mullins & Servais (2008), including acritarchs, prasinophytes and zygneмаaceans. In order to avoid sampling biases and bias due to the variable length of stages, the relative diversity fluctuations were estimated based on the maximum number of taxa reported by a single study in each time interval. The paper by Lei et al. (2013) concerned the biodiversity of the Permian phytoplankton based on a review of the data listed by Fensome et al. (1990) and data from subsequent literature.

While many previous studies are confined either to certain regions (palaeocontinents) or to a smaller timescale or both, our study represents a new attempt to construct comprehensive global diversity curves for the organic-walled microphytoplankton for the whole Palaeozoic. Moreover, most previous studies concerning Palaeozoic phytoplankton diversity had limitations in the choice of sources, with often outdated data, and analytical methods, making the results prone to different biases. Several new diversity metrics to account for biases were developed in more recent years, allowing better, more robust estimates of true richness.

### **3. Material and methods**

#### *3.1. Dataset*

The database used in this study represents a continuous attempt to compile all available occurrence data of the Palaeozoic organic-walled microphytoplankton on a global level based on extensive literature surveying. It originated in the PhytoPal Project (Mullins et al., 2005; 2006). A global diversity curve was constructed during this project, which included more than 6,000 species, and was presented at several meetings (e.g., Mullins et al., 2005), but it had never been published. Parts of it, however, were included in certain publications: Moczydłowska (2011) presented a curve for the Cambrian based on the PhytoPal database, the Middle Cambrian–Llandovery was shown in Servais et al. (2008) and the Devonian in Klug et al. (2010). The database is a sample-based exhaustive incidence dataset, with references acting as samples. The occurrences are derived from all palaeocontinents. The data was filtered and cleaned by removing or reassigning illegitimate, questionable and synonymous taxa, and converting local to global chronostratigraphic units. For the calculations, 580 genera and 4053 species in 568 publications were used.

#### *3.2. Biodiversity metrics*

Since the fossil record represents the only direct evidence of ancient biodiversity, the construction of biodiversity curves of past life is strongly depending on the quality of palaeontological data. This includes the completeness of the fossil record, the accuracy of taxonomy, and the precision of stratigraphic correlations and chronometric dating (e.g., Sepkoski, 1997). Palaeobiodiversity analyses have to deal with various biases that arise from differences in the amount of studies in a certain region or a certain time interval (sampling bias), the quantity of sediment, and the quality of preservation (taphonomic bias) (e.g., Sepkoski, 1997; Aberhan & Kiessling, 2012; Alroy et al., 2008). The aim is not to determine true diversity in a given time, but to construct representative trajectories for diversity trends correcting for the different biases.

The calculations were done with chronostratigraphic stages as time bins. Given the often rather unprecise age determinations in literature, a more precise scale, such as biozones, was abandoned. In order to account for the various facets of biodiversity and correct for the different biases, various counting methods were applied (Fig. 2): (1) the sampled in bin method (SIB) counts all actual occurrences in a given time interval. It therefore does not give assumptions on taxa that could be present in the bin but might not be sampled. Given the different durations of stages, their use as the stratigraphic intervals (bins) for the diversity calculations inherits a bias: Longer stages may show higher taxonomic richness than shorter ones, as they may have a higher coverage. In order to correct for this bias, rates per Myr were calculated for SIB diversity. (2) The range-through method (RT-) counts all occurrences recorded in an interval and the taxa that are inferred to be present in the interval by their stratigraphic range. Singletons can be included (RTinS) or excluded (RTexS). (3) The metric of boundary crossers (BCR) counts the taxa that are inferred to occur at the boundaries between two bins, i.e. that are present before and after the boundary. Therefore, singletons are omitted. (4) As only few taxa completely range through the bins in which they first or last appear, species ranges are

overestimated. Normalised diversity (NORM) based on Sepkoski (1975) is used as a measure to compensate for this. It sums the taxa that appear before and after the interval, half the number of taxa originating or going extinct within the interval, and half the number of singletons. Normalised diversity has been proven a good approximation of mean standing diversity in model datasets (Cooper, 2004). (5) In order to correct for sampling bias, a coverage-based rarefaction method known as Shareholder Quorum Subsampling (SQS) has been applied, which is a subsampling method based on an equal sample coverage (e.g., Alory, 2010; 2013). (6) An approach to estimate sampling bias and absolute richness is provided with Poisson-based resampling (TriPs: ‘true richness estimation using Poisson sampling’). This method uses the number of times each species occurs at different points in time to estimate its probable fossilisation potential in order to assess the number of species potentially missing. The sampling bias is also addressed by calculating correlations between the number of references per time interval and the biodiversity metrics using Spearman’s rho (R.rho) and Kendall’s tau (R.tau) coefficients (Fig. 6).

*Fig. 1 near here*

Rates of taxonomic change were calculated for all stages (Fig. 3). Extinction rates represent the number of taxa going extinct within a stratigraphic interval; origination rates the number of taxa first appearing within it. Taxonomic turnover rates are the sum of origination and extinction rates. Additionally, a poly-cohort analysis was applied (Fig. 4). The poly-cohort survivorship indicates the percentage of a cohort, i.e., an assemblage of taxa present in a given time bin (here: stage), that is still present in later intervals (Raup, 1978; Van Valen, 1979). Poly-cohort prenasence (‘backward survivorship’) illustrates the proportion of an assemblage in a given time bin present in earlier intervals. Thus, survivorship and prenasence indicate the proportion of taxa surviving and originating, respectively, through time, and document the relative constancy of extinction and origination rates through time intervals (e.g., Raup, 1978; Van Valen, 1979; Foote, 2001). Poly-cohorts of survivorship and prenasence are presented herein for all stages and plotted on a logarithmic scale (Fig. 4). Within these diagrams, linear curves would imply constant rates; changes over time or between cohorts may indicate changing rates or biases.

The various analyses of taxonomic richness of the data available in the database were performed using the environment R (version 3.5.3; R Core Team, 2019) with the package ‘ePaleo’ (Monnet, 2019, unpublished) at species level.

## **4. Results**

### *4.1. Palaeozoic phytoplankton biodiversity*

Global diversity trajectories for the phytoplankton of the Palaeozoic are shown in Fig. 2. The diversity trajectories show significant global trends, with general high diversity in the lower and middle Palaeozoic (Cambrian–Devonian), and low diversity in the late Palaeozoic (Carboniferous–Permian). Diversity peaks are observable in the Cambrian (Miaolingian, Furongian), Ordovician (Middle, Upper), Silurian (Llandovery, Ludlow) and Upper Devonian. Significant diversity drops appear in the latest Ordovician, late Silurian–Lower Devonian and Upper Devonian–Carboniferous. While the Silurian to Permian interval of the diversity curves based on the different measures are very similar, several differences are observed in the Cambrian and Ordovician.

*Fig. 2 near here*

#### *4.1.1. Cambrian*

The Cambrian period starts with relatively high diversity levels. A decrease in Cambrian Series 2 is evident, with the timing differing in the various curves: In the SQS and TRiPS diversities it is visible from stage 2 to 3, in the SIB (per stage) and range-through diversities from stage 4 to 5, with reduced values until the Series 3/Furongian boundary. The normalised and boundary-crosser diversities record the decrease from stages 3 to 5, followed however by a short-term recovery noticeable in a positive excursion in the Drumian and another diversity drop in the Guzhangian. The diversity increase at the Series 3/Furongian boundary is observed in all metrics, but yet another negative excursion occurs in the NORM and BCR diversities after a pronounced peak in the Jiangshanian, while the other diversities remain relatively high throughout the Furongian.

#### 4.1.2 Ordovician

The Ordovician is characterised by generally very high biodiversity, including the highest values for the whole Palaeozoic. A pronounced increase in diversity marks the Lower Ordovician in all diversity metrics, which is continued in the Middle Ordovician in the NORM diversity, reaching a peak in the Darriwilian. SIB (per stage), range-through, BCR and TRiPS diversities, however, record a more or less pronounced decrease from the Floian to Dapingian. In the SQS70 curve, a negative peak occurs before, in the Floian, with increasing diversity in the Dapingian to Darriwilian. A decrease is visible in the Sandbian in all metrics but BCR and SQS, which appears relatively strong in the SIB (per stage) and range-through diversities, while only slightly marked in the NORM measures. The SQS40 curve, however, record the highest values in the Sandbian. A high peak is reached in the Katian or Katian/Hirnantian boundary, respectively in all metrics except SQS, with the latter documenting a decrease already from the Sandbian. The Hirnantian shows a rapid and marked decrease in all metrics, to values comparable with those at the beginning of the Ordovician.

#### 4.1.3 Silurian

The diversity curves for the Silurian all show very similar trends, but with the time interval of peaks differing. The Silurian is characterized by generally high diversity values. A rapid recovery from the pronounced negative excursion at the Ordovician–Silurian boundary is evident in the Llandovery (Rhuddanian–Aeronian/Telychian). A peak is recorded in the Telychian in most trajectories, at the Aeronian/Telychian boundary in the BCR diversity, and in the Aeronian in the SQS40 curve. Afterward, the diversity is falling slightly until the Sheinwoodian/Homerian. While the Homerician shows lowered diversity in the SIB, range-through and BCR curves, an increase is visible in the SQS and TRiPS diversities. Another peak is shown in the Homerician/Gorstian, followed by a rapid decrease that continues through the Silurian–Devonian boundary.

#### 4.1.4 Devonian

The diversity trends in the Devonian to Permian interval are very similar in all metrics. The diversity decrease that started in the late Silurian continues throughout the Lower and early Middle Devonian, but is not as steep as in the Pridoli. The values become lowest in the Middle Devonian, followed by a rise in diversity with a peak in the Frasnian. After this the diversity is decreasing rapidly. It should be noted, that the Frasnian peak appears more pronounced in the SQS curve, with biodiversity reaching similar values as in the Middle and Upper Ordovician.

#### 4.1.5 Carboniferous–Permian

The late Palaeozoic (Carboniferous–Permian) is characterised by generally very low biodiversity. Throughout the Mississippian, the decrease, which began in the Late Devonian, continues. A slight increase is visible in the earliest Pennsylvanian. A slight but pronounced decline happens in the

NORM and BCR diversities after the Kasimovian, with very low values continuing through the Carboniferous–Permian boundary to the Asselian. Another increase follows in the Sakmarian and Artinskian. After the Artinskian the diversity falls to the lowest levels, continuing until the Capitanian. A slight increase is visible in the latest Permian just before the Permian–Triassic boundary in all trajectories. The TRiPS curve shows high values in the Cisuralian and Guadalupian, but the error at this interval is quite large.

#### *4.2 Taxonomic changes*

Curves for origination and extinction rates, as well as taxonomic change are provided in Fig. 3.

##### *4.2.1 Extinctions*

The Cambrian shows four phases of extinction. Low extinction rates are met in Cambrian stage 2, high rates occur in stage 4, the Guzhangian and stage 10. The values at stage 10 are second highest for the Palaeozoic. The Lower Ordovician is characterised by low (Tremadocian) to moderate (Floian) extinction rates. Extinction rates in the Middle Ordovician reach a peak in the Darriwilian. A major extinction event is recorded in the Hirnantian, with extinction reaching the highest values for the Palaeozoic. The Silurian shows three minor extinctions in peaks in the Telychian, the Homerian and the Ludfordian to Pridoli. The latter extinction is continued attenuated in the Lochkovian. While extinction in the remaining part of the Lower Devonian and the Middle Devonian to Frasnian is low; a distinct peak is reached in the Famennian. This extinction event is continued to a lesser extent in the Carboniferous. The extinction values during the late Palaeozoic remain low, due to the small number of taxa. Small peaks are reached in the latest Carboniferous (Gzhelian) and the Kungurian.

##### *4.2.2 Originations*

Three intervals of origination are recorded during the Cambrian: A moderate peak occurs in stage 3, high peaks in stage 5 and the Paibian. The Lower Ordovician is characterised by generally high values, with the highest in the Palaeozoic appearing in the Floian. Major peaks of origination are recorded for the Darriwilian and the Katian. The early Silurian shows high to moderate origination rates, with a peak in the Rhuddanian. A second peak is reached in the Gorstian. The Devonian is characterised mostly by low origination, with moderate values occurring in the Lochkovian and the Frasnian. The Late Palaeozoic shows generally low origination rates, again, due to the low number of taxa recorded. Small peaks are found in the earliest Permian (Asselian) and Wuchiapingian.

*Fig. 3 near here*

##### *4.2.3 Taxonomic turnover*

High turnover rates are observed in the Cambrian stages 4–5. A second phase of high turnover occurs in the Guzhangian–Paibian. The uppermost Cambrian and Lower Ordovician record a long interval of high to very high turnover, with a peak observed in the Floian. After low turnover rates in the Dapingian, a very high peak occurs in the Darriwilian, with the highest values reached for the Palaeozoic. While turnover rates decrease strongly in the Sandbian, the interval Katian–Rhuddanian show again high to very high values with a peak in the Hirnantian. The Silurian is characterised by moderate turnover, with peaks visible in the Telychian and Gorstian. The interval Gorstian–Lochkovian show elevated turnover values. The Pragian–Givetian are characterised by small to moderate rates. Turnover increases in the Frasnian–Famennian. The Tournasian still shows elevated turnover rates, followed by low values in the remaining parts of the upper Palaeozoic. A small peak is observed in the Asselian–Sakmarian.



#### 4.2.4 Poly-cohort analysis

The survivorship poly-cohorts indicate several intervals with high extinction. In the Cambrian, distinct decreases in survivorship are recorded in stage 5 and in the Guzhangian. A strong decline is also visible in the Tremadocian, documenting an extinction event at the Cambrian/Ordovician boundary. The Ordovician shows until the Hirnantian relative stable survivorship rates except for a minor change from the Darriwilian to the Sandbian. From the Hirnantian to the Rhuddanian a marked drop of survivorship is observable. The Llandovery and Wenlock have relatively gentle slopes, indicating high survivorship of taxa. The decline is faster in the Ludlow to Lochkovian. The Pragian to Famennian interval is characterised by gentle slopes. The survivorship decreases faster from the Famennian to the Serpukhovian, then becomes more gentle again until the latest Carboniferous. A fast change is observed at the Carboniferous/Permian boundary. The Permian survivorship is relatively slowly decreasing, with changes to faster declines from the Kungurian to the Roadian and in the uppermost Permian.

*Fig. 4 near here*

The prenascence curves show several intervals of change indicate several significant shifts in phytoplankton composition: Distinct changes occur at the Cambrian/Ordovician boundary, at the Ordovician/Silurian boundary and at the Carboniferous/Permian boundary; smaller changes are observed in the Middle Ordovician, in the Wenlock–Ludlow interval, at the Silurian/Devonian boundary and in the Devonian/Carboniferous boundary interval.

#### 3.3. Distribution of coverage/studies over time

**Fig. 5.** Correlation of taxonomic diversity and number of references per bin.

*Fig. 5 near here*

The number of references per time bin is varying significantly throughout the Palaeozoic (Fig. 5). The coverage in the Cambrian is moderate, while the Ordovician shows a high focus, with most references in the Floian, Darriwilian and Katian. The Silurian is again moderately covered. After a moderate number of studies concerning the Lochkovian, the Devonian shows a continuous increase in references from the Pragian to the Upper Devonian from a low number in the Pragian to a moderate number in the Famennian. The coverage decreases throughout the Upper Palaeozoic, with very low numbers of references in the Permian. These results indicate a good correlation of the distribution of references through time with the biodiversity trajectories. Tests for correlation (Fig. 6) show significant correlation with the range-through ( $R.\rho = 0.924$ ;  $R.\tau = 0.783$ ) and SIB diversities ( $R.\rho = 0.931$ ;  $R.\tau = 0.801$ ) and moderate correlation with the SQS ( $R.\rho = 0.567$ ;  $R.\tau = 0.409$ ) and TRiPS diversities ( $R.\rho = 0.744$ ;  $R.\tau = 0.556$ ).

*Fig. 6 near here*

## 5. Discussion

### 5.1 Comparison with previous studies

The observed diversity trends of the Palaeozoic microphytoplankton show many similarities to diversity curves from previous studies. Considering the simplistic approach of Tappan & Loeblich (1973), the results therein are well matching with ours. The lower to middle Palaeozoic is characterised by high species numbers, with higher diversity in the Ordovician, and the late Palaeozoic exhibit very low numbers. The Silurian in Loeblich & Tappan (1973) shows a smaller

number than the Devonian, but this is due to the shorter duration of the Silurian, as already pointed out by the authors. The trajectories shown by Katz et al. (2004) and Strother (2008) are also matching in long-term trends. Therein, the highest diversity values are in the lower and middle Palaeozoic (Cambrian–Devonian) with a distinct diversity drop afterwards and the subsequent ‘Late Palaeozoic Phytoplankton Blackout’ (Riegel, 2008; Servais et al., 2016a). These curves also show a strong diversification occurring from the late Cambrian to the Middle Ordovician. Furthermore, in the diversity curve presented by Katz et al. (2004) the peaks of diversity, i.e. in the Ordovician, in the Silurian and in the Upper Devonian are roughly coinciding with our results. However, when going in detail, many differences are observable. The curve of Strother (2008) does not include a distinct drop in diversity at the Ordovician–Silurian boundary. Moreover, it is missing a diversity peak in the Late Devonian. Rather, it shows the diversity decrease leading to the ‘Late Palaeozoic Phytoplankton Blackout’ occurring earlier, around the Middle Devonian.

The diversity curve for the Precambrian to Permian based on data from the Ordovician of the British Isles shown in Servais et al. (2004) differs significantly from the results herein. During the Cambrian the diversity is highest in the Terreneuvian and, after a decrease, stays low until the Cambrian/Ordovician boundary. An increase from the Lower Ordovician to a peak in the Middle Ordovician is similar to the normalised diversity curve in our study, but a following very strong continuous decline up until the Ordovician–Silurian boundary cannot be confirmed in the new results. The curve of Servais et al. (2004) shows the highest peak in the Silurian. While our results also exhibit high diversity during most part of this period, the values are lower than peak diversities during the Ordovician. The Devonian appears quite different in the curve of Servais et al. (2004), with a peak in the Emsian and a smaller increase in the Late Devonian. While a very slight peak in the Emsian is visible in some metrics (SIB per stage, range-through diversities), our results show a more pronounced increase in the late Devonian. The diversity decrease at the Devonian/Carboniferous boundary appears in both, Servais et al. (2004) and herein.

Despite the fact that Moczyłowska (2011) included a global diversity curve for the Cambrian based on a very similar database as this study, the trajectories shown are quite different from those presented herein. The curve based on the PhytoPal project in Moczyłowska (2011) shows a constant increase in diversity throughout the Cambrian. Beside the cleaning and updating of the database, it has to be pointed out that the trajectory in Moczyłowska (2011) has a different precision, with time bins appearing to be on epoch level rather than the more precise stage level of this study, probably omitting smaller-scale diversity changes. The other curves presented by Moczyłowska (2011), a global diversity curve based on Grey (2005), Moczyłowska (1998) and new data, and a regional curve with new data for Baltica, also show a general increase in diversity throughout the Cambrian, but include an interval with decreasing values somewhere around the Series 2/Miaolingian boundary. Moczyłowska (2011) addresses this change, referring it to as the ‘early-middle Cambrian taxonomic turnover’ (see also Moczyłowska, 1999). This turnover event is also observed in our results, with high extinction rates in Cambrian Stage 4 and high origination rates in Stage 5. The extinction event will be addressed later (5.2.1) as the end-Botoman extinction. The curves in the more comprehensive analysis of the Cambrian phytoplankton biodiversity by Nowak et al. (2015) show several differences. While the studies agree in an increasing diversity from the Stage 2 to Stage 3, the new results display a pronounced decrease in the following two stages. In the global species and genus diversity curves of Nowak et al. (2015) a slight decrease is visible in Stage 4, but followed by increasing diversity to Stage 5. Herein, Stage 5 is found to exhibit a diversity low. The following peak in the Drumian, too, differs from Nowak et al. (2015), which shows a decrease in the Drumian to Guzhangian. However, both studies agree in a negative peak in the Guzhangian. Another difference is visible in the Jiangshanian, which shows a pronounced positive excursion in our study, which is not visible in Nowak et al. (2015). Similarly, the diversity in Stage 10 is at a low in our study, but increasing in

Nowak et al. (2015). The diversity curves for the Ordovician of North Africa by Vecoli & Le Hérissé (2004) are similar to our results, showing a rise of diversity in the Lower and Middle Ordovician, and a peak in the Darriwilian, followed by a decrease at the Middle/Upper Ordovician boundary. Differences are a small peak in the Tremadocian that does not appear in our results, and decreased diversity throughout the Upper Ordovician. Additionally, a decrease in the Dapingian is shown in some metrics herein, does not occur as pronounced in the results of Vecoli & Le Hérissé (2004). The diversity curve produced by Li et al. (2007) for the Ordovician of South China differs more significantly from the new results. Here, peak diversity is reached at the Lower/Middle Ordovician boundary, with a decline after and decreased values until the late Upper Ordovician. The total diversity curve for the Middle Cambrian to Llandovery by Servais et al. (2008), also based on the PhytoPal database, is very similar to the results herein. Smaller differences might be due to the use of British stages instead of global stages. The total and normalised diversities for acritarch from Baltica by Hints et al. (2010) shows a small decrease from the Tremadocian to the Floian, followed by an increase to highest values at late Darriwilian to earliest Katian, and a decrease thereafter, which is relatively similar to the normalised and the SQS diversities herein. The diversity curves for the Devonian published in Klug et al. (2010) are almost identical to the results of our study, which is not surprising since they are based on the same database, with both showing relatively low values in the Lower and Middle Devonian and high values in the Upper Devonian, followed by a distinct decline. A slight peak in the Emsian appears also in both, Klug et al. (2010) and herein. Similarly, the diversity trends for the Carboniferous in Mullins & Servais (2008) match well our results, with declining acritarch diversity from the Tournaisian to Visean and generally low diversity in the Serpukhovian and Late Carboniferous. The results for the Permian differ from those of Lei et al. (2013). Therein is, however, only genus diversity documented. A peak in the Kungurian is not confirmed in our study. Rather, highest diversity is reached in the Sakmarian and Artinkian. A trend of increasing diversity in the Lopingian, however, is observed in both studies.

### *5.2 Comparison with other marine organisms*

Since the phytoplankton represent a major part of the food at the base of marine trophic chains, changes of their composition certainly have impacts on heterotroph marine organisms, and, on the foodweb in whole. Therefore, it is useful to compare phytoplankton biodiversity trajectories with those of other marine organisms. Changes in the marine trophic web might be indicated by correlations between the diversities of the phytoplankton and marine invertebrates. Moreover, it can provide information about the efficiency of the trophic transfer of primary production into invertebrates over time. Katz et al. (2004) already presented an attempt to correlate marine invertebrate faunal and phytoplankton diversities and community composition. The results therein show a high correlation of the diversity of Mesozoic and Cenozoic phytoplankton (diatoms, dinoflagellates, calcareous nannoplankton) with invertebrate diversity. However, acritarch diversity is weakly correlated according to the data used (Katz et al. 2004).

The strong increase of phytoplankton biodiversity in the Early to Middle Ordovician coincides with major changes in the trophic chain. The late Cambrian and Early Ordovician is characterised by a radiation of zooplankton and a major diversification of suspension feeders (Servais et al., 2016b). While planktic groups started to radiate in the late Cambrian, they experienced an explosive increase in the Ordovician. The diversity curves of different planktic groups show close similarities with those of the acritarchs (cf., Servais et al., 2008). Graptolites are interpreted to represent primary consumers, feeding on phytoplankton (Bulman, 1964; Berry & Wilde, 1990; Underwood, 1993). Planktic graptolites radiated in the Ordovician (Chen et al., 2006; Cooper et al., 2013; Crampton et al., 2016). The diversity increase in the Early to Middle Ordovician, with a peak in the Darriwilian mirrors that recorded for acritarchs. Similarly, the global diversity changes of chitinozoans in the Ordovician



(Paris et al., 2004; Achab & Paris, 2007) closely correlates with the normalised phytoplankton diversity curve, as shown by Vecoli & Le Hérissé (2004). Here, too, an increase is recorded from the Tremadocian to a peak in the Darriwilian. The diversity decreases to lower values in the Sandbian, followed by yet another increase to a peak in the Katian. The latest Ordovician is characterised by a continuous decrease in diversity. Radiolarians are known to directly interact with phytoplanktic organisms. Some recent radiolaria taxa are known to use dinoflagellates as symbionts, others are feeding on phytoplankton. Since data are sparse, the Ordovician diversity trends of radiolarians are not well studied. According to Noble & Danelian (2004), the Tremadocian to Floian is characterised by a complete faunal turnover, therefore shows no correlation to the phytoplankton biodiversity changes in this interval. However, the Middle to Upper Ordovician diversity trends are quite similar, with a peak in the Darriwilian, lower values in the Sandbian and another diversity increase thereafter (Noble & Danelian, 2004). The Silurian, too, is mirroring the phytoplankton diversity curves, showing an early Silurian increase, a peak in the Telychian, a low in the Homerian, followed by a peak in the Gorstian and a decrease in the Ludfordian and Pridoli (Tetard et al., 2017).

### *5.2.1 Extinction events*

#### *5.2.1.1 Cambrian extinction events*

The Cambrian phytoplankton biodiversity is characterised by succeeding extinction and radiation events. A decrease in diversity is visible after Cambrian Stage 4, or, respectively, after Stage 3 in the normalised curve. A pronounced peak in extinction rates occurs in stage 4. This extinction is mirroring an extinction of marine metazoans during Stages 4 and 5 ('end-Botomian mass extinction event'). As to the causes of this event, there are several hypotheses. There are evidences for anoxia/euxinia events (Zhuravlev & Wood, 1996; Hough et al., 2006; Pagès et al., 2016). While Hough et al. (2006) attributed these events partly to climate warming related to the Kalkarindji Large Igneous Province, Zhuravlev & Wood (1996) and Pagès et al. (2016) argued that the phytoplankton played a role in this extinction. They described anoxia evidenced in pyrite-rich black shales as a possible cause. Zhuravlev & Wood (1996) recorded abundant monospecific acritarchs within pyrite-rich black shales, indicating blooming of phytoplankton resulting in anoxic conditions. Similarly, Pagès et al. (2016) found evidences for phytoplankton blooms in the increase in algal-derived biomarker concentrations. The latter authors describe the rise in phytoplanktic productivity occurring after the main euxinia events, which they attribute to a sea-level rise. They interpreted the phytoplankton blooms as being caused by an increased nutrient supply deriving from decaying marine organisms due to the mass mortality during the euxinia, and from terrestrial sediments due to increased erosion and transport of terrestrial sediments during a regression event. The indices of taxonomic change indicate a shift in the phytoplankton communities, with high taxonomic turnover in stages 4 and 5, with a relative large number of taxa going extinct in stage 4 and many new taxa originating in stage 5. This shift in the composition of the phytoplankton is also observed in a change in the biomarker ratios (Pagès et al., 2016): While C<sub>28</sub> steranes were prevailing before the euxinic interval, C<sub>29</sub> sterane became predominant after this interval. An increase in C<sub>27</sub> steranes during the euxinia is attributed to red algae, which become more abundant under euxinic conditions (Schwark & Empt, 2006). Apart from short-term changes, C<sub>29</sub> sterane-producing phytoplanktic organisms remain the dominant throughout the Palaeozoic until another shift happens at the Devonian–Carboniferous boundary (Schwark & Empt, 2006). C<sub>28</sub> steranes were previously associated to shifts to prasinophytes as "disaster species" (Tappan, 1980) during other mass extinction events (Schwark & Empt, 2006).

After an apparent recovery in the Drumian, another extinction happens in the Guzhangian, visible in a drop in diversity and a peak in extinction rates. Here, too, a corresponding extinction event is known from the diversity of marine metazoans, called the 'Dresbachian extinction event'. This event is named

after a North American regional stage approximately corresponding to parts of the Guzhangian and Paibian stages. While some authors argue that the Dresbachian extinction might be an artefact of poor fossil record (Bond & Grasby, 2017), faunal crises are widely reported (Öpik, 1966; Palmer, 1979; 1984; 1998; Ludvigsen & Westrop, 1985; Saltzman et al., 2000; Shergold & Cooper, 2004). Moreover, a pronounced  $\delta^{13}\text{C}$  positive excursion is recorded in the Paibian, known as the SPICE (Steptoean Positive Carbon Isotope Excursion; e.g., Glumac & Walker, 1998; Saltzman et al., 2000), indicating major disturbances of the carbon cycle. The relation between Early to Middle Palaeozoic  $\delta^{13}\text{C}$  excursions and primary productivity is debated in literature (Bickert et al., 1997; Munnecke et al., 2003; Kaljo et al., 2004; Cramer & Saltzman, 2005; Melchin & Holmden, 2006; Stricanne et al., 2006). A possible relation between temporal shifts in  $\delta^{13}\text{C}_{\text{carb}}$  and major biotic events in the early Cambrian has been proposed by Brasier et al. (1994), with negative shifts correlating with reduced primary productivity and extinction, and positive shifts correlating with enhanced productivity and radiation. A positive sulphur isotope excursion is coinciding with the SPICE, which is interpreted to reflect increases in organic carbon and pyrite burial under anoxic and euxinic conditions (Gill et al., 2011). It has been hypothesized that these conditions may have been a result of upwelling during sea-level rise and caused the extinction at the base of the Paibian (Gill et al., 2011). A fundamental shift in the phytoplankton communities is known to follow the SPICE excursion, with the appearance of "modern" dinoflagellate-like acritarchs and the introduction of new morphologies (e.g., galeate acritarchs, diacromorphs) (Servais et al., 2008, 2016b). A shift is indeed visible at the Guzhangian/Paibian boundary in high turnover rates in both intervals, with many taxa going extinct in the Guzhangian while the Paibian shows high origination rates. A third interval of extinction is recorded in the uppermost Cambrian. This correlates well with the global Cambrian–Ordovician extinction event of other marine organisms, such as trilobites, brachiopods and cephalopods (e.g., Loch et al., 1993; Sepkoski, 1995; Fang et al., 2019).

#### 5.2.1.2 Late Ordovician Extinction Event

During the Hirnantian Extinction the phytoplankton diversity shows a clear cut, with very high extinction rates recorded in the Hirnantian, which represent the highest in the Palaeozoic. This extinction event is well studied in terms of taxonomic changes of the microphytoplankton (e.g., Paris et al., 2000; Ghavidel-Syooki et al., 2011; Delabroye, 2010; Delabroye & Vecoli, 2010; Delabroye et al., 2012). The extinction event is characterised by a stepwise pattern with the extinction of different groups of organisms occurring at different times (e.g., Munnecke et al., 2003). While no extinction event in direct relation to the glaciation is observed, a reduction of diversity and abundance of acritarchs, with a shift to an overrepresentation of opportunistic taxa, such as *Micrhystridium*, *Multiplicisphaeridium* and *Veryhachium* is detected in glacial sediments (Paris et al., 2000; Vecoli & Le Hérisse, 2004; Vecoli, 2008). Ghavidel-Syooki et al. (2011) note an abrupt palynofloral change during the onset of the Gondwanan glaciation at Katian–Hirnantian boundary, but with no new taxa appearing. The major turnover with the extinction of Ordovician forms and the appearance of Silurian type taxa occurred in the uppermost Hirnantian (Paris et al. 2000; Ghavidel-Syooki et al., 2011) after a post-glacial recovery of the phytoplankton, therefore after the glacial event during a time of warming (Paris et al., 2000). Our results show that the major episode of originations indeed happened after the Hirnantian, with a pronounced peak in origination rates in the Rhuddanian. According to Munnecke et al. (2003), the extinction of the microphytoplankton occurred after all other groups of marine invertebrates, and it is coinciding with a strong decrease in  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{18}\text{O}$  values (Brenchley et al., 1995; Paris et al., 2000). This decrease comes after a pronounced positive  $\delta^{13}\text{C}_{\text{carb}}$  excursion. While no direct indication is known from the fossil record, these high  $\delta^{13}\text{C}_{\text{carb}}$  values are interpreted as a result of high primary productivity (Brenchley et al., 1995). Brenchley et al. (1995) suggest changes in ocean circulation as a driver of the Hirnantian Extinction Event. They argue that while during glaciations the ocean was deeply ventilated, the ocean basins filled with warm saline water during the interglacials.

The extinctions at the beginning of the Hirnantian are coinciding with upwelling of nutrient-rich deeper waters, causing this enhanced productivity (Brenchley et al., 1995). It should be noted, that a high abundance of teratological forms of acritarchs is recorded in the upper Hirnantian, during or close to the maximum ice-sheet extensions of the Gondwanan glaciation, an interval corresponding to strong perturbations in the carbon cycle (Delabroye et al., 2012).

### *5.2.1.3 Silurian Extinction Events*

In the Silurian three significant marine turnover events are known: The Ireviken, Mulde and Lau events are associated with clear positive excursions of the carbon isotope curve, and therefore interpreted as reflecting perturbations in the global carbon cycle and climate (Talent et al., 1993; Samtleben et al., 1996; 2000; Kaljo et al., 1997; 2003; 2006; Saltzman, 2001; Munnecke et al., 2003; Cramer & Saltzman, 2005; Calner et al., 2006; Cramer et al., 2006; Lenz et al., 2006). A decrease in diversity following a peak in the Telychian is visible in all diversity metrics. Additionally, a peak in extinction rates is recorded in the Telychian. This signal is coinciding with the Ireviken Event, which occurred at the Telychian–Sheinwoodian boundary. Like the Hirnantian Extinction, the Ireviken Event shows a stepwise extinction pattern (Munnecke et al., 2003; Geslthorpe, 2004). A significant turnover in the microphytoplankton communities is known to have occurred during this event (Le Hérissé, 1989; Gelsthorpe, 2002, 2004; Munnecke et al., 2003). Relatively high turnover values are indeed demonstrated in our results for the Telychian, with both, high extinction and origination rates at this stage. A high number of originations distributed throughout the event was recognised by Gelsthorpe (2004). As in the Hirnantian Event, most extinctions of the phytoplankton are recorded at the end of the event, notably after the extinctions of other marine organisms (Munnecke, et al., 2003; Gelsthorpe, 2004; Calner, 2008). This is coinciding with a sea-level rise and a widespread expansion of euxinic and local anoxic conditions from deeper marine settings into shallower shelf environments (Munnecke, et al., 2003; Smolarek et al., 2016; Young et al., 2019). The Mulde Event occurred at the base of the Gorstian. While the normalised diversity and the SIB curves show a rise rather than a decrease in diversity, the SQS curve does display a decrease from the Homerian to the Gorstian. A small peak in extinction rates in the Homerian is proven in the present study, followed by a pronounced peak in origination rates. The number of originations in the Gorstian is higher than the number of extinctions in the Homerian. Thus, the Homerian–Gorstian interval is characterised by relatively high turnover rates with a peak in in the Gorstian. The Mulde Event primarily affected pelagic organisms (Calner, 2008). A considerable reduction of acritarch diversity and abundance is recorded (Porębska et al., 2004). Just prior to the onset of the event, a significant short-time increase in abundance of acritarchs is known from Gotland (Calner et al., 2006) and Poland (Porębska et al., 2004). The event is associated with phosphorite formation in shaly successions (Pittau et al., 2006; Jaeger, 1991). Phosphorites are mainly formed biologically in shallow seas close to the shelf slope where cold, phosphate-rich waters are brought up. A large part of phosphorites are the result of enrichment of phosphorus in phytoplankton. A rapid decrease in biodiversity is recorded from the Ludfordian onward, with relatively high numbers of extinctions in the Ludfordian, Pridoli and Lochkovian. Origination rates in the Ludfordian and Pridoli are low, hence the steep decline in biodiversity. The onset of this extinction is coinciding with the late Ludfordian Lau Event. This event has been related to the highest  $\delta^{13}\text{C}$  positive excursion recorded in the Palaeozoic. Here again, the extinctions occurred stepwise, with benthic preceding planktic groups (e.g., Munnecke et al., 2003; Stricanne et al., 2006; Calner, 2008). A turnover of the phytoplankton is described to have occurred after hemipelagic planktic and nektic organisms such as graptolites and conodonts (Stricanne et al., 2006). While  $\delta^{13}\text{C}$  positive excursions are often attributed to enhanced productivity (e.g., Berger & Vincent, 1986; Kump & Arthur, 1999; Herrle et al., 2003), Stricanne et al. (2006) recorded a strong decrease in abundance of acritarchs and prasinophytes during the  $\delta^{13}\text{C}$  excursion, indicating reduced primary production. Moreover, it has been argued, that the extreme amplitude of the Ludfordian  $\delta^{13}\text{C}$  positive excursion is too high to be

explained by enhanced productivity (Bickert et al., 1997). Rather it is explained by oceanic-climatic models for the Silurian describing an alternation between humid and arid conditions in low latitudes (Jeppsson, 1990; Bickert et al., 1997; Cramer & Saltzman, 2005). High  $\delta^{13}\text{C}$  values correspond to arid conditions, with low terrestrial input resulting in decreases in phytoplankton productivity. Humid episodes show low  $\delta^{13}\text{C}$  values and are characterised by high terrestrial input and enhanced upwelling resulting in increased primary production. Jeppsson & Calner (2002) suggested a larger role of changes in the phytoplankton in the Mulde and Lau events. According to the authors a severe drop in phytoplankton primary productivity might have caused mass mortality amongst planktic larvae in non-coastal settings.

#### *5.2.1.4 Late Devonian Extinction Events and the 'Late Palaeozoic Phytoplankton Blackout'*

The Upper Devonian is characterised by high taxonomic turnover, with a peak in extinction in the Famennian. Extinction rates remain high in the Tournaisian. Here, a relation to the Late Devonian mass extinctions can be inferred. According to the results, the Kellwasser Event at the Frasnian/Famennian boundary did not affect the organic-walled phytoplankton significantly, since the extinction rates in the Frasnian are relatively low. But a decrease in biodiversity is recorded, as the number of originations in the Famennian is very low. The results show a more severe extinction event at the Devonian/Carboniferous boundary coinciding with the Hangenberg event. The causes for the decrease of biodiversity beginning in the Late Devonian and for the succeeding apparent 'Late Palaeozoic Phytoplankton Blackout' are not well understood and widely discussed in literature (e.g., Riegel, 2008; Strother, 2008; Strother et al., 2010). Servais et al. (2006; 2016a) noted that the 'Phytoplankton Blackout' is but an artifact. They argue that the absence of resting cysts does not necessarily imply the absence of phytoplanktic organisms, since only a very small part of dinoflagellates in modern oceans produce preservable resting cysts (e.g., Head, 1996). With the focus on spores and pollen grains, acritarchs have been neglected in palynological studies concerning the Permian (Lei et al., 2013). Several indices pointing to a change in the composition of the phytoplankton somewhere close to the Devonian–Carboniferous boundary. Larger cysts become absent from the fossil record during the Carboniferous and Permian. Lei et al. (2013) noticed that acritarchs in the Permian are generally very small ( $< 20 \mu\text{m}$ ). Therefore, such forms are lost in standard palynological preparation techniques using sieves with a mesh size of  $20 \mu\text{m}$ . A distinct increase in the  $\text{C}_{28}/\text{C}_{29}$ -sterane ratio is observed by Schwark & Emt (2006) coinciding with the Hangenberg Event, with values remaining permanently higher after this event. This implies a shift from more primitive phytoplanktic organisms, which produce mainly  $\text{C}_{29}$ -steranes, to more modern forms, producing  $\text{C}_{28}$ -steranes. Before this event, short-term increases in the  $\text{C}_{28}/\text{C}_{29}$ -sterane ratio are known from certain mass extinction events (Kacak and Kellwasser Events), which lead to a rise in prasinophytes. Prasinophytes are known as 'disaster species' due to their abundance in sediments related to anoxia (Tappan, 1980; Van de Schootbrugge et al., 2005). Recent prasinophytes are known to produce predominantly  $\text{C}_{28}$ -members in their steroid composition (Volkman et al., 1994). But while these events did not seem to have lasting changes in the phytoplankton assemblages, as the  $\text{C}_{28}/\text{C}_{29}$ -sterane ratios rapidly recovered afterwards, the elevated values remained for the Carboniferous and Permian after the increase during the Hangenberg Event. Therefore a fundamental shift in the composition of the phytoplankton must have occurred at this time (Schwark & Emt, 2006). As the gap in phytoplankton diversity in the late Palaeozoic is not reflected in a decline in benthic invertebrate communities, it possibly represents an artifact. Strother (1996) suggests the presence of a non-encysting group of phytoplankton. This hypothesis is supported by the observed change in  $\text{C}_{28}/\text{C}_{29}$ -sterane ratios. This shift coincides with the appearance of euspondyle and metaspondyle Dasycladales in the Tournaisian/Mississippian (Roux, 1985; 1986) and the global spread of filamentous Codiacea (Siphonales) (Schwark & Emt, 2006). It should be noted, that the prasinophytes, which showed short-term abundance increases in anoxia-related extinction events, also



experienced a decline of biodiversity throughout the Carboniferous (Mullins & Servais, 2008). A change in phytoplankton composition at the D/C boundary is also reflected in the morphological evolution of Bryozoans that suggest a change in food specialisation (A. Ernst, personal communication). It is still unclear what caused this fundamental change in phytoplankton composition. Martin & Quigg (2012) proposed a shift to more nutrient-rich phytoplankton in the late Palaeozoic. They considered the Cambrian to Devonian as being characterised by low nutrient availabilities (cf., Martin, 1996). The increased nutrient availability during the Carboniferous and Permian could be due to falling sea level, the spread of forests, higher weathering, enhanced ocean circulation, oxygenation and upwelling (Martin & Servais, 2019). According to Strother (2008) the apparent change in acritarch diversity was a response to extrinsic changes in sea-water chemistry, with a decline of cysts in the fossil record reflecting decreasing atmospheric pCO<sub>2</sub> levels (e.g., Berner, 2008; Royer, 2014) as well as a change from low-Mg to high Mg calcite and aragonite seas (e.g., Sandberg, 1983; Ries, 2010). A Large Igneous Province Event (LIP) in two pulses (377–373; 364–363 Ma) is recorded from the Upper Devonian of the Eastern Siberian Craton. The Ma Yakutsk-Vilyui LIP has been related to the Late Devonian Extinction Events (Ricci et al., 2013). The first phase indeed coincides with the Kellwasser Event; the second phase, however, is older than the Hangenberg Event.

#### *5.2.1.5 Late Palaeozoic Extinction Events*

A decline in biodiversity is recorded at the Carboniferous–Permian boundary, with a small peak in taxonomic turnover, elevated extinction in the Gzhelian and increased origination in the Asselian. This interval follows a change in palaeoclimate to cooler and more arid conditions (e.g., Gulbranson et al., 2015), and the related Carboniferous rainforest collapse (Moscovian–Kasimovian). Moreover, CO<sub>2</sub> concentrations decreased to the lowest values of the Phanerozoic in the late Carboniferous–early Permian interval (e.g., Berner & Kothavala, 2001; Royer et al., 2004; Fig. 10). Also, two LIP events are known from the Carboniferous–Permian boundary interval: A major eruption of the Skagerrak-Centered LIP is dated 297 ± 4 Ma (Asselian; Torsvik et al., 2008); the Barguzin-Vitim LIP was active at 305–257 Ma. Both events have been related to the Carboniferous rainforest collapse (e.g., Kravchinsky, 2012).

#### *5.2.2 Diversification events and relation to biotic events*

##### *5.2.2.1 ‘Cambrian Explosion’ and the ‘Cambrian Substrate Revolution’*

During the Cambrian almost all phyla and classes originated. A slight diversification of the phytoplankton from Stage 2 to Stage 3 is visible, which coincides with the radiation of metazoans (Sepkoski, 1997; Na & Kießling, 2015). While it can be argued that a causal link between the diversities of the phytoplankton and other marine metazoans exists, the extent of the interrelations and therefore the role of the phytoplankton in the ‘Cambrian Explosion’ have to remain unclear, since the peak is minor and the preceding Stage 2 is poorly covered. A similar conclusion is given by Nowak et al. (2015), who observed the same radiation. Butterfield (1997) also describes a marked radiation of phytoplankton coinciding with the ‘Cambrian Explosion’ and a change to morphologically more complex forms at this interval. However, he argues that this shift was not acting as a trigger for the Cambrian Explosion, but rather represents a response of the phytoplankton to the expansion of metazoan activities into it by the introduction of small planktic herbivorous metazoans, thus a top-down effect (Butterfield, 1997). The comparably small radiation of the phytoplankton diversity during the interval of the Cambrian Explosion confirms a remark by Servais et al. (2008): The real ‘explosion’ in respect to phytoplankton diversity did not happen before the Late Cambrian.

A diversification occurs in the Miaolinguan from a low in stage 5 to a peak in the Drumian. The start of bioturbation of the expanding benthos during the middle Cambrian, termed the ‘Cambrian Substrate

Revolution' (e.g., Bottjer et al., 2000) enhanced the evolution of biogeochemical cycles in the oceans. It allowed the oxidation of dead organic matter and the recycling of nutrients back to the water column. Apart from higher nutrient availability, bioturbation might have played a role in the Cambrian evolution of plankton as a stress to escape benthic communities (Signor & Vermeij, 1994; Servais et al., 2016b).

#### 5.2.2.2 'Ordovician Plankton Revolution' and the Great Ordovician Biodiversification Event

The late Cambrian to Ordovician is characterised by significant ecological changes in marine communities. While the Cambrian ecosystems were dominated by benthic and nekto-benthic organisms in shallow water environments (e.g., Burzin et al., 2001), the water column and pelagic habitats became fully colonised during the Ordovician. According to Signor & Vermeij (1994), the fossil record suggests the diversification of plankton and suspension feeders during the late Cambrian–Early Ordovician interval, with the plankton evolution likely representing a response to benthic predation and bioturbation. The development of planktotrophy in invertebrate larvae also occurred during this interval (Peterson, 2005; Nützel et al., 2006; 2007). Servais et al. (2008; 2016b) concern this ecological shift including a significant diversification of the plankton and suspension feeders and the development of planktotrophy in larval stages. With respect to the organic-walled phytoplankton, Servais et al. (2008; 2016b) describe a fundamental shift in the phytoplankton communities following the SPICE excursion, with the appearance of "modern" dinoflagellate-like acritarchs and the introduction of new morphologies (e.g., galeate acritarchs, diacromorphs), and a rise in taxonomic diversity. The indices of taxonomic change show indeed a shift in phytoplankton communities between the Guzhangian and the Paibian, and a diversification of the organic-walled phytoplankton in the Guzhangian and the Jiangshanian. However, Nowak et al. (2015) found no evidence of great morphological innovation and high origination until the uppermost Cambrian. While our results indicate a shift as suggested by Servais et al. (2008; 2016b), this younger change in phytoplankton composition is also evident: another extinction event is recorded from the Cambrian stage 10, leading to yet another shift in the phytoplankton communities as visible in the indices for taxonomic change. Interestingly, the poly-cohorts of survivorship show the assemblages of the Jiangshanian and Stage 10 with the steepest curves, indicating a greater number of short-ranging species. Additionally, the pre-nascence curves show the most distinct change at the Cambrian/Ordovician boundary, indicating the major shift in phytoplankton composition to more modern forms happening at this interval and not before. However, many of the typical Early Ordovician acritarch forms, such as the 'diacromorphs' and the 'galeate' acritarchs indeed originated in the late Cambrian (Servais & Eiserhardt, 1995). A major increase of the phytoplankton is following the taxonomic shift at the Cambrian/Ordovician boundary during the Lower to Middle Ordovician. This diversification coincides with the onset of the Great Ordovician Biodiversification Event (GOBE), one of the most important radiations of life in the Phanerozoic. During the Ordovician, a rapid increase in the number of families, genera, and species of marine organisms occurred. The GOBE saw the rise of the Palaeozoic fauna. Several authors consider the GOBE as the sum of diversification events of different fossil groups in different ages over a longer time rather than a single diversification event (e.g., Miller, 2004; Servais & Harper, 2018). The indices of taxonomic change show two major phases of high origination: the first in the Lower Ordovician, the second in the Darriwilian, with no new taxa appearing in the Dapingian. Therefore, the diversification of the phytoplankton during the GOBE may have happened in two episodes rather than a single continuous event.

#### 5.2.2.3 'Devonian Nekton Revolution'

From the Silurian to the Carboniferous a diversification of nektic organisms is recognised (Klug et al., 2010; Whalen & Briggs, 2018). While Klug et al. (2010) described a rather rapid diversification event

("Devonian Nekton Revolution"), Whalen & Brigg concluded that the nekton diversified gradually with no evidence for a "revolution". In their work about the "Devonian Nekton Revolution", Klug et al. (2010) discussed the role of the phytoplankton in this major evolutionary and ecological event. They argue that it might have acted as a trigger for the recorded changes in the ecosystems. Hypotheses were presented in which the rise of land plants provided an increase of organic input into the oceans that lead to eutrophication and this in turn to plankton blooms (Algeo & Schlecker, 1998). One hypothesis stated that the increase in food availability supported diversification throughout the marine food web causing increasing competition leading to increasing mobility (Klug et al., 2010). Another suggested the anoxia events caused by the great masses of accumulating organic carbon would create a selectional pressure in favour of non-benthic and nondemersal groups (Klug et al., 2010). Klug et al. (2010) observed a rough correlation of the Devonian phytoplankton diversity curve and that of ammonoids, placoderms, and bony and cartilaginous fish tracks, while it is different from that of jawless fishes and acanthodians. Our results show an increase in phytoplankton biodiversity in the Devonian not before the Givetian–Frasnian interval. Diversity was rather declining in the Lower to Middle Devonian. Therefore a causal relation of phytoplankton biodiversity and the gradual diversification of the Nekton from the Silurian onward is not supported.

### *5.3 Possible causes of the recorded diversity changes*

#### *5.3.1 Ecospace*

It is well known that global species diversity is often reflecting the distribution of suitable habitat area. Radiations are associated with expansion of ecospace, diversity declines with decreases in ecospace (e.g., Sepkoski, 1984; Sepkoski & Miller, 1985; Rosenweig, 1995). One factor controlling the availability of marine ecospace, and therefore representing a major influence on the global biodiversity of marine organisms, is plate tectonics, i.e., the palaeogeographic constellation of land masses (e.g., Valentine & Moores, 1970; Zaffos et al., 2017). In times of high continental fragmentation more and smaller land masses and, relating thereto, an increased total length of coastline and a higher amount of shelf regions exist, whereas the amount of shelf area is reduced in phases of supercontinents. Additionally, the fragmentation of continents and the related formation of oceans permitted nutrients from the interior parts of those continents to be transported into the seas (Katz et al., 2004). According to Valentine & Moores (1972), supercontinent rifting produces topographic dispersal barriers, which increases genetic isolation and biodiversity. This holds true for the phytoplankton also. Katz et al. (2004) noticed that acritarch radiations in the Proterozoic appear to correlate with rifting phases of the supercontinents Rodinia and Pannotia, while the most important modern phytoplankton groups radiated after the breakup of Pangaea in the Late Triassic to Early Jurassic (Katz et al., 2004). A high separation of land masses from each other limits communication of faunas and floras in-between them and fosters provincialism. Indeed, a pronounced provincialism in acritarch floras is known from the Early to Middle Ordovician (e.g., Vavrdová, 1974; Li, 1989; Molyneux et al., 2013), a time with great separation of continental masses (e.g., Scotese & McKerrow, 1990).

*Fig. 7 near here*

The Palaeozoic was characterised by continental breakups and formations and the related openings and closures of seas and oceans. The comparison of the diversity trajectories with the curve of continental fragmentation based on Zaffos et al. (2017) reveals a good correlation (Fig. 7) concerning the long-term trends. In times of high fragmentation (i.e., from the latest Cambrian to Silurian, in the Upper Devonian) the biodiversity of the phytoplankton shows the highest values. The detachment of terranes, such as Avalonia, Canderia, Carolina and Meguma, and the related opening and widening of the Rheic Ocean in the latest Cambrian and throughout the Ordovician created new habitable areas for

the phytoplankton. These events were accompanied by the input of large amounts of terrestrial sediments, and therefore nutrients, into the oceans. A marked drop in biodiversity after a peak in the Gorstian (Silurian) is coinciding with the final stages of the Caledonide Orogeny, including the closure of the Iapetus Ocean during the merging of Avalonia-Baltica with Laurentia. The decrease in diversity following the Upper Devonian peak is set during a time of radical palaeogeographical change. The remaining parts of the Rheic Ocean were finally closed in the earliest Carboniferous, followed by the closure of the Proto-Tethys during the assembly of the supercontinent Pangaea in the Variscan Orogeny.

### *5.3.2 Sea level*

Sea level is known to affect the diversity of marine organisms. Transgressions result in more continental area being flooded. Therefore, high diversities are expected in times of high sea levels. Many studies discuss the correlation of phytoplankton biodiversity with sea-level changes and the related amount of flooded continental area. Katz et al. (2004) observed a high correlation in regard of Mesozoic and Cenozoic phytoplankton. The radiation of the major phytoplankton groups in recent oceans (dinoflagellates, diatoms, coccolithophores) occurred in the Early Mesozoic. This radiation is paralleling a long-term sea-level rise and the related expansion of flooded continental shelf area (Falkowski et al., 2004). Particularly the diversity curve of dinoflagellates shows a high correlation with the Mesozoic and Cenozoic global sea-level curve (Stover et al., 1996). It can therefore be inferred that sea level has a major influence on the biodiversity of the marine phytoplankton. However, not always is a direct correlation observed: While a diversity decline of calcareous nannoplankton and dinoflagellates from the Palaeogene onward is coinciding with a long-term sea-level decrease, diatom diversity has increased during the same time (Katz et al., 2004).

Several attempts to correlate sea-level changes with regional Palaeozoic phytoplankton diversity exist. Vecoli & Le Hérisse (2004) found no apparent correlation of acritarch diversity to second-order sea-level oscillations in the Ordovician of the "northern Gondwana margin" (North Africa and other locations), but a rough correlation of first-order transgressional phases with increasing diversity. Li et al. (2007) found diversity patterns of Ordovician acritarchs from the Chinese palaeocontinents partly correlating with regional and global sea-level changes, with peaks of biodiversity corresponding to sea-level highstands. A reverse result from the Early Ordovician of Avalonia is presented by Molyneux (2009). While diversity changes are paralleling sea-level changes, the highest diversity was observed in times of sea-level lowstands and vice versa. This might be the result of a lateral movement of high-diversity assemblages on- and offshore during trans- and regressions (Molyneux, 2009). Hints et al. (2010) compared their acritarch diversity curves for the Ordovician of Baltica with the global sea-level curve of Haq & Schutter (2008) and observed a rough correlation, with the highest diversity occurring during a sea-level highstand.

### *Fig. 8 near here*

In general, our phytoplankton diversity curves are roughly paralleling the Palaeozoic global sea-level curve (e.g., Haq & Schutter, 2008) (Fig. 8). A long-term increase in sea level is reflected in a radiation of the phytoplankton in the Lower and Middle Ordovician, and is followed by a decrease during the latest Ordovician to earliest Silurian, likewise paralleling the diversity curves. High diversity during the Silurian is also coinciding with sea-level high stands. A decrease in sea level in the latest Silurian and the Lower Devonian mirrors a decline in phytoplankton diversity. A long-term sea-level fall in the upper Palaeozoic coincides with the 'phytoplankton blackout'. Likewise, a comparison with changes in the total continental area covered by seas (Ronov, 1994) shows a rough correlation (Fig. 8), with



highest diversity occurring during intervals with high amounts of the continents flooded, i.e., the Middle Ordovician, the Silurian, the Middle to Upper Devonian.

### 5.3.3 Nutrients

It is well established that phytoplankton distribution in time and space is crucially controlled by nutrient availability (Strother, 2008; Martin & Quigg, 2012; Martin & Servais, 2019). Nutrients are essential for the growth of phytoplanktic organisms, particularly nitrate, phosphate and iron. Studies on recent phytoplankton show that resource limitation decreases survival and therefore community diversity (Sommer, 1985; Li, 2002; Goebel et al., 2013; Vallina et al., 2014). Based on the theory of ecological stoichiometry, Martin & Servais (2019) argue that nutrient input, especially phosphorus, is responsible for an increase in primary productivity and an enhanced stoichiometry of the phytoplankton through geological time. Thus, it can be inferred that the evolution of the Palaeozoic phytoplankton is most presumably related to the nutrient evolution of Palaeozoic oceans. There are different sources of these nutrients, such as terrestrial sediment input, volcanic activity and upwelling. Therefore it is reasonable to compare the biodiversity fluctuations of the Palaeozoic with changes in nutrient availability in the Palaeozoic oceans.

While many studies see a relation between high nutrient availability and high phytoplankton diversity (e.g., Tappan, 1980; Bambach, 1993; Riegel, 2008), Martin (1996) and Martin & Quigg (2012) present a different conclusion. They regard the lower and middle Palaeozoic (Cambrian to Devonian) as superoligotrophic, i.e. extremely low nutrient conditions, given generally slow terrestrial nutrient inputs and low recycling rates during the early to middle Palaeozoic. In contrast, the upper Palaeozoic (Carboniferous–Permian) was characterised by increased nutrient availability due to falling sea levels, the spread of forrests, higher weathering, enhanced ocean circulation, oxygenation and upwelling, according to Martin & Quigg (2012). Martin (1996) argues that modern phytoplankton diversity is lowest in nutrient-rich regimes and highest in oligotrophic conditions. According to Martin & Quigg (2012), pulses of higher nutrient inputs would have had a greater effect on phytoplankton biodiversification, since they promoted eutrophication and destabilisation of marine ecosystems associated with extinctions.

#### 5.3.3.1 Terrestrial sediments

Marine productivity is known to have been stimulated by terrestrial nutrient input derived from orogenic activities, weathering and enhanced upwelling of nutrients (e.g., Martin, 1996; 2002; 2003). Strontium isotope values are used, among other purposes, as a proxy for terrestrial sediment influx into the oceans (e.g., Faure, 1986; Taylor & Lasaga, 1999; Martin, 2003), since continental runoff is enriched in  $^{87}\text{Sr}$ , as opposed to  $^{86}\text{Sr}$  typically associated with sea-floor spreading and hydrothermal weathering (Edmond, 1992). The strontium isotope curve (e.g., Prokoph et al., 2008) shows strong excursions during large-scale tectonic events, such as the Neoproterozoic–Cambrian Pan-African Orogeny, the Late Ordovician Taconic Orogeny, the Late Devonian Acadian and Antler orogenies and the Carboniferous–Permian Alleghenian Orogeny. While the  $^{87}\text{Sr}/^{86}\text{Sr}$  trends are not or not well correlated with the phytoplankton biodiversity throughout the whole of the Palaeozoic (Fig. 9), it does parallel it from the late Lower Devonian to the Carboniferous, with a decrease between the Lochkovian (Lower Devonian) and the Eifelian (Middle Devonian), followed by an increase to a peak in the Famennian and a decrease after.

*Fig. 9 near here*

While the curve for Phanerozoic sediment flux by Flögel et al. (2000) (Fig. 9) is also only in parts correlating with the biodiversity of the Palaeozoic phytoplankton, it is more similar to the

phytoplankton diversity trends than the  $^{87}\text{Sr}/^{86}\text{Sr}$  curve. It shows a major peak in the Middle Ordovician, coinciding with high phytoplankton diversity. This interval is characterised by increased volcanic (Stillman, 1984; Barnes, 2004) as well as orogenic activity (e.g., Miller & Mao, 1995), to which a higher nutrient influx into the oceans can be related. An increasing sediment flux is observed during the Middle to Upper Devonian. This is mirroring the rise of diversity during this interval. A decline of runoff, erosion rates and suspended/dissolved loads is observed from the Carboniferous to the end of the Palaeozoic, coinciding with the 'phytoplankton blackout'. This reflects increasing interior drainage and aridity during the Pangaea assembly (Martin, 2003). Moreover, a decrease of phosphorite deposition suggests a decline of upwelling of nutrients (Parrish, 1982; 1987; Hotinski et al., 2001).

The Devonian was a period of environmental change. During the Devonian land plants underwent major evolutionary changes, from primitive non- or shallowly rooted small forms to multi-storied forests. The expansion of terrestrial vegetation and the development of deeper roots lead to a breakup of the rocky ground and to the formation of soil, which in turn caused an increase of sedimentary runoff into the oceans (Algeo et al., 1995; Algeo & Scheckler, 1998). This supply of nutrients had major effects on the phytoplankton and the marine ecosystems. Among a number of other factors (McLaren 1982; Wilde & Berry 1984; Johnson et al. 1985; Copper 1986; Geldsetzer et al. 1987; Ettensohn et al. 1988; Wang 1992), the Late Devonian Extinctions have been attributed to vast bottom water anoxia events, which probably were caused by an enhanced primary production leading to high rates of organic carbon burial.

Iron represents a micronutrient that is needed for the biological utilisation of nitrate. Phytoplankton growth is therefore limited by iron availability (e.g., Martin & Fitzwater, 1988; Boyd et al., 2001). Acritarchs are considered to include organisms of the green algal lineages (Falkowski et al., 2004; Katz et al., 2004). These forms use chlorophyll *b*, rather than chlorophyll *c* for the photosynthetic processes (Katz et al., 2004). Algae with green plastids have higher requirements for iron, zinc and copper as nutrients (Quigg et al., 2003, 2011) in comparison to the most important Mesozoic and Cenozoic phytoplankton groups, which belong to the red algal lineage. Iron is more soluble in low oxygen conditions. The atmospheric oxygen concentrations during the early to middle Palaeozoic were lower. Therefore, it is possible that the higher availability of iron has facilitated the high diversity of the phytoplankton in this interval.

### 5.3.3.2 *Upwelling*

Coastal upwelling is a process that brings colder, nutrient-rich waters from the deeper parts to the photic zone, creating areas of high organic productivity. The upper layers of sea water are transported by wind off the shore and water masses replaced from below. The wind direction relative to the shoreline is therefore essential for upwelling. Due to Coriolis forces, water is transported to the right of the direction of the wind in the Northern hemisphere and to the left in the Southern hemisphere. Given the prevailing winds in the atmospheric circulation, large upwelling zones are typically associated with eastern boundaries of oceans. Therefore, past upwelling zones can be reconstructed in palaeogeographic ocean and atmosphere circulation models: Parrish (1982) related Palaeozoic hydrocarbon source rocks with predicted areas of upwelling; Moore et al. (1993) reconstructed upwelling zones for the Wenlockian (Silurian); Servais et al. (2014) proposed regions with coastal and equatorial upwelling for the Ordovician–Silurian boundary. These models agree in presuming coastal upwelling zones at the western margins of Laurentia and the extended southwest-northeast stretching margin of Gondwana in the lower Palaeozoic.

The role of upwelling in extinction events has also been discussed in literature. Phosphate formations, recorded globally in the early Botomian (Shergold & Brasier, 1986; Bakhturov et al., 1988), indicate nutrient-enriched upwelling, coinciding with a widespread anoxic event. The SPICE has been related to enhanced coastal upwelling and associated extinction (Saltzman et al., 2000; Gill et al., 2011). According to Gill et al. (2011), upwelling at the base of the Paibian lead to increases in organic carbon and pyrite burial under anoxic and euxinic conditions during sea-level rise. The extinctions at the Hirnantian base are coinciding with upwelling causing enhanced productivity (Brenchley et al., 1995). Phosphorite formation associated with the Gorstian Mulde Event (Pittau et al., 2006; Jaeger, 1991) indicates upwelling.

#### *5.3.3.3 Volcanism*

Volcanism represents an important source for nutrients and is found to enhance primary production (Ducklow & Plank 2019; Wilson et al., 2019). Increased phytoplankton growth and abundance as well as altered species composition are observed responses to volcanic activity in recent oceans (Wilson et al., 2019). Oceanic iron concentrations can be enhanced by volcanic ash, and nitrate-rich deep waters can be mobilised and brought into the photic zone by heat ('lava-induced upwelling'; Wilson et al., 2019).

It can be assumed that phytoplankton diversification was facilitated during intervals with increased volcanic activity, e.g., Cambrian (Glass & Phillips, 2006; Hanley & Wingate, 2000), Ordovician (Stillman, 1984; Barnes, 2004), Upper Devonian (Kravchinsky et al., 2002; Courtillot et al., 2010; Kravchinsky, 2012).

#### *5.3.4 CO<sub>2</sub> concentrations*

The effects of increased CO<sub>2</sub> concentrations on phytoplankton are not well known. While some studies have reported negative (Gao & Zheng, 2010; Rokitta & Rost, 2012) or neutral (Tortell & Morel, 2002; Feng et al., 2009) responses in primary production, several cultural experiments with recent phytoplankton show an enhanced primary production under elevated CO<sub>2</sub> concentrations (Hein & Sand-Jensen, 1997; Riebesell et al., 2007; Iglesias-Rodriguez et al., 2008; Huang et al., 2018). The biodiversity of the phytoplankton is roughly correlated to the atmospheric CO<sub>2</sub> curves based on GEOCARB III (Berner & Kothavala, 2001), GEOCARBSULF (Berner, 2006) and proxies (Royer et al., 2004) (Fig. 10). The lower Palaeozoic is characterised by high atmospheric CO<sub>2</sub> concentrations (e.g., Berner, 2008; Royer, 2014), coinciding with high phytoplankton diversity. Middle to late Palaeozoic CO<sub>2</sub> trends are mirroring the diversity curves, with declining CO<sub>2</sub> concentration from the Silurian to Lower Devonian followed by a rise in the Middle to early Upper Devonian and a marked decrease in the Upper Devonian and Carboniferous correlating with the coinciding diversity trends. It can be inferred, that changes in atmospheric CO<sub>2</sub> concentrations had an impact on the phytoplankton (compare Strother et al., 2010). Particularly, a relation between the marked decrease in atmospheric CO<sub>2</sub> and the corresponding decrease in biodiversity in the Late Devonian is probable. Therefore, the development of terrestrial plants consuming atmospheric CO<sub>2</sub> and sequestering it in their growing biomass might not only have had caused a fertilisation of the oceans leading to enhanced primary production and subsequent widespread anoxia/euxinia events, but also a reduced CO<sub>2</sub> availability. Additionally, it is certainly possible that an increase in phytoplankton biomass during the Devonian, for example due to the fertilisation of the oceans, contributed to the reduction of CO<sub>2</sub> from the atmosphere.

*Fig. 10 near here*

## 5. Conclusions

The present study is the first exhaustive study to analyse the biodiversity changes of organic-walled microphytoplankton over the course of the Palaeozoic era. A relative high correlation with literature references has been identified. Several diversity metrics have been used in order to account for potential bias. The produced diversity trajectories show several diversifications and extinctions. The lower Palaeozoic (Cambrian–Devonian) shows generally high diversity, with high peaks in the Ordovician and Silurian, while the late Palaeozoic is characterised by low values ('Late Palaeozoic Phytoplankton Blackout'). Indices of taxonomic change as well as a poly-cohort analysis help to identify important shifts in the composition of the phytoplankton. Distinct extinctions could be correlated to known extinction events, such as the late Cambrian, the Hirnantian, the Silurian (Ireviken, Mulde, Lau events) and the Late Devonian extinction events. Two intervals of high origination coincide with the Great Ordovician Biodiversification Event. The results show no clear direct relations to certain biotic events, such as the Cambrian Explosion and the Devonian Nekton Revolution. However, phytoplankton diversity changes during the Ordovician and Silurian are mirroring trends of other planktic organisms, such as radiolarian, chitinozoans and graptolites.

Several factors are discussed that probably controlled long-term diversity trends. The amount and distribution of ecospace, as given by continental distribution/palaeogeography at a certain time, is shown to correlate with the diversity curves, with high diversity occurring in intervals of high continental fragmentation and separation and *vice versa*. Furthermore, diversity is found highest in intervals with high sea level and high amount of flooded continental area. We found that phytoplankton diversity might also be controlled by sediment supply, since a correlation to curves for  $^{87}\text{Sr}/^{86}\text{Sr}$  and sediment influx is observed in certain intervals. It can be inferred that nutrient influx, e.g., by terrestrial sediment runoff, upwelling and volcanic activity, facilitated primary production and diversification. Enhanced primary production probably played a role in extinction events by causing widespread anoxia events, which in turn had a negative effect on phytoplankton biodiversity. A rough correlation of the diversity curves with atmospheric  $\text{CO}_2$  concentration with high values in the early to middle, and low values in the late Palaeozoic, indicates an interconnection of these two parameters.  $\text{CO}_2$  availability might have facilitated diversification of the phytoplankton on the one hand, but increasing phytoplankton biomass might have reduced atmospheric  $\text{CO}_2$  concentrations on the other.

## Acknowledgements

We thank Ken Dorning, Alain Le Hérisse, Małgorzata Moczyłowska, Stewart Molyneux, and Reed Wicander for their initial work on the PhytoPal project. We acknowledge the University of Lille for the support. This paper is a contribution to the IGCP Project 653 'The Great Ordovician Biodiversification Event'.

## References

- Aberhan, M., Kiessling, W., 2012. Phanerozoic Marine Biodiversity: A Fresh Look at Data, Methods, Patterns and Processes. In: Talent, J.A. (ed.), *Earth and Life, International Year of Planet Earth*. Springer, Dordrecht.
- Achab, A., Paris, F., 2007. The Ordovician chitinozoan biodiversification and its leading factors. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245, 5–19.
- Algeo, T.J., Berner, R.A., Maynard, J.B., Scheckler, S.E., 1995. Late Devonian Anoxic Events and Biotic Crises: "Rooted" in the Evolution of Vascular Land Plants? *GSA Today* 5(3), 64–66.
- Algeo, T.J., Scheckler, S.E., 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society B: Biological Sciences* 353(1365), 113–130.
- Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J., Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomašových, A., Visaggi, C.C., 2008. Phanerozoic Trends in the Global Diversity of Marine Invertebrates. *Science* 321, 97–100.
- Alroy, J., 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* 53, 1211–1235.
- Alroy, J., 2013. The shifting balance of diversity among major marine animal groups. *Science* 329, 1191–1194.
- Bakhturov, S.F., Evtushenko, V.M., Pereladov, V.S., 1988. Kuonamka bituminous group: *Akademiya Nauk SSSR, Sibirskoye Otdeleniye, Trudy Instituta Geologii i Geofiziki* 671, 161 pp.
- Bambach, R.K., 1993. Seafood through time: changes in biomass, energetic, and productivity in the marine ecosystem. *Paleobiology* 19, 372–397.
- Barnes, C.R., 2004. Was there an Ordovician Superplume event? In: Webby, B.D., Droser, M.L., Paris, F., Percival, I. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 77–80.
- Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42(1), 1–20.
- Berger, W.H., Vincent, E., 1986. Deep-sea carbonates: reading the carbon-isotope signal. *Geologische Rundschau* 75, 249–269.
- Berner, R.A., 2006. GEOCARBSULF: A combined model for Phanerozoic atmospheric O<sub>2</sub> and CO<sub>2</sub>. *Geochimica et Cosmochimica Acta* 70, 5653–5664.
- Berner, R.A., 2008, Addendum to "inclusion of the weathering of volcanic rocks in the GEOCARBSULF model" (R. A. Berner, 2006, v. 306, p. 295–302). *American Journal of Science* 308, 100–103.

- Berner, R.A., Kothavala, Z., 2001. GEOCARB III: A revised model of atmospheric CO<sub>2</sub> over Phanerozoic time. *American Journal of Science* 301, 182–204.
- Berry, W.B.N., Wilde, P., 1990. Graptolite biogeography: implications for palaeogeography and palaeoceanography. In: McKerrow, W.S., Scotese, C.R. (eds), *Palaeozoic Palaeogeography and biogeography*. Geological Society Memoir 12, 129–137.
- Bickert, T., Pätzold, J., Samtleben, C., Munnecke, A., 1997. Paleoenvironmental changes in the Silurian indicated by stable isotopes in brachiopod shells from Gotland, Sweden. *Geochimica et Cosmochimica Acta* 61, 2717–2730.
- Bond, D.P.G., Grasby, S.E., 2017. On the causes of mass extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 478, 3–29.
- Bottjer, D.J., Hagadorn, J.W., Dornbos, S.Q., 2000. The Cambrian substrate revolution. *GSA Today* 10(9), 1–7.
- Boyd, P.W., Crossley, A.C., Di Tullio, G.R., Griffiths, F.B., Hutchins, D.A., Queguiner, B., Sedwick, P.N., Trull, T.W., 2001. Control of phytoplankton growth by iron supply and irradiance in the Subantarctic Southern Ocean: experimental results from the SAZ project. *Journal of Geophysical Research* 106(C12), 31585–31595.
- Brasier, M.D., Rozanov, A.Y., Zhuravlev, A.Y., Corfield, R.M., Derry, L.A. 1994. A carbon isotope reference scale for the Lower Cambrian succession in Siberia: report of IGCP Project 303. *Geological Magazine* 131, 767–783.
- Brenchley, P.J., Carden, G.A.F., Marshall, J.D., 1995. Environmental changes associated with the ‘first’ strike of the late Ordovician mass extinction. *Modern Geol.* 20, 69–82.
- Bulman, O.M.B., 1964. Lower Palaeozoic plankton. *Journal of the Geological Society of London* 120, 457–476.
- Burzin, M.B., Debrenne, F., Zhuravlev, A.Yu., 2001. Evolution of shallow-water level-bottom communities. In: Zhuravlev, A.Yu., Riding, R. (eds), *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, pp. 217–237
- Butterfield, N.J., 1997. Plankton ecology and the Proterozoic–Phanerozoic transition. *Paleobiology* 23(2), 247–262.
- Butterfield, N.J., Rainbird, R.H., 1998. Diverse organic-walled fossils, including ‘possible dinoflagellates’, from the early Neoproterozoic of arctic Canada. *Geology* 26(11), 963–966.
- Calner, M., 2008. Silurian global events – at the tipping point of climate change. In: Elewa, A.M.T. (ed.), *Mass Extinction*. Springer, Berlin, Heidelberg, pp. 21–57.
- Calner, M., Kozłowska, A., Masiak, M., Schmitz, B., 2006. A shoreline to deep basin correlation chart for the middle Silurian coupled extinction-stable isotopic event. *GFF* 128, 79–84.
- Chen, X., Zhang, Y.-D., Fan, J.-X., 2006: Ordovician graptolite evolutionary radiation: a review. *Geological Journal* 41, 289–301.



- Colbath, G.K., Grenfell, H.R., 1995. Review of biological affinities of acid-resistant, organic-walled eukaryotic algal microfossils (including 'acritarchs'). *Review of Palaeobotany and Palynology* 86, 287–314.
- Cooper, P., 1986. Frasnian/Famennian mass extinction and cold-water oceans. *Geology* 14, 835–839.
- Cooper, R.A., 2004. Measures of diversity. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 52–57.
- Cooper, R.A., Sadler, P.M., Munnecke, A., Crampton, J.S., 2013. Graptoloid evolutionary rates track Ordovician–Silurian global climate change. *Geological Magazine* 151(2), 349–364.
- Courtillot, V., Kravchinsky, V.A., Quidelleur, X., Renne, P.R., Gladkochub, D.P., 2010. Preliminary dating of the Viluy traps (Eastern Siberia): Eruption at the time of Late Devonian extinction events? *Earth and Planetary Science Letters* 102(1–2), 29–59.
- Cramer, B.D., Saltzman, M.R. 2005. Sequestration of  $^{12}\text{C}$  in the deep ocean during the early Wenlock (Silurian) positive carbon isotope excursion. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219, 333–349.
- Cramer, B.D., Kleffner, M.A., Saltzman, M.R., 2006. The Late Wenlock Mulde positive carbon isotope ( $\delta^{13}\text{C}_{\text{carb}}$ ) excursion in North America. *GFF* 128, 85–90.
- Crampton, J.S., Cooper, R.A., Sadler, P.M., Foote, M., 2016. Greenhouse–icehouse transition in the Late Ordovician marks a step change in extinction regime in the marine plankton. *PNAS* 113(6), 1498–1503.
- Cruz, N.M., 2011. Acritarcs. In: Carvalho, I.S. (ed.), *Paleontologia – Microfósseis, Paleoinvertebrados*. Editora Interciência, Rio de Janeiro, 2, 221–228.
- Delabroye, A., Vecoli, M., 2010. The end-Ordovician glaciations and the Hirnantian Stage: A global review and questions about Late Ordovician event stratigraphy. *Earth-Science Reviews* 98, 269–282.
- Delabroye, A., Munnecke, A., Servais, T., Vandenbroucke, T.R.A., Vecoli, M., 2012. Abnormal forms of acritarchs (phytoplankton) in the upper Hirnantian (Upper Ordovician) of Anticosti Island, Canada. *Review of Palaeobotany and Palynology* 173, 46–56.
- Delabroye, A., 2010. Dynamiques du phytoplancton à travers la limite Ordovicien-Silurien aux faibles paléolatitudes (Laurentia : Île d'Anticosti, Québec, Canada ; Baltica : Valga, Estonie) : compléments aux données des hautes latitudes glaciaires du Gondwana. Dissertation, University of Lille 1, 464 pp.
- Downie, C., 1984. Acritarchs in British Stratigraphy. 17. Geological Society London, Special Report, pp. 1–26.
- Downie, C., Evitt, W.R., Sarjeant, W.A.S., 1963. Dinoflagellates, hystrichospheres, and the classification of the acritarchs. *Stanford University Publications in Geological Sciences* 7, 1–16.
- Ducklow, H., Plank, T., 2019. Volcano-stimulated marine photosynthesis. *Science* 365(6457), 978–979.

- Edmond, J.M., 1992. Himalayan tectonics, weathering processes, and the strontium isotope record in marine limestones. *Science* 258, 1594–1597.
- Ettensohn, F.R., Miller, M.L., Dillman, S.B., Elam, T.D., Geller, K.L., Swager, D.R., Markowitz, G., Woock, R.D., Barron, L.S., 1988. Characterization and implications of the Devonian–Mississippian black-shale sequence, eastern and central Kentucky, USA: pycnoclines, transgression, regression, and tectonism. In: McMillan, N.J., Embry, A.J., Glass, D.J. (eds), *Devonian of the world. 2. Sedimentation*. Canadian Society of Petroleum Geologists Memoir 5, pp. 323–345.
- Evitt, W.R., 1963. A discussion and proposals concerning fossil dinoflagellates, hystriospheres and acritarchs, II. *Proceedings of the National Academy of Sciences of the United States of America* 49(3), 298–302.
- Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305, 354–360.
- Fang, X., Kröger, B., Zhang, Y.-D., Zhang, Y.-B., Chen, T.E., 2019. Palaeogeographic distribution and diversity of cephalopods during the Cambrian–Ordovician transition. *Palaeoworld* 28(1–2), 51–57.
- Faure, G., 1986. *Principles of Isotope Geology*. Wiley, New York.
- Feng, Y.Y., Warner, M.E., Zhang, Y., Sun, J., Fu, F.X., Rose, J.M., Hutchins, D.A., 2009. Interactive effects of increased pCO<sub>2</sub>, temperature and irradiance on the marine coccolithophore *Emiliana huxleyi* (Prymnesiophyceae). *European Journal of Phycology* 43(1), 87–98.
- Fensome, R.A., Williams, G.L., Sedley Barss, M., Freeman, J.M., Hill, J.M., 1990. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. *American Association of Stratigraphic Palynologists Foundation* 25, 1–771.
- Fensome, R.A., Williams, G.L., MacRae, R.A., Moldowan, J.M., Taylor, F.J.R., 1996. The early Mesozoic radiation of dinoflagellates. *Paleobiology* 22, 329–338.
- Field, C., Behrenfeld, M., Randerson, J., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–40.
- Flögel, S., Wold, C., Hay, W., 2000. Evolution of sediments and ocean salinity. Abstracts volume, 31<sup>st</sup> International Geological Congress, Rio de Janeiro, Brazil, August 6–17, 2000, 4 pp.
- Foote, M., 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* 26, 74–102.
- Foote, M., 2001. Evolutionary rates and the age distributions of living and extinct taxa. In: Jackson, J.B.C., McKinney, F.K., Lidgard, S. (eds), *Evolutionary Patterns: Growth, Form, and Tempo in the Fossil Record*. University of Chicago Press, Chicago, pp. 245–294.
- Gao, K.S., Zheng, Y.Q., 2010. Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). *Global Change Biology* 16(8), 2388–2398.
- Geldsetzer, H.H.J., Goodfellow, W.D., McLaren, D.J., Orchard, M.J., 1987. Sulfur-isotope anomaly associated with the Frasnian–Famennian extinction, Medicine Lake, Alberta, Canada. *Geology* 15, 393–396.



- Gelsthorpe, D., 2002. Microplankton changes across a mass extinction: the Early Silurian Ireviken Event. *IPC2002 Geol. Soc. Austr. Abstr.* 86, 64.
- Gelsthorpe, D.N., 2004. Microplankton changes through the early Silurian Ireviken extinction event on Gotland, Sweden. *Review of Palaeobotany and Palynology* 130, 89–103.
- Ghavidel-Syooki, M., Hassanzadeh, J., Vecoli, M., 2011. Palynology and isotope geochronology of the Upper Ordovician–Silurian successions (Ghelli and Soltan Maidan Formations) in the Khoshyeilagh area, eastern Alborz Range, northern Iran; stratigraphic and palaeogeographic implications. *Review of Palaeobotany and Palynology* 164, 251 – 271.
- Gill, B.C., Lyons, T.W., Young, S.A., Kump, L.R., Knoll, A.H., Saltzman, M.R., 2011. Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* 469, 80–83.
- Glass, L.M., Phillips, D., 2006. The Kalkarindji Continental Flood Basalt Province: a new Cambrian large igneous province in Australia with possible links to faunal extinctions. *Geology* 34(6), 461–464.
- Glumac, B., Walker, K.R., 1998. A Late Cambrian positive carbon-isotope excursion in the southern Appalachians: relation to biostratigraphy, sequence stratigraphy, environments of deposition, and diagenesis. *Journal of Sedimentary Research* 68, 1212–1222.
- Goebel, N.L., Edwards, C.A., Zehr, J.P., Follows, M.J., Morgan, S.G., 2013. Modeled phytoplankton diversity and productivity in the California Current System. *Ecological Modelling* 264, 37–47.
- Grey, K., 2005. Ediacaran palynology of Australia. *Memoir of the Association of Australasian Palaeontologists* 31, 1–439
- Gulbranson, E.L., Montanez, I.P., Tabor, N.J., Limarino, C.O., 2015. Late Pennsylvanian aridification on the southwestern margin of Gondwana (Paganzo Basin, NW Argentina): A regional expression of a global climate perturbation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 417, 220–235.
- Guy-Ohlson, D., 1996. Prasinophycean algae. In: Jansonius, J., McGregor, D.C. (eds), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, pp. 181–189.
- Hanley, L., Wingate, M., 2000. SHRIMP zircon age for an Early Cambrian dolerite dyke: an intrusive phase of the Antrim Plateau Volcanics of northern Australia, *Australian Journal of Earth Science* 47(6), 1029–1040.
- Haq, B.U., Shutter, S.R., 2008. A Chronology of Paleozoic Sea-Level Changes. *Science* 322, 64–68.
- Head, M.J., 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansonius, J., McGregor, D.C., (eds), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation. Publishers Press, Salt Lake City, Utah, USA, pp. 1197–1248.
- Hein, M., Sand-Jensen, K., 1997. CO<sub>2</sub> increases oceanic primary production. *Nature* 388(6642), 526–527.
- Herrle, J.O., Pross, J., Friedrich, O., Kössler, P., Hemleben, C., 2003. Forcing mechanisms for Mid-Cretaceous black shale formation: evidence from the Upper Aptian and Lower Albian of the Vocontian Basin (SE France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 190, 399–426.

- Hints, O., Delabroye, A., Nölvak, J., Servais, T., Uutela, A., Wallin, Å., 2010. Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: Comparison with other fossil groups and sea-level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294, 161–173.
- Hotinski, R.M., Bice, K.L., Kump, L.R., Najjar, R.G., Arthur, M.A., 2001. Ocean stagnation and end-Permian anoxia. *Geology* 29, 7–10.
- Hough, M.L., Shields, G.A., Evins, L.Z., Strauss, H., Henderson, R.A., Mackenzie, S., 2006. A major sulphur isotope event at *c.* 510 Ma: a possible anoxia-extinction-volcanism connection during the Early-Middle Cambrian transition?: Global warming as a major determining factor in biosphere evolution. *Terra Nova*, 18(4): 257–263.
- Huang et al., 2018. Effects of increasing atmospheric CO<sub>2</sub> on the marine phytoplankton and bacterial metabolism during a bloom: A coastal mesocosm study. *Science of the Total Environment* 633, 618–629.
- Huntley, J.W., Xiao, S.-H., Kowalewski, M., 2006a. 1.3 billion years of acritarch history: an empirical morphospace approach. *Precambrian Res.* 144, 52–68.
- Huntley, J., Xiao, S.-H., Kowalewski, M., 2006b. On themorphological history of Proterozoic and Cambrian acritarchs. In: Xiao, S., Kaufman, A.J. (eds.), *Neoproterozoic Geobiology and Paleobiology, Topics in Geobiology*. Springer, Netherlands, pp. 23–56.
- Iglesias-Rodriguez, M.D., Halloran, P.R., Rickaby, R.E., Hall, I.R., Colmenero-Hidalgo, E., Gittins, J.R., Green, D.R., Tyrrell, T., Gibbs, S.J., von Dassow, P., Rehm, E., Armbrust, E.V., Boessenkool, K.P., 2008. Phytoplankton calcification in a high-CO<sub>2</sub> world. *Science* 320(5874), 336–340.
- Jaeger, H., 1991. New standard graptolite zonal sequence after the "big crisis" at the Wenlockian/Ludlovian boundary (Silurian). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 182, 303–354.
- Jeppsson, L., 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. *Journal of the Geological Society, London* 147, 663–674.
- Jeppsson, L., Calner, M., 2002. The Silurian Mulde Event and a scenario for secundo-secundo events. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 93, 135–154.
- Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin* 96, 567–587.
- Kaljo, D., Kiipli, T., Martma, T., 1997. Correlation of carbon isotope event markers through the Wenlock-Pridoli sequence at Ohesaare (Estonia) and Priekule (Latvia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 132, 211–223.
- Kaljo, D., Martma, T., Männik, P., Viira, V., 2003. Implications of Gondwana glaciations in the Baltic late Ordovician and Silurian and a carbon isotopic test of environmental cyclicality. *Bull. Soc. Géol. Fr.* 174, 59–66.
- Kaljo, D., Hints, L., Martma, T., Nölvak, J., Oraspold, A., 2004. Late Ordovician carbon isotope trend in Estonia, its significance in stratigraphy and environmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 210, 165–185.

- Kaljo, D., Martma, T., 2006. Application of carbon isotope stratigraphy to dating Baltic Silurian rocks. *GFF* 128, 161–168.
- Katz, M.E., Vinkel, Z.V., Grzebyk, D., Knoll, A.H., Falkowski, P.G. 2004. Evolutionary Trajectories and Biogeochemical Impacts of Marine Eukaryotic Phytoplankton. *Annu. Rev. Evol. Syst.* 35, 523–556.
- Kaźmierczak, J., Kremer, B., 2009. Spore-like bodies in early Paleozoic acritarchs: clues to chlorococcalean affinities. *Acta Palaeontologica Polonica* 54(3), 541–551.
- Klug, C., Kröger, B., Kiessling, W., Mullins, G., Servais, T., Frýda, J., Korn, D., Turner, S., 2010. The Devonian nekton revolution. *Lethaia* 43, 465–477.
- Knoll, A.H., 1994. Proterozoic and Early Cambrian protists: evidence for accelerating evolutionary tempo.
- Kravchinsky, V.A., Konstantinov, K.M., Courtillot, V., Valet, J.-P., Savrasov, J.I., Cherniy, S.D., Mishenin, S.G., Parasotka, B.S., 2002. Palaeomagnetism of East Siberian traps and kimberlites: two new poles and palaeogeographic reconstructions at about 360 and 250 Ma. *Geophysical Journal International* 148, 1–33.
- Kravchinsky, V.A., 2012. Paleozoic large igneous provinces of Northern Eurasia: Correlation with mass extinction events. *Global and Planetary Change* 86–87.
- Kump, L.R., Arthur, M.A., 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. *Chemical Geology* 161, 181–198.
- Le Hérisse, A., 1984. Microplankton à paroi organique du Silurien de Gotland (Suède): observations au microscope électronique de structures de desenkystement. *Review of Palaeobotany and Palynology* 43, 217–236.
- Le Hérisse, A., 1989. Acritarches et kystes d'algues Prasinophycées du Silurien de Gotland, Suède. *Palaeontographia Italica* 76, 57–302.
- Le Hérisse, A., Dorning, K.J., Mullins, G.L., Wicander, R., 2009. Global patterns of organic-walled phytoplankton biodiversity during the late Silurian to earliest Devonian. *Palynology* 33(1), 25–75.
- Lei, Y., Servais, T., Feng, Q., 2013. The diversity of the Permian phytoplankton. *Review of Palaeobotany and Palynology* 198, 145–161.
- Lenz, A.C., Noble, P.J., Masiak, M., Poulson, S.R., Kozłowska, A., 2006. The *lundgreni* Extinction Event: integration of paleontological and geochemical data from Arctic Canada. *GFF* 128, 153–158.
- Li, W.K.W., 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419, 154–157.
- Li, J., 1989. Early Ordovician Mediterranean Province acritarchs from Upper Yangtze Region, China. In: *Developments in Geoscience: contributions to the 28th International Geological Congress, 1989, Washington D.C.* Chinese Academy of Science, Beijing, 231–234.
- Li, J., Servais, T., Yan, K., Zhu, H., 2007. A nearshore-offshore trend in the acritarch distribution of the Early-Middle Ordovician of the Yangtze Platform, South China. *Review of Palaeobotany and Palynology* 130, 141–161.

- Loch, J.D., Stitt, J.H., Derby, J.R., 1993. Cambrian-Ordovician boundary interval extinctions: implications of revised trilobite and brachiopod data from Mount Wilson, Alberta, Canada. *Journal of Paleontology* 67, 497-517.
- Ludvigsen, R., Westrop, S.R., 1985. Three new Upper Cambrian stages for North America. *Geology* 13, 139-143.
- Martin, F., 1993. Acritarchs: a review. *Biological Reviews* 68, 475-538.
- Martin, R.E., 1996. Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. *Palaios* 11, 209-219.
- Martin, R.E., 2002. Cyclic and secular trends in preservation through geologic time: implications for the evolution of biogeochemical cycles. In: Derenzi, M., Alonso, M.V.P., Belinchón, M., Peñalver, E., Montoya, P., & Márquez-Aliaga, A. (eds), *Current Topics on Taphonomy and Fossilization: Taphos 2002, 3rd Meeting on Taphonomy and Fossilization, Valencia*, 67-76.
- Martin, R.E., 2003. The fossil record of biodiversity: nutrients, productivity, habitat area and differential preservation. *Lethaia* 36, 179-193.
- Martin, J.H., Fitzwater, S.E., 1988. Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature* 331, 341-343.
- Martin, R.E., Quigg, A., 2012. Evolving Phytoplankton Stoichiometry Fueled Diversification of the Marine Biosphere. *Geosciences* 2, 130-146.
- Martin, R.E., Servais, T., 2019. Did the evolution of the phytoplankton fuel the diversification of the marine biosphere? *Lethaia*, in press.
- Martin, R.E., Quigg, A., Podkovyrov, V., 2008. Marine biodiversification in response to evolving phytoplankton stoichiometry. *Palaeogeography, Palaeoclimatology, Palaeoecology* 258, 277-291.
- McLaren, D.J., 1982. Frasnian-Famennian extinctions. In: Silver, L.T., Schultz, P.H. (eds), *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America, Special Paper 190, Boulder, CO, pp. 477-484.
- Melchin, M.J., Holmden, C., 2006. Carbon isotope chemostratigraphy of the Llandovery in Arctic Canada: implications for global correlation and sea-level change. *GFF* 128, 173-180.
- Mendelson, C., 1993. Acritarchs and Prasinophytes. In: Lipps, J.H. (ed.), *Fossil Prokaryotes and Protists*. Blackwell Scientific, Boston, pp. 77-104.
- Miller, A.I., 2004. The Ordovician Radiation: towards a new global synthesis. In: Webby, B.D., Droser, M.L., Paris, F., Percival, I.G. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 380-388.
- Miller, A.I., Mao, S., 1995. Association of orogenic activity with the Ordovician radiation of marine life. *Geology* 23, 305-308.
- Moczydłowska, M., 1998. Cambrian acritarchs from Upper Silesia, Poland – biochronology and tectonic implications. *Fossils and Strata* 46, 121 pp.

- Moczyłowska, M., 1999. The Lower-Middle Cambrian boundary recognised by acritarchs in Baltica and at the margin of Gondwana. *Bolletino della Societa Paleontologica Italiana* 38, 27–225.
- Moczyłowska, M., 2010. Life cycle of early Cambrian microalgae from the *Skiagia*-plexus acritarchs. *Journal of Paleontology* 84(2), 216–230.
- Moczyłowska, M., 2011. The early Cambrian phytoplankton radiation: acritarch evidence from the Lükati Formation, Estonia. *Palynology* 35(1), 103–145.
- Moldowan, J.M., Talyzina, N.M., 1998. Biogeochemical Evidence for Dinoflagellate Ancestors in the Early Cambrian. *Science* 281(5380), 1168–1170.
- Moldowan, J.M., Dahl, J., Jacobson, S.R., Huizinga, B.J., Fago, F.J., Shetty, R., Watt, D.S., Peters, K.E., 1996. Chemostratigraphic reconstruction of biofacies: molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology* 24, 159–162.
- Molyneux, S.G., 2009. Acritarch (marine microphytoplankton) diversity in an Early Ordovician deep-water setting (the Skiddaw Group, northern England): Implications for the relationship between sea-level change and phytoplankton diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275, 59–76.
- Molyneux, S.G., Delabroye, A., Wicander, R., Servais, T., 2013. Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton. *Geological Society, London, Memoirs* 38, 365–397.
- Monnet, C., 2019. epaleo: an R package for paleontological data analysis. University of Lille, France (unpublished)
- Moore, G.T., Hayashida, D.N., Ross, C.A., 1993. Late Early Silurian (Wenlockian) general circulation model-generated upwelling, graptolitic black shales, and organic-rich source rocks – An accident of plate tectonics? *Geology* 21, 17–20.
- Mullins, G.L., Servais, T., 2008. The diversity of the Carboniferous phytoplankton. *Review of Palaeobotany and Palynology* 149, 29–49.
- Mullins, G.L., Aldridge, R.J., Dorning, K.J., Le Hérisse, A., Moczyłowska-Vidal, M., Molyneux, S., Servais, T., Wicander, R., 2005. The diversity of the Lower Paleozoic phytoplankton: The PhytoPal Project. 38th Annual Meeting of the AASP, St. Louis, Missouri, Program and Abstracts, 43.
- Mullins, G.L., Aldridge, R.J., Dorning, K.J., Le Hérisse, A., Moczyłowska-Vidal, M., Molyneux, S., Servais, T., Wicander, R., 2006. The diversity of the lower Palaeozoic phytoplankton: The phytopal project. *Palynology* 30, 224.
- Munnecke, A., Samtleben, C., Bickert, T., 2003. The Ireviken Event in the lower Silurian of Gotland, Sweden – relation to similar Palaeozoic and Proterozoic events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 99–124.
- Na, L., Kießling, W., 2015. Diversity partitioning during the Cambrian radiation. *PNAS* 112(15), 4702–4706.
- Noble, P.J., Danelian, T., 2004. Radiolarians. In: Webby, B.D., Droser, M.L., Paris, F., Percival, I. (eds), *The Great Ordovician Biodiversification Event*, 97 – 101. Columbia University Press, New York.

- Nowak, H., Servais, T., Monnet, C., Molyneux, S.G., Vandenbroucke, T.R.A., 2015. Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity. *Earth-Science Reviews* 151, 117–131.
- Nützel, A., Lehnert, O. & Fryda, J., 2006. Origin of planktotrophy – evidence from early molluscs. *Evolution & Development* 8, 325–330.
- Nützel, A., Lehnert, O. & Fryda, J., 2007. Origin of planktotrophy – evidence from early molluscs: a reply to Freeman & Lundelius. *Evolution & Development* 9, 312–317.
- Öpik, A.A., 1966. The Early Upper Cambrian crisis and its correlation. *Journal and Proceedings of the Royal Society of New South Wales* 100, 9–14.
- Pagès, A., Schmid, S., Edwards, D., Barnes, S., He, N., Grice, K., 2016. A molecular and isotopic study of palaeoenvironmental conditions through the middle Cambrian in the Georgina Basin, central Australia. *Earth and Planetary Science Letters* 447, 21–32.
- Palmer, A.R., 1979. Biome boundaries re-examined. *Alcheringa* 3, 33–41.
- Palmer, A.R., 1984. The biome problem: Evolution of an idea. *Journal of Paleontology* 58, 599–611.
- Palmer, A.R., 1998. A proposed nomenclature for stages and series for the Cambrian of Laurentia. *Canadian Journal of Earth Sciences* 35, 323–328.
- Palynodata Inc., White, J.M., 2008. Palynodata Datafile 2006 version, with introduction by J. M. White. Geological Survey of Canada Open File 5793 (1 CD-ROM).
- Paris F., Bourahrouh, A., Le Hérisse, A., 2000. The effects of the final stages of the Late Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well NI-2 (NE Algerian Sahara). *Review of Palaeobotany and Palynology* 113, 87–104.
- Paris, F., Achab, A., Asselin, E., Nölvak, J., Wang, X-F, Chen, X-H, Grahn, Y., Sennikov, N., Obut, O., Samuelsson, J., Vecoli, M., Verniers, J., Winchester-Seeto, T., 2004. Chitinozoans. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (eds), *The Great Ordovician Biodiversification Event*. Columbia Univ. Press, New York, pp. 294–311.
- Parrish, J.T., 1982. Upwelling and petroleum source beds, with reference to Paleozoic. *American Association of Petroleum Geologists Bulletin* 66(6), 750–774.
- Parrish, J.T., 1987. Palaeo-upwelling and the distribution of organic-rich rocks. In: Brooks, J., Fleet, A.J. (eds), *Marine Petroleum Source Rocks*. Geological Society Special Publication 26, 199–205.
- Peterson, K.J., 2005. Macroevolutionary interplay between planktic larvae and benthic predators. *Geology* 33, 929–932.
- Pittau, P., Cotza, F., Cristini, S., Del Rio, M., Loi, M., 2006. Palaeontologic and biogeochemical characterization of the *Cyrtograptus lundgreni* event in the black shales of eastern Mid-Sardinia, Italy. *Lethaia* 39, 111–127.
- Quigg, A., Finkel, Z.V., Irwin, A.J., Rosenthal, Y., Ho, T.-Y., Reinfelder, J.R., Schofield, O., Morel, F.M.M., Falkowski, P.G., 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425, 291–294.



- Quigg, A., Irwin, A.J., Finkel, Z.V., 2011. Evolutionary imprint of endosymbiosis of elemental stoichiometry: Testing inheritance hypotheses. *Proceedings of the Royal Society Series B* 278, 526–534.
- Porębska, E., Kozłowska-Dawidziuk, Masiak, M., 2004. The lundgreni event in the Silurian of the East European Platform, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213, 271–294.
- Prokoph, A., Shields, G.A., Veizer, J., 2008. Compilation and time-series analysis of marine carbonate  $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ ,  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{34}\text{S}$  databases through Earth history. *Earth Science Reviews* 87, 113–133.
- Rasul, S.M., 1974. The Lower Palaeozoic acritarchs *Priscogalea* and *Cymatiogalea*. *Palaeontology* 17(1), 41–63.
- Raup, D.M., 1978. Cohort analysis of generic survivorship. *Paleobiology* 4, 1–15.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>
- Ricci, J., Quidelleur, X., Pavlov, V., Orlov, S., Shatsillo, A., Courtillot, V., 2013. New  $^{40}\text{Ar}/^{39}\text{Ar}$  and K–Ar ages of the Viluy traps (Eastern Siberia): Further evidence for a relationship with the Frasnian–Famennian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 384, 531–540.
- Riebesell, U., Schulz, K.G., Bellerby, R.G., Botros, M., Fritsche, P., Meyerhofer, M., Neill, C., Nondal, G., Oschlies, A., Wohlers, J., Zollner, E., 2007. Enhanced biological carbon consumption in a high CO<sub>2</sub> ocean. *Nature* 450(7169), 545–548.
- Riegel, W., 2008. The Late Palaeozoic phytoplankton blackout – arefact or evidence of global change? *Review of Palaeobotany and Palynology* 148, 73–90.
- Ries, J.B., 2010. Review: geological and experimental evidence for secular variation in seawater Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification. *Biogeosciences* 7, 2795–2894.
- Rokitta, S.D., Rost, B., 2012. Effects of CO<sub>2</sub> and their modulation by light in the life-cycle stages of the coccolithophore *Emiliana huxleyi*. *Limnology and Oceanography* 57(2), 607–618.
- Ronov, A.B., 1994. Phanerozoic transgressions and regressions on the continents: a quantitative approach based on areas flooded by the sea and areas of marine and continental deposition. *American Journal of Science* 294, 777–801.
- Rosenweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Roux, A., 1985. Introduction à l'Étude des Algues Fossiles Paléozoïques (de la bactérie à la Tectonique des Plaques). *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 9, 253–699.
- Roux, A., 1986. Microflores Algaires Paléozoïques (Tendances Évolutives, Répartitions) et Tectonique globale. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 10, 555–563.
- Royer, D.L., 2014. Atmospheric CO<sub>2</sub> and O<sub>2</sub> during the Phanerozoic: Tools, patterns, and impacts. In: Holland, H., Turekian, K. (eds), *Treatise on Geochemistry*, Vol. 6, 2nd Edition, Elsevier, Amsterdam, pp. 251–261.

- Royer, D.L., Berner, R.A., Montañez, I.P., Tabor, N.J., Beerling, D.J., 2004. CO<sub>2</sub> as a primary driver of Phanerozoic climate. *GSA Today* 14(3), 4–10.
- Saltzman, M.R., Ripperdan, R.L., Brasier, M.D., Lohmann, K.C., Robison, R.A., Chang, W.T., Peng, S.C., Ergaliev, G.Kh., Runnegar, B., 2000. Global carbon isotope excursion (SPICE) during the Late Cambrian: Relation to trilobite extinctions, organic-matter burial and sea level. *Palaeogeography, Palaeoclimatology, Palaeoecology* 162, 211–223.
- Saltzman, M.R., 2001. Silurian  $\delta^{13}\text{C}$  stratigraphy: A view from North America. *Geology* 29, 671–674.
- Samtleben, C., Munnecke, A., Bickert, T., Pätzold, J., 1996. The Silurian of Gotland (Sweden): Facies interpretation based on stable isotopes in brachiopod shells. *Geologische Rundschau* 85, 278–292.
- Samtleben C., Munnecke, A., Bickert, T., 2000. Development of facies and C/O-isotopes in transects through the Ludlow of Gotland: Evidence for global and local influences on a shallow-marine environment. *Facies* 43, 1–38.
- Sandberg, P.A., 1983. An oscillating trend in Phanerozoic non-skeletal carbonate mineralogy. *Nature* 305(5929), 19–22.
- Schwark, L., Emt, P., 2006. Sterane biomarkers as indicators of palaeozoic algal evolution and extinction events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 240, 225–236.
- Scotese, C.R., McKerrow, W.S., 1990: Revised world maps and introduction. In: McKerrow, W.S., Scotese, C.R. (eds), *Palaeozoic Palaeogeography and Biogeography*, Memoir Geological Society of London 12, 1–21.
- Saltzman, M.R., Ripperdan, R.L., Brasier, M.D., Lohmann, K.C., Robison, R.A., Chang, W.T., Peng, S., Ergaliev, E.K., Runnegar, B., 2000. A global carbon isotope excursion (SPICE) during the Late Cambrian: relation to trilobite extinctions, organic-matter burial and sea level. *Palaeogeography, Palaeoclimatology, Palaeoecology* 162, 211–223.
- Sepkoski, J.J., Jr., 1975. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology* 1, 343–355.
- Sepkoski, J.J. Jr., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Sepkoski, J.J., 1995. The Ordovician radiations: diversification and extinctions shown by global genus-level taxonomic data. In: Cooper, J.D., Droser, M.L., Finney, S.C. (eds), *Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System*. Pacific Section, Society for Sedimentary Geology (SEPM), California, pp. 393–396.
- Sepkoski, J.J., Jr., 1997. Biodiversity: Past, Present, and Future. *Journal of Paleontology* 71(4). 533–539.
- Sepkoski, J.J. Jr., Miller, A.I., 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In: Valentine, J.W. (ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton University Press and Pacific Division, American Association for the Advancement of Science, Princeton, NJ, pp. 393–396.
- Servais, T., 1996. Some considerations on acritarch classification. *Review of Palaeobotany and Palynology* 93, 9–22.



- Servais, T., Eiserhardt, K.H., 1995. A discussion and proposals concerning the lower Paleozoic “galeate” acritarch plexus. *Palynology* 19, 191–210.
- Servais, T. & Harper, D.A.T., 2018. The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration. *Lethaia* 51(2), 151–164.
- Servais, T., Paris, F., 2000. Ordovician palynology: balance and future prospects at the beginning of the third millenium. *Review of Palaeobotany and Palynology* 113, 1–14.
- Servais, T., Li, J., Stricanne, L., Vecoli, M., Wicander, R., 2004. Acritarchs. In: Webby, B., Paris, F., Percival, I. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 348–360.
- Servais, T., Nützel, A., Mullins, G., 2006. Was there a phytoplankton blackout in the late Paleozoic? *Palynology* 30, 228.
- Servais, T., Lehnert, O., Li, J., Mullins, G.L., Munnecke, A., Nützel, A., Vecoli, M., 2008. The Ordovician Biodiversification: revolution in the oceanic trophic chain. *Lethaia* 41, 99–109.
- Servais, T., Danelian, T., Harper, D.A.T., Munnecke, A., 2014. Possible oceanic circulation patterns, surface water currents and upwelling zones in the Early Palaeozoic. *GFF* 136(1), 229–233.
- Servais, T., Martin, R.E., Nützel, A., 2016a. The impact of the ‘terrestrialisation process’ in the late Palaeozoic: pCO<sub>2</sub>, pO<sub>2</sub>, and the ‘phytoplankton blackout’. *Review of Palaeobotany and Palynology* 224, 26–37.
- Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R., Munnecke, A., Nowak, H., Nützel, A., Vancembroucke, T.R.A., Williams, M., Rasmussen, C.M.Ø., 2016b. The onset of the ‘Ordovician Plankton Revolution’ in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 458, 12–28.
- Shergold, J.H., Brasier, M.D., 1986. Proterozoic and Cambrian phosphorites — Special studies: Biochronology of Proterozoic and Cambrian Phosphorites. In: Cook, P.J., Shergold, J.H. (eds), *Proterozoic and Cambrian phosphorites*. Cambridge, United Kingdom, Cambridge University Press, 295–396.
- Shergold, J.H., Cooper, R.A., 2004. The Cambrian Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (eds), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, UK., pp. 147–164.
- Signor, P.W., Vermeij, G., 1994. The plankton and the benthos: origins and early history of an evolving relationship. *Paleobiology* 20, 297–319.
- Smolarek, J., Trela, W., Bond, D., Marynowski, L., 2017. Lower Wenlock black shales in the northern Holy Cross Mountains, Poland: sedimentary and geochemical controls on the Ireviken Event in a deep marine setting. *Geological Magazine* 154, 246–264.
- Sommer, U., 1985. Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. *Limnology and Oceanography* 30(2), 335–346.
- Stillman, C.V., 1984. Ordovician volcanicity. In: Bruton, D.L. (ed.), *Aspects of the Ordovician System*. *Palaeontological Contributions from the University of Oslo* 295, University of Oslo, Oslo, pp. 183–194.

Stover L.E., Brinkhuis H., Damassa S.P., Verteuil, L., De Helby, R.J., Monteil, E., Patridge, A.D., Powell A.J., Riding, J.B., Smelror, M., Williams, G.L., 1996. Chapter 19. Mesozoic–Tertiary dinoflagellates, acritarchs and prasinophytes. In: Jansonius, J., McGregor, D.G. (eds): *Palynology: Principles and Application*, 641–750. American Association of Stratigraphic Palynologists Foundation. Publishers Press, Salt Lake City, USA.

Stricanne, L., Munnecke, A., Pross, J., 2006. Assessing mechanisms of environmental change: Palynological signals across the late Ludlow (Silurian) positive isotope excursion ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ) on Gotland, Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology* 230, 1–31.

Strother, P.K., 1996. Acritarchs. In: Jansonius, J., McGregor, D.C., (eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Salt Lake City, pp. 81–106.

Strother, P.K., 2008. A speculative review of factors controlling the evolution of phytoplankton during Paleozoic time. *Revue de micropaléontologie* 51, 9–21.

Strother, P.K., Servais, T., Vecoli, M., 2010. The effects of terrestrialization on marine ecosystems: the fall of  $\text{CO}_2$ . In: Vecoli, M., Clément, G., Meyer-Berthaud, B. (eds), *Geological Society: London, Special Publications* 339, pp. 37–48.

Summons, R.E., Thomas, J., Maxwell, J.R., Boreham, C.J., 1992. Secular and environmental constraints on the occurrence of dinosterane in sediments. *Geochimica et Cosmochimica Acta* 56(6), 2437–2444.

Talent, J.A., Mawson, R., Andrew, A.S., Hamilton, P.J., Whitford, D.J., 1993. Middle Palaeozoic events: Faunal and isotopic data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 104, 139–152.

Talyzina N.M., Moczyłowska, M., 2000. Morphological and ultrastructural studies of some acritarchs from the Lower Cambrian Lukati Formation, Estonia. *Review of Palaeobotany and Palynology* 112, 1–21.

Talyzina, N.M., Moldowan, J.M., Johannisson, A., Fago, F.J., 2000. Affinities of Early Cambrian acritarchs studied by using microscopy, fluorescence flow cytometry and biomarkers. *Review of Palaeobotany and Palynology* 108, 37–53.

Tappan, H., 1980. *The Palaeobiology of Plant Protists*. Freeman, San Francisco. 1028 pp.

Tappan, H., Loeblich Jr., A.R., 1972. Fluctuating rates of protistan evolution, diversification and extinction, in: 24th International Geological Congress, Section 7. pp. 205–213.

Tappan, H., Loeblich Jr., A.R., 1973. Evolution of the oceanic plankton. *Earth Science Reviews* 9, 207–240.

Taylor, A.G., Lasaga, A.C., 1999. The role of basalt weathering in the Sr isotope budget of the oceans. *Chemical Geology* 161, 59–88.

Tedard, M., Monnet, C., Noble, P.J., Danelian, T., 2017. Biodiversity patterns of Silurian Radiolaria. *Earth Science Reviews* 173, 77–83.

Tortell, P.D., Morel, F.M.M., 2002. Sources of inorganic carbon for phytoplankton in the eastern subtropical and equatorial Pacific Ocean. *Limnology and Oceanography* 47(4), 1012–1022.

- Underwood, C.J., 1993. The position of graptolites within Lower Palaeozoic planktic ecosystems. *Lethaia* 26, 189–202.
- Valentine, J.W., Moores, E.M., 1970. Plate-tectonic regulation of faunal diversity and sea level: A model. *Nature* 228, 657–659.
- Valentine, J.W., Moores, E.M., 1972. Global tectonics and the fossil record. *Journal of Geology* 80, 167–184.
- Vallina, S.M., Follows, M.J., Dutkiewicz, S., Montoya, J.M., Cermeno, P., Loreau, M., 2014. Global relationship between phytoplankton diversity and productivity in the ocean. *Nature Communications* 4299, 1–10.
- Van de Schootbrugge, B., Bailey, T., Rosenthal, Y., Katz, M.E., Wright, J.D., Feist-Burkhardt, S., Miller, K.G., Falkowski, P.G., 2005. Early Jurassic climate change and the radiation of organic-walled phytoplankton in the Tethys Ocean. *Paleobiology* 31, 73–97.
- Van Valen, L., 1979. Taxonomic survivorship curves. *Evolutionary Theory* 4, 129–142.
- Vavrdová, M., 1974. Geographical differentiation of Ordovician acritarch assemblages in Europe. *Review of Palaeobotany and Palynology* 18, 171 – 175.
- Vecoli, M., 2000. Palaeoenvironmental interpretation of microphytoplankton diversity trends in the Cambrian–Ordovician of the northern Sahara Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology* 160, 329–346.
- Vecoli, M., 2008. Fossil microphytoplankton dynamics across the Ordovician–Silurian boundary. *Review of Palaeobotany and Palynology* 148, 91–107.
- Vecoli, M., Le Hérisse, A. 2004. Biostratigraphy, taxonomic diversity and patterns of morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton from the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes. *Earth-Science Reviews* 67, 267–311.
- Vidal, G., Knoll, A.H., 1982. Radiations and extinctions of plankton in the late Proterozoic and early Cambrian. *Nature* 297, 57–60.
- Vidal, G., Moczyłowska-Vidal, M., 1997. Biodiversity, speciation, and extinction trends of Proterozoic and Cambrian phytoplankton. *Paleobiology* 23, 230–246.
- Volkman, J.K., 2003. Sterols in microorganisms. *Applied Microbiology and Biotechnology* 60, 495–506.
- Wall, D., 1962. Evidence from recent plankton regarding the biological affinities of *Tasmanites Newton 1875* and *Leiospheridia Eisenack 1958*. *Geological Magazine* 99, 353–362.
- Wang, K., 1992. Glassy microspherules (microtektites) from an Upper Devonian limestone. *Science* 256, 1547–1550.
- Whalen & Briggs, 2018. The Palaeozoic colonization of the water column and the rise of global nekton. *Proceedings of the Royal Society B* 285, 1–9.

Wilde, P., Berry, W.B.N., 1984. Destabilization of the oceanic density structure and its significance to marine 'extinction' events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 48, 143–162.

Wilson, S.T., Hawco, N.J., Armbrust, V., Barone, B., Björkman, K.M., Boysen, A.K., Burgos, M., Burrell, T.J., Casey, J.R., DeLong, E.F., Dugenne, M., Dutkiewicz, S., Dyrman, S.T., Ferrón, S., Follows, M.J., Foreman, R.K., Funkey, C.P., Harke, M.J., Henke, B.A., Hill, C.N., Hynes, A.M., Ingalls, A.E., Jahn, O., Kelly, R.L., Knapp, A.N., Letelier, R.M., Ribalet, F., Shimabukuro, E.M., Tabata, R.K.S., Turk-Kubo, K.A., White, A.E., Zehr, J.P., John, S., Karl, D.M., 2019. Kīlauea lava fuels phytoplankton bloom in the North Pacific Ocean. *Science* 365(6457), 1040–1044.

Yan, K., Servais, T., Li, J., Wu, R., Tang, P., 2011. Biodiversity patterns of Early–Middle Ordovician marine microphytoplankton in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299, 318–334.

Young, S.A., Kleinberg, A., Owens, J.D., 2019. Geochemical evidence for expansion of marine euxinia during an early Silurian (Llandovery–Wenlock boundary) mass extinction. *Earth and Planetary Science Letters* 513, 187–196.

Zaffos, A., Finnegan, S., Peters, S.E., 2017. Plate tectonic regulation of global marine animal diversity. *PNAS* 114(22), 5653–5658.

Zhuravlev, A.Y., 2001. Biotic diversity and structure during the Neoproterozoic–Ordovician transition. In: Zhuravlev, A.Y., Riding, R. (eds), *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, pp. 173–199.

Zhuravlev, A.Y. & Wood, R.A., 1996. Anoxia as the cause of the mid-Early Cambrian (Botoman) extinction event. *Geology* 24(4), 311–314.

Fig. 1. Classes of taxa within and among stratigraphic intervals (time bins). After Foote (2000).

Fig. 2. Global species diversity of phytoplankton throughout the Palaeozoic. A, sampled-in-bin diversity (SIB) per stage and per Myr; range-through diversity including singletons (RTinS) and excluding singletons (RTextS). B, normalised diversity (after Sepkowski, 1975) per stage (NORM); boundary-crossing diversity (BCR). C, diversity based on shareholder quorum subsampling at 40 % coverage (SQS40) and 70 % coverage (SQS70); diversity based on Posson-based resampling (TriPs).

Fig. 3. Taxonomic changes of global Palaeozoic phytoplankton species diversity per stage. A, origination and extinction rates. B, turnover rates.

Fig. 4. Poly-cohort analyses. A, cohort survivorship. B, cohort pre-nascence.

Fig. 5. Number of references per stage.

Fig. 6. Correlation of taxonomic (species per stage) and monographic (number of references per stage) diversity.

Fig. 7. Comparison of phytoplankton diversity with indices of continental fragmentation after Zaffos et al. (2007).

Fig. 8. Comparison of phytoplankton diversity with sea-level changes (after Haq and Shutter, 2008), and amount of continental area covered by sea (after Ronov, 1994).

Fig. 9. Comparison of phytoplankton diversity with changes in  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios (after Prokoph et al., 2008), and terrestrial sediment influx (after Flögel et al., 2000).

Fig. 10. Comparison of phytoplankton diversity with changes in atmospheric  $\text{CO}_2$  concentrations (after Berner & Kothavala, 2001; Royer et al., 2004).

Figure 1

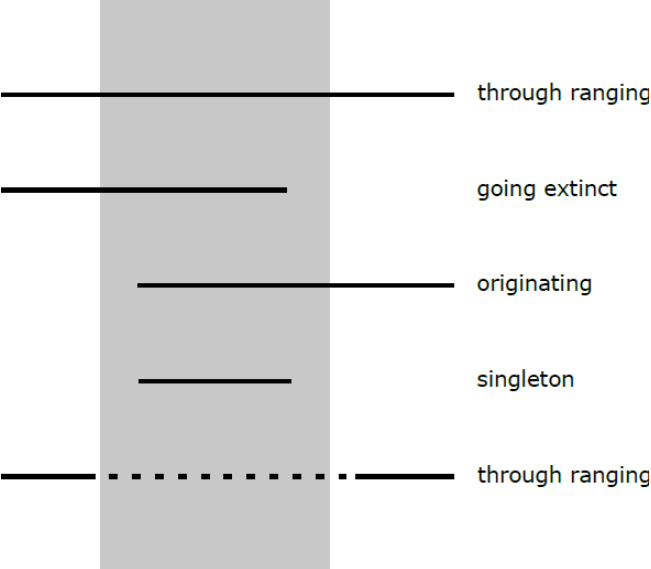


Figure 2

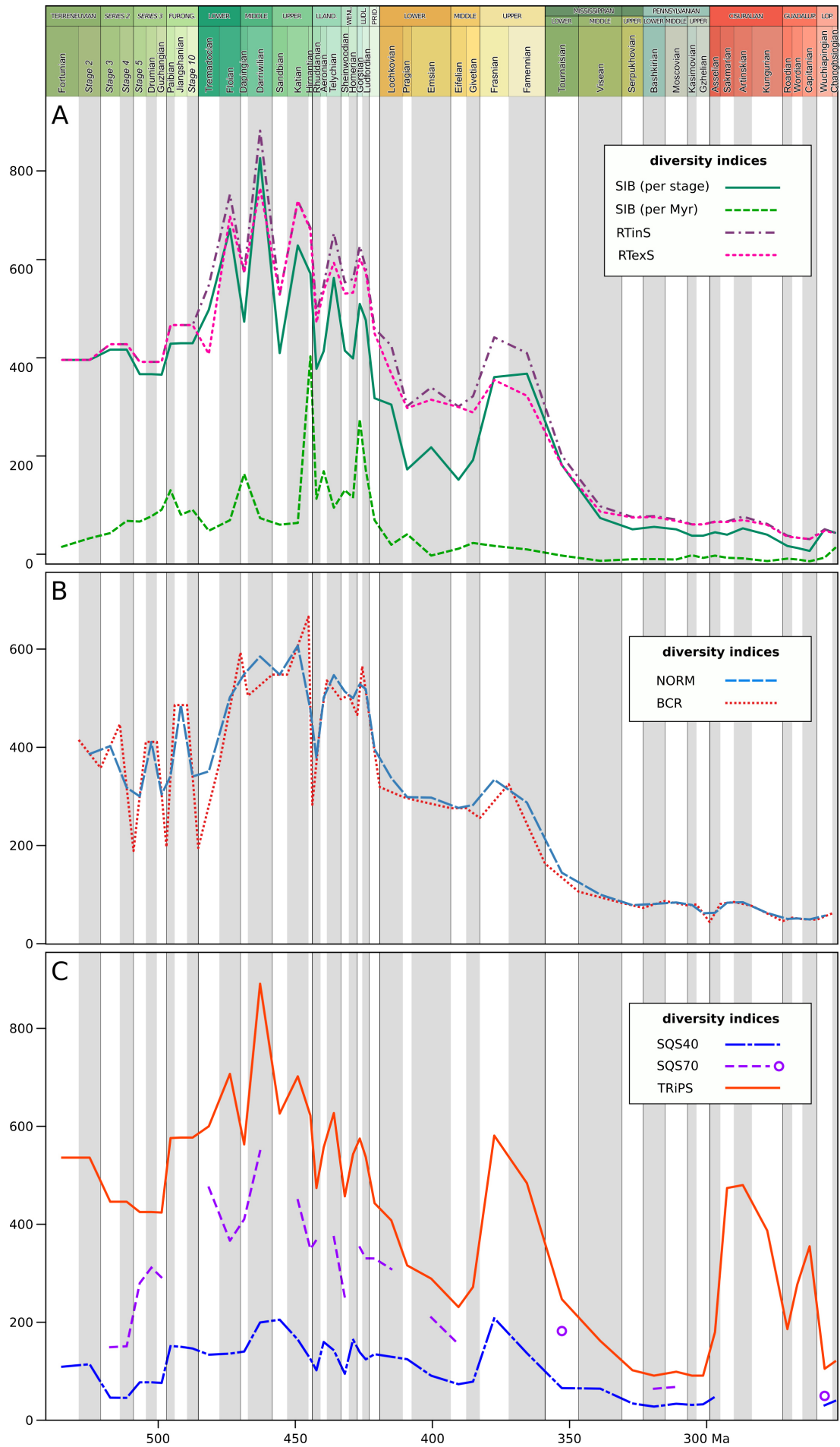


Figure 3

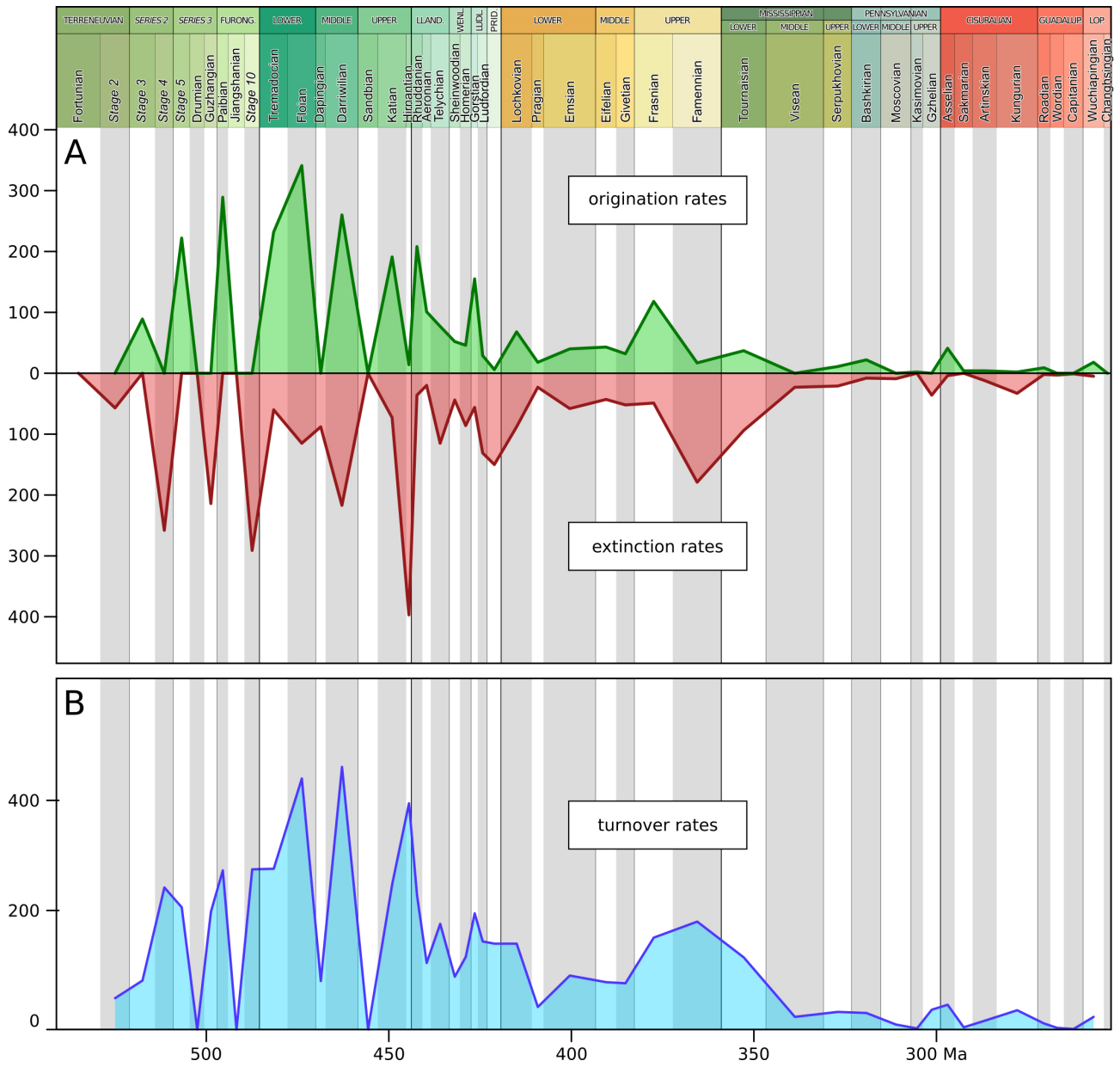




Figure 4

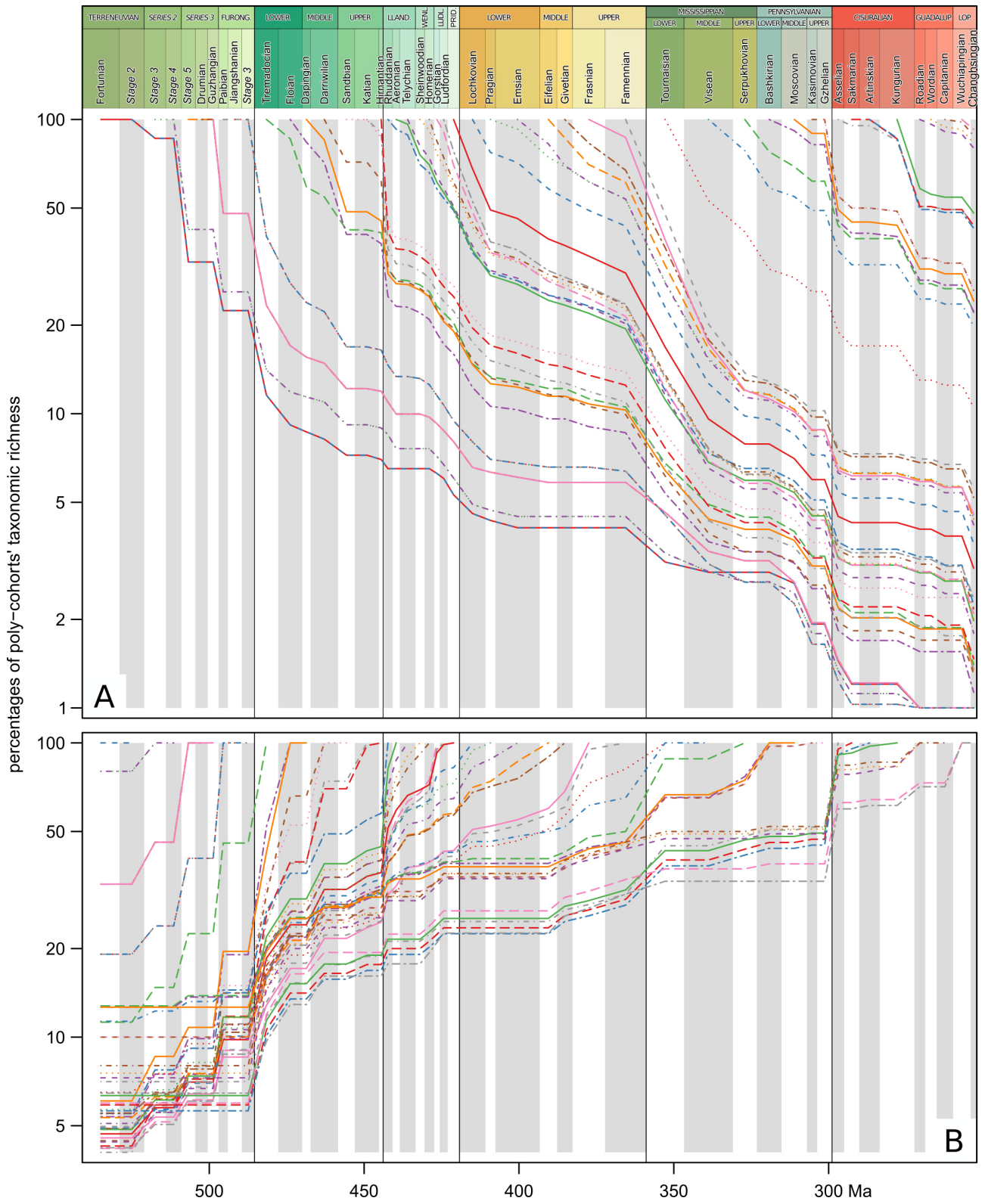


Figure 5

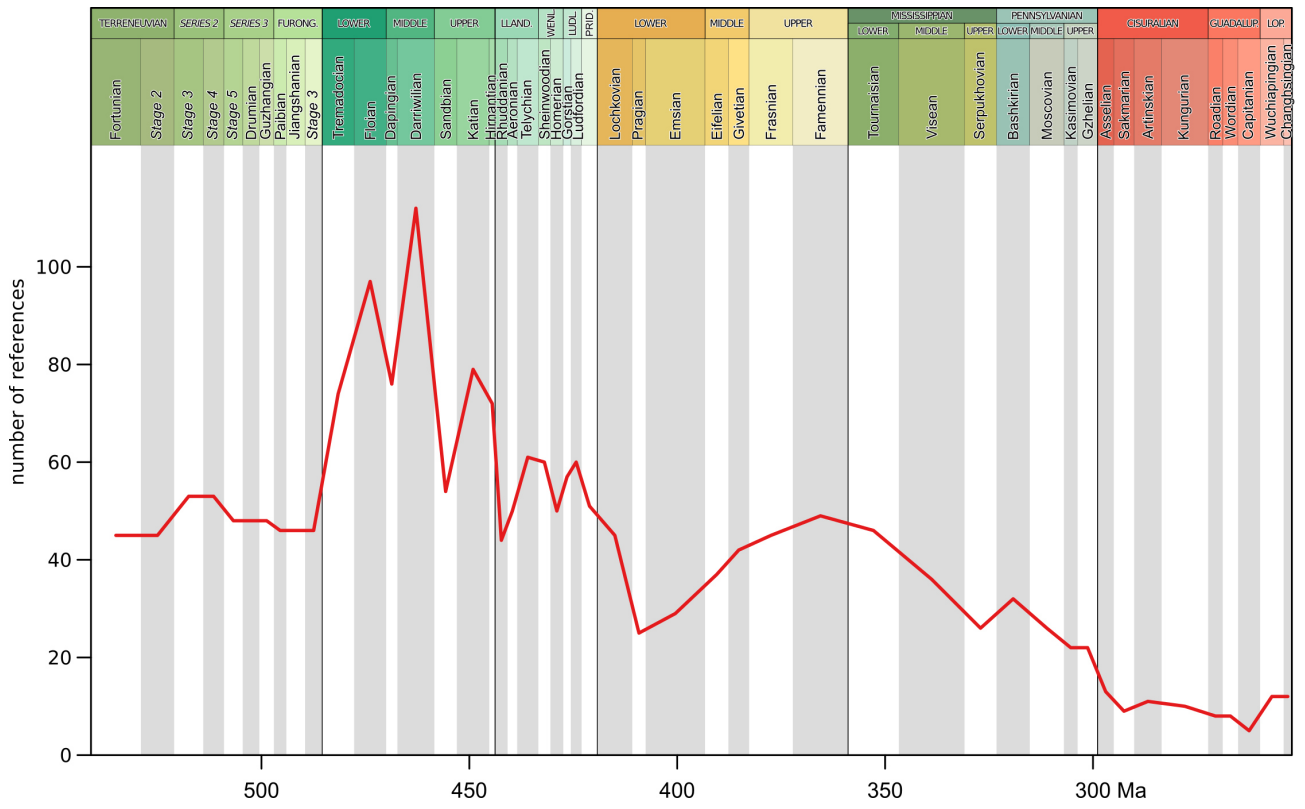


Figure 6

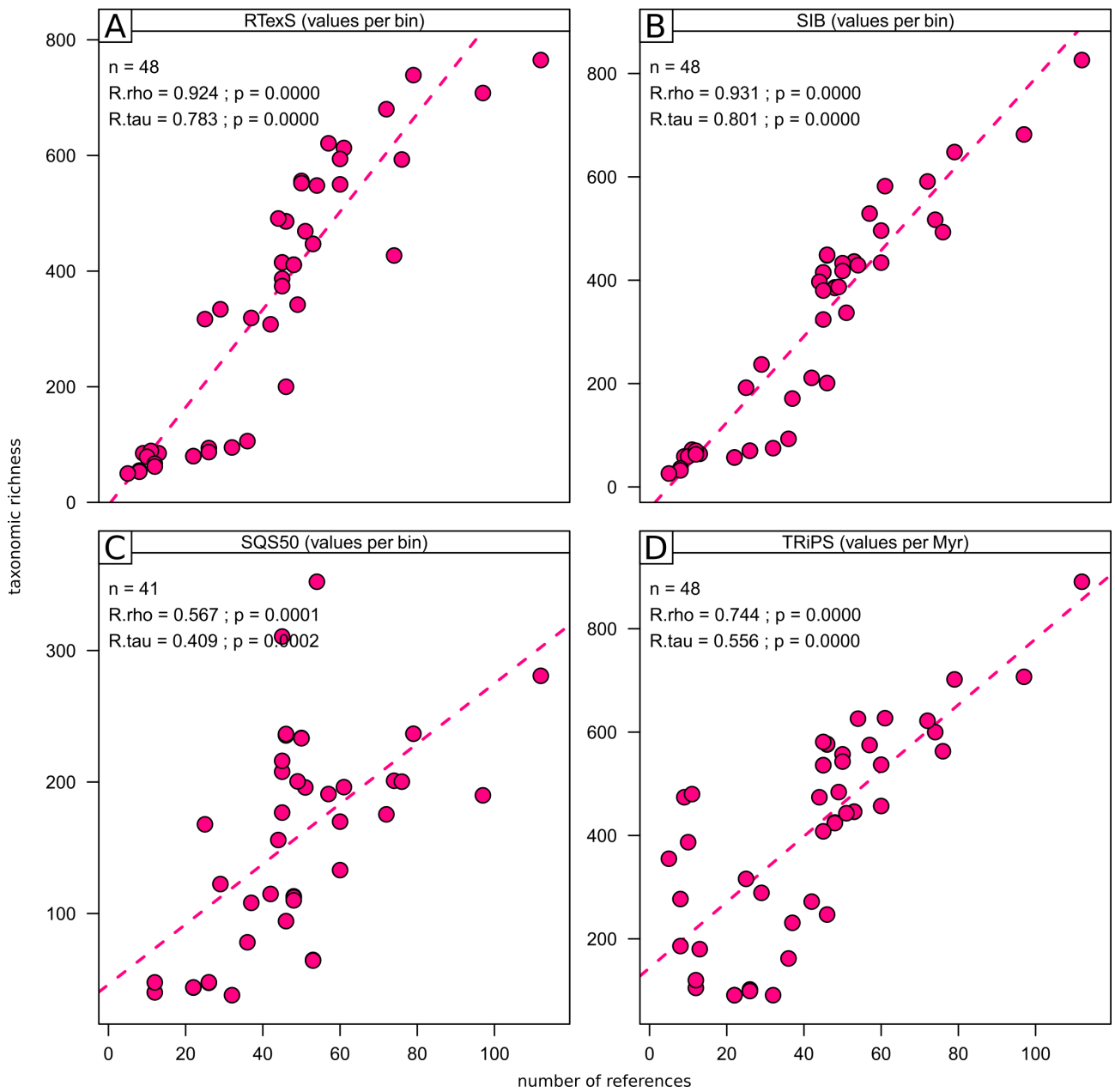


Figure 7

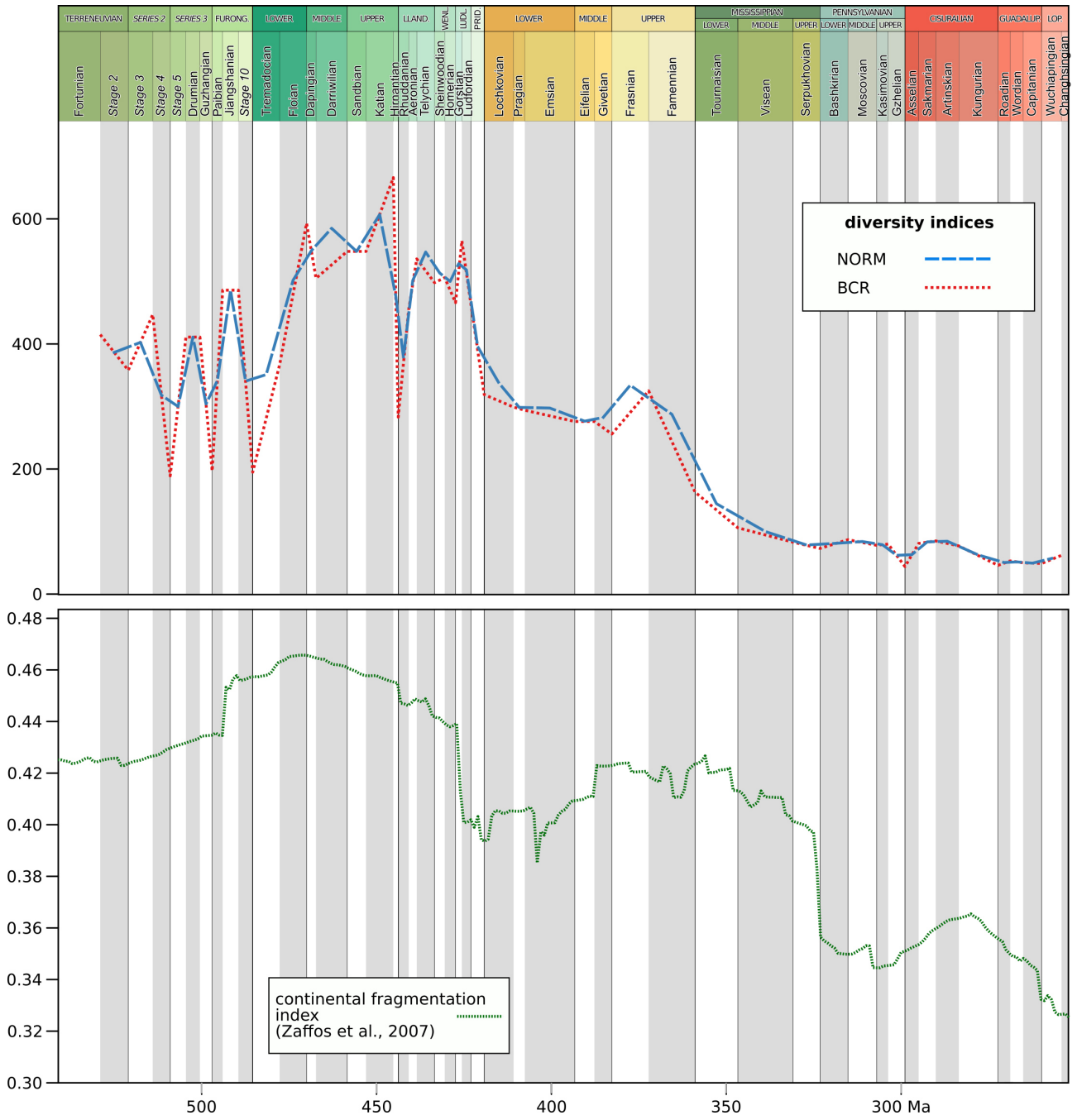


Figure 8

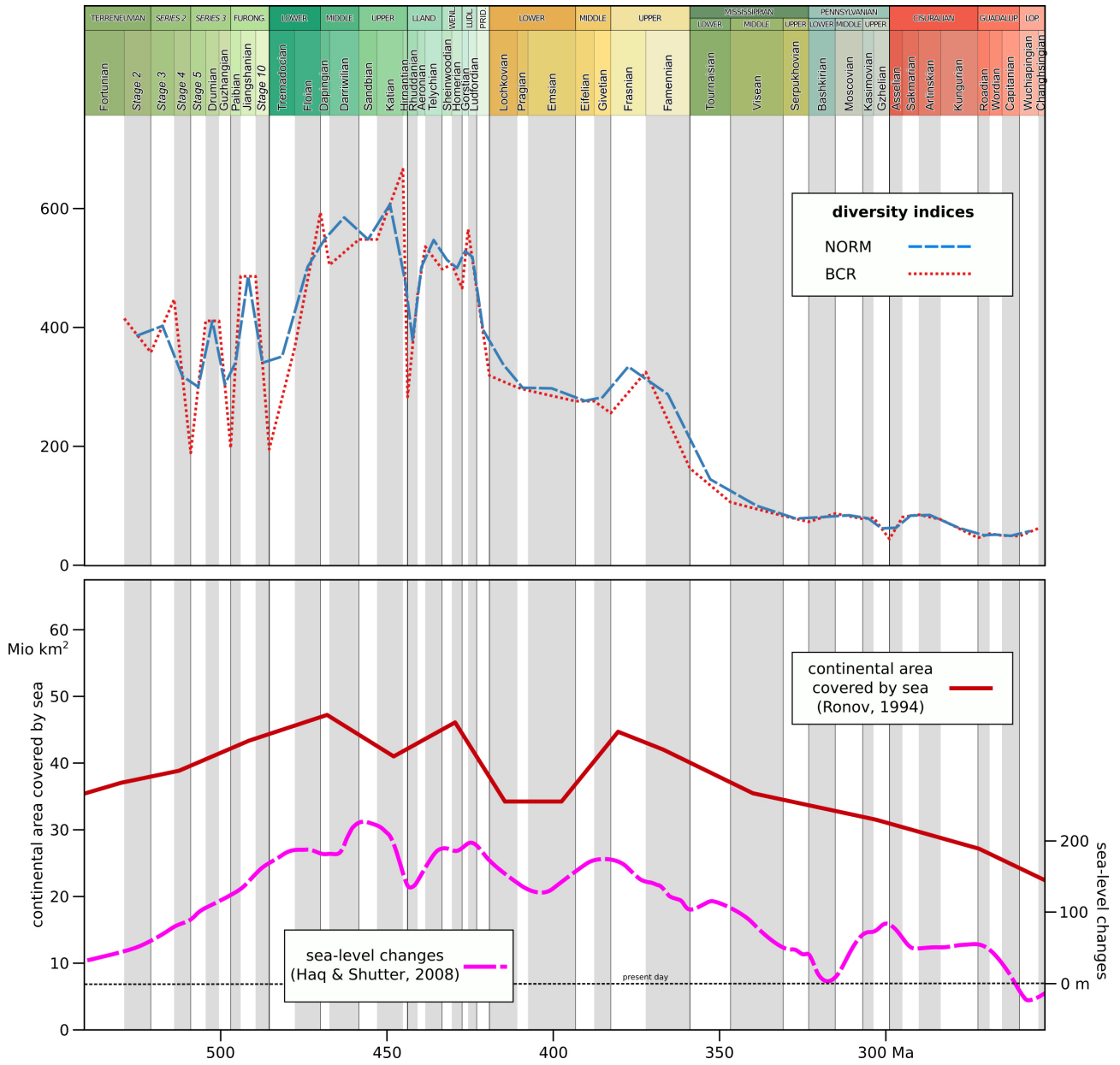


Figure 9

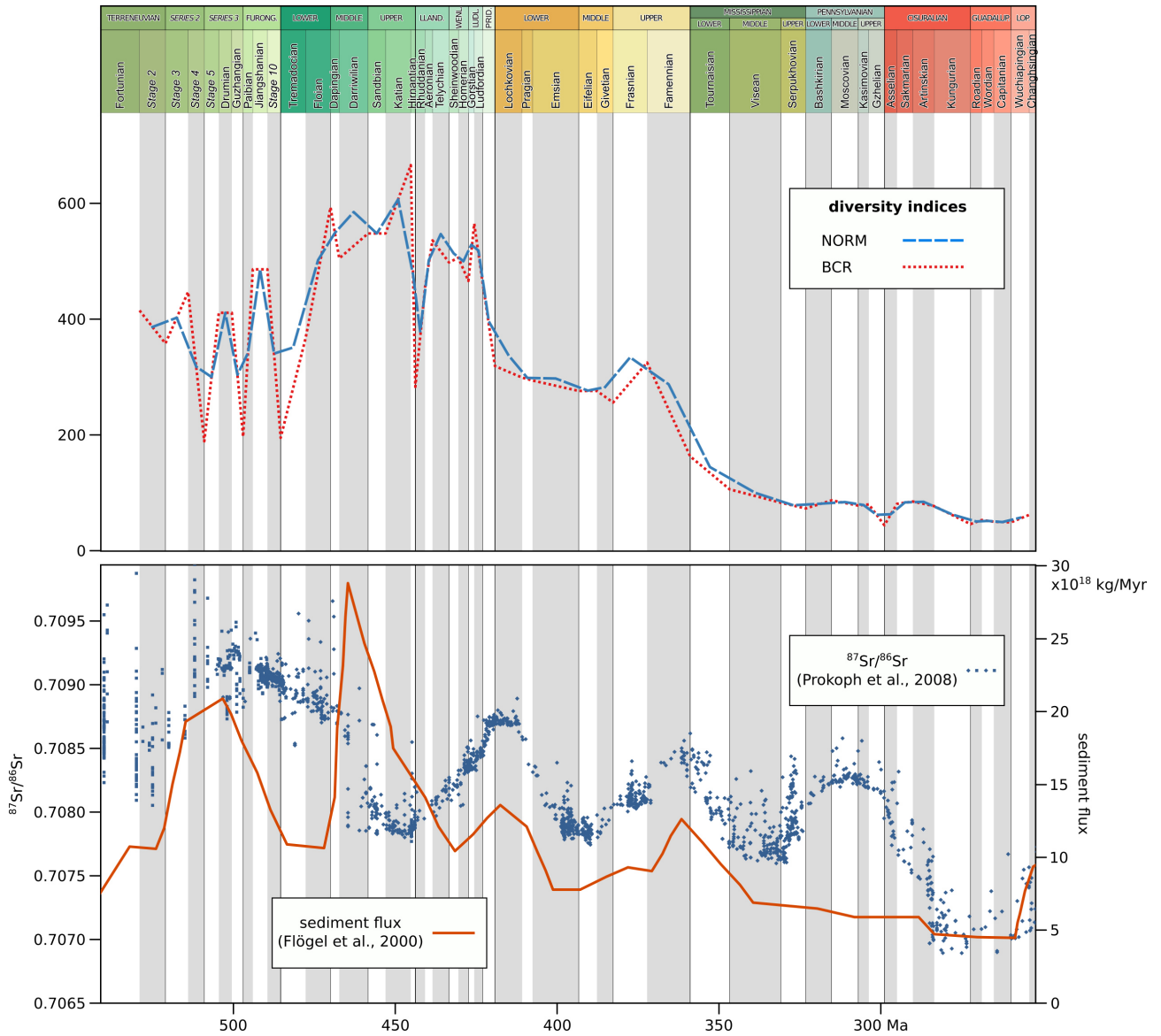
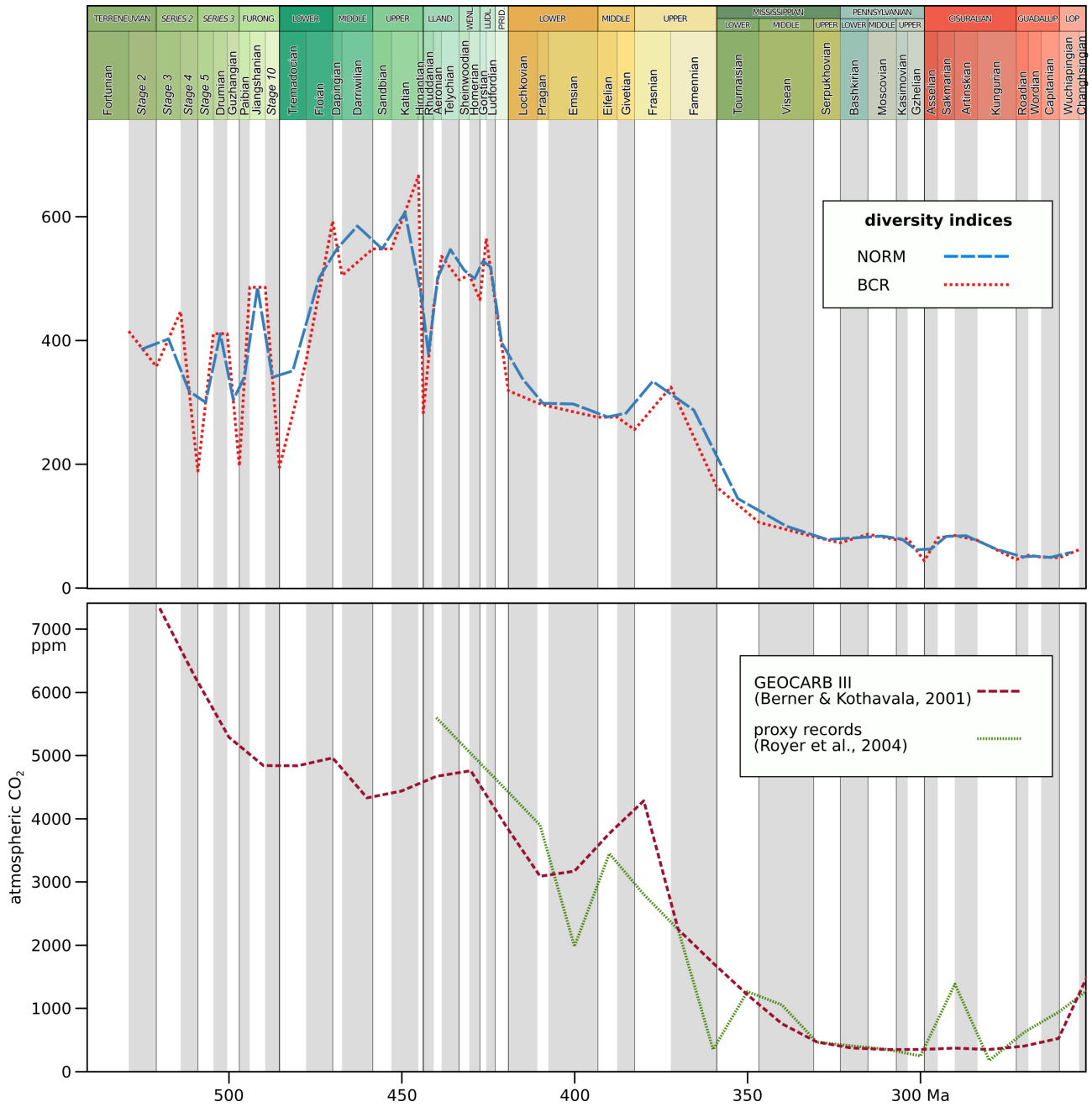


Figure 10



## **Article II**

### **Revision of the Cambro-Ordovician acritarch genus *Vulcanisphaera* Deunff, 1961**

David Kroeck, Mathilde Blanchon, Axelle Zacaï, Navid Navidi-Izad, Houcine Benachour, Claude Monnet, Elena Raevskaya, Zbigniew Szcapanik, Thomas Servais

submitted to *Review of Palaeobotany and Palynology*.





## Manuscript Details

<b>Manuscript number</b>	PALBO_2019_125_R2
<b>Title</b>	Revision of the Cambro-Ordovician acritarch genus <i>Vulcanisphaera</i> Deunff, 1961
<b>Article type</b>	Research paper

### Abstract

After its first description in Cambrian–Ordovician boundary strata from Gondwana, the acritarch genus *Vulcanisphaera* Deunff, 1961 has been found subsequently on most other palaeocontinents, with in total 32 species assigned to this genus. A comprehensive revision of the published literature indicates that the genus contains only three species that are easily differentiable: (1) *V. africana* Deunff, 1961; (2) *V. mougnoana* Martin, 1973; and (3) *V. simplex* Jardiné et al., 1974. The other species are either synonymous with these three or must be excluded from the genus. The generic and specific diagnoses of *Vulcanisphaera* are emended herein. The new classification scheme is tested and validated by using quantitative multivariate analyses based on morphometric studies on abundant material from England, Algeria and Iran. The species show large morphological variability, and transitional forms between *V. africana* and *V. mougnoana* are observed. The stratigraphic ranges of the species have been determined. *V. mougnoana* occurs from the Miaolingian to the Early Ordovician, *V. africana* is found with certainty from the Furongian to the Floian and *V. simplex* is recorded in the latest Furongian and throughout the Tremadocian. The genus *Vulcanisphaera* shows a cosmopolitan palaeogeographic distribution with most occurrences recorded in higher palaeolatitudes.

<b>Keywords</b>	microphytoplankton; early Palaeozoic; biostratigraphy; palaeogeography; taxonomy; morphometry
<b>Manuscript category</b>	Palaeozoic And Mesozoic Palynological Biostratigraphy And Taxonomy
<b>Corresponding Author</b>	David Kroeck
<b>Corresponding Author's Institution</b>	Lille University
<b>Order of Authors</b>	David Kroeck, Mathilde Blanchon, Axelle Zacaï, Navid Navidi-Izad, Houcine Benachour, Claude Monnet, Elena Raevskaya, Zbigniew Szczepanik, Thomas Servais
<b>Suggested reviewers</b>	Claudia Rubinstein, JUN LI, Kui Yan, Stewart Molyneux

## Submission Files Included in this PDF

### File Name [File Type]

Kroeck\_et\_al\_revision\_letter\_and\_correction\_list\_2020.docx [Response to Reviewers]  
Manuscript\_Kroeck\_et\_al\_revised\_with\_changelog\_2020.docx [Revised Manuscript with Changes Marked]  
Highlight\_Kroeck\_et\_al\_Vulcanisphaera.docx [Highlights]  
Abstract\_revised\_2020.docx [Abstract]  
Manuscript\_Kroeck\_et\_al\_revised\_2020.docx [Manuscript File]  
Fig\_3\_LDA.pdf [Figure]  
Stratigraphical\_distribution\_final.pdf [Figure]  
Palaeogeographical\_distribution.pdf [Figure]  
Conflict\_of\_Interest.doc [Conflict of Interest]

## Submission Files Not Included in this PDF

### File Name [File Type]

Complete\_Geographical map Project2.png [Figure]

Vulcanisphaera\_Plate2.png [Figure]

Figure3.png [Figure]

Vulcanisphaera\_Plate1\_revised.png [Figure]

Figure1.png [Figure]

Figure2.png [Figure]

To view all the submission files, including those not included in the PDF, click on the manuscript title on your EVISE Homepage, then click 'Download zip file'.

## Research Data Related to this Submission

**Data set** <https://data.mendeley.com/datasets/zdzhhbwb53/draft?a=6d1d67c9-f5a3-4a3e-bb43-77e36e2ee13a>

Data for: Revision of the Cambro-Ordovician acritarch genus *Vulcanisphaera* Deunff, 1961

Morphometric measurements of specimens of *Vulcanisphaera* Deunff, 1961 from Cambrian–Ordovician strata of three localities: Shineton Shales in England, NI-2 Borehole in the Hassi R'mel region in Algeria, Ghelli area in the eastern Alborz, Iran.

- Only three of 32 described species of *Vulcanisphaera* Deunff, 1961 can be maintained
- *Vulcanisphaera* is recorded from the Miaolingian to the Lower Ordovician
- *Vulcanisphaera* is palaeogeographically widespread in rather higher latitudes

## Abstract

After its first description in Cambrian–Ordovician boundary strata from Gondwana, the acritarch genus *Vulcanisphaera* Deunff, 1961 has been found subsequently on most other palaeocontinents, with in total 32 species assigned to this genus. A comprehensive revision of the published literature indicates that the genus contains only three species that are easily differentiable: (1) *V. africana* Deunff, 1961; (2) *V. mougnoana* Martin, 1973; and (3) *V. simplex* Jardiné et al., 1974. The other species are either synonymous with these three or must be excluded from the genus. The generic and specific diagnoses of *Vulcanisphaera* are emended herein. The new classification scheme is tested and validated by using quantitative multivariate analyses based on morphometric studies on abundant material from England, Algeria and Iran. The species show large morphological variability, and transitional forms between *V. africana* and *V. mougnoana* are observed. The stratigraphic ranges of the species have been determined. *V. mougnoana* occurs from the Miaolingian to the Early Ordovician, *V. africana* is found with certainty from the Furongian to the Floian and *V. simplex* is recorded in the latest Furongian and throughout the Tremadocian. The genus *Vulcanisphaera* shows a cosmopolitan palaeogeographic distribution with most occurrences recorded in higher palaeolatitudes.

1 **Revision of the Cambro-Ordovician acritarch genus *Vulcanisphaera* Deunff,**  
2 **1961**

3  
4 **David M. Kroeck<sup>1, \*</sup>, Mathilde Blanchon<sup>1</sup>, Axelle Zacaï<sup>1</sup>, Navid Navidi-Izad<sup>1, 2</sup>, Houcine B.**  
5 **Benachour<sup>1, 3, 4</sup>, Claude Monnet<sup>1</sup>, Elena Raevskaya<sup>5</sup>, Zbigniew Szczepanik<sup>6</sup>, Thomas Servais<sup>1</sup>**

6  
7 <sup>1</sup> *Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France*

8 <sup>2</sup> *Department of Geology, Faculty of Earth Sciences, Kharazmi University, 49 Mofatteh Avenue, 15614 Tehran, Iran*

9 <sup>3</sup> *Laboratoire de Recherche n° 25 «PRHPM-LECT», Département des Sciences de la Terre et de l'Univers, Université*  
10 *de Tlemcen, Tlemcen 13000, Algeria*

11 <sup>4</sup> *Département Hydraulique, Faculté de Génie civil et d'architecture, Université de Chlef, Ouled Fares Chlef 02180,*  
12 *Algeria*

13 <sup>5</sup> *AO “Geologorazvedka”, Fayansovaya str., 20, block 2, Saint-Petersburg, 192019, Russia*

14 <sup>6</sup> *Holy Cross Branch of the Polish Geological Institute – National Research Institut, Agoda 21, PL-25-953 Kielce,*  
15 *Poland*

16  
17 **Abstract**

18  
19 After its first description in Cambrian–Ordovician boundary strata from Gondwana, the acritarch  
20 genus *Vulcanisphaera* Deunff, 1961 has been found subsequently on most other palaeocontinents,  
21 with in total 32 species assigned to this genus. A comprehensive revision of the published literature  
22 indicates that the genus contains only three species that are easily differentiable: (1) *V. africana*  
23 Deunff, 1961; (2) *V. mougnoana* Martin, 1973; and (3) *V. simplex* Jardiné et al., 1974. The other  
24 species are either synonymous with these three or must be excluded from the genus. The generic  
25 and specific diagnoses of *Vulcanisphaera* are emended herein. The new classification scheme is  
26 tested and validated by using quantitative multivariate analyses based on morphometric studies on  
27 abundant material from England, Algeria and Iran. The species show large morphological  
28 variability, and transitional forms between *V. africana* and *V. mougnoana* are observed. The

29 stratigraphic ranges of the species have been determined. *V. mougnoana* occurs from the  
30 Miaolingian to the Early Ordovician, *V. africana* is found with certainty from the Furongian to the  
31 Floian and *V. simplex* is recorded in the latest Furongian and throughout the Tremadocian. The  
32 genus *Vulcanisphaera* shows a cosmopolitan palaeogeographic distribution with most occurrences  
33 recorded in higher palaeolatitudes.

34

35 *Keywords:* microphytoplankton; early Palaeozoic; biostratigraphy; palaeogeography; taxonomy;  
36 morphometry

37

38 \* Corresponding author. *E-mail address:* [davidmarius.kroeck.etu@univ-lille.fr](mailto:davidmarius.kroeck.etu@univ-lille.fr)

39

## 40 **1 Introduction**

41 The acritarchs represent a major group of palynomorphs in the Palaeozoic. These organic-walled  
42 microfossils, abundant in marine sediments, are widely used in international biostratigraphic  
43 correlation, as well as in palaeobiogeographic and palaeoenvironmental studies. The taxonomic  
44 classification of acritarchs represents a major problem for the study of this group, as it is purely  
45 phenetic, therefore not based on biological affinities but relying only on morphological aspects.  
46 Until the late 1980s, most studies focused on biostratigraphic usability (Brocke et al., 1995), and  
47 were based on purely descriptive approaches. Also, most of these studies were based on a restricted  
48 number of specimens, and did not take into account palaeobiological and palaeoecological aspects,  
49 or the presence of high intraspecific morphological variabilities. This led to the establishment of a  
50 very large number of genera and species. This is a general problem in palaeontological taxonomic  
51 investigations that holds for acritarchs: when only isolated specimens, which have been found in a  
52 certain locality and stratigraphic interval, are available to examine, the full morphological range of a  
53 taxon remains largely unknown (Fatka and Brocke, 2008). During the last decades, multiple  
54 quantitative analyses of biometric parameters based on large sample sizes of the same taxon  
55 highlighted high levels of morphological variability in acritarch species, and recognised the

56 importance of acritarchs for palaeoecological reconstructions (Le Hérisse, 1989; Servais, 1993;  
57 Servais et al., 1996, 2004; Stricanne and Servais, 2002; Wang et al., 2017). Also, these studies  
58 allow the unveiling of morphological transitions among taxa that were originally considered to be  
59 separate species or even genera (e.g., Brocke et al., 1997). Therefore, it is likely that many  
60 described taxa are synonymous and represent different (eco-)phenotypes of the same taxon.  
61 Accordingly, a critical systematic revision of acritarch taxa is necessary.

62 Many acritarch taxa have already been investigated in detail, for taxonomic revision as well as  
63 biostratigraphic and palaeogeographic analyses (e.g., Albani et al., 2007; Fatka et al., 1997; Fatka  
64 and Brocke, 1999; Li et al., 2014; Moczyłowska and Stockfors, 2004; Navidi-Izad et al., 2020;  
65 Servais, 1997; Servais et al., 2007, 2008; Vanguetaine, 2002; Vecoli et al., 1999; Wang et al.,  
66 2015; Yan et al., 2010, 2017). The present study represents a continuation of these works on the  
67 description and revision of Palaeozoic microphytoplankton with the aim to enhance the taxonomic  
68 knowledge of acritarchs and their biostratigraphic correlation before conducting palaeobiodiversity  
69 and macroevolutionary studies. It also aims to demonstrate the importance of palaeoecological  
70 aspects involved in the mechanisms influencing acritarch morphology. In this account we revise the  
71 Cambrian–Ordovician genus *Vulcanisphaera* Deunff, 1961 and document its morphological  
72 variability, based on a re-evaluation of the morphological parameters and a multivariate  
73 morphometric analysis. This abundant and widespread genus contains more than thirty species.  
74 However, the boundaries between the different species are not always clear, and intraspecific  
75 variability has rarely been taken into consideration in the original descriptions. Thus, it is important  
76 to revise the genus *Vulcanisphaera*, especially to improve its biostratigraphic, palaeobiogeographic,  
77 and palaeoecological value.

78 The revision of the data available in previously published papers, together with the  
79 reinvestigation of abundant material of *Vulcanisphaera* from the type-localities in Algeria and  
80 England, as well as assemblages from Iran, allows a new classification and a revision of the  
81 biostratigraphy and palaeobiogeography of the genus.



82

## 83 **2 Material and methods**

84

85 Palynological analysis was carried out on material from three localities (Figs. 1, 2), the  
86 Tremadocian Shingleton Shales in the Shropshire, England; a Cambrian–Ordovician boundary  
87 sequence from the NI-2 well in the Hassi-R'mel area, Algeria, and the Tremadocian of the Ghelli  
88 area in Iran. The samples were processed using standard preparation techniques, which include the  
89 use of HF and HCl and micrometric mesh filter extraction. All material used here is  
90 stratigraphically distributed between the Upper Cambrian and the Lower Ordovician.

91

### 92 *2.1 Algerian Sahara*

93

94 The Algerian material comes from a subsurface stratigraphic sequence of the Sahara Platform,  
95 derived from the NI-2 borehole in the Hassi-R'Mel area, north-central Algeria. The Cambrian–  
96 Ordovician study interval comprises siliciclastic sediments: mainly alternating coarse to fine-  
97 grained sandstones, siltstones, and shales, with occasional microconglomeratic and ferruginous-  
98 oolitic horizons. The lithostratigraphic column including the positions of sampling levels is  
99 provided in Figure 2. The abundant and well preserved organic-walled microfossils, as well as the  
100 macrofossil content (graptolites, brachiopods) in localised horizons throughout the section, allowed  
101 detailed taxonomic studies and precise stratigraphic correlation (e.g. Legrand, 1974; Vecoli et al.,  
102 1995; Vecoli, 1999; Vecoli and Le Hérissé, 2004; Spina, 2015).

103 Legrand (1985) published an attempt at a stratigraphic synthesis for the lower Palaeozoic of  
104 Algeria. Deunff and Massa (1975) and Massa (1988) established a detailed stratigraphic framework  
105 of the Ordovician of the Sahara platform for Libya, and Oulebsir (1992) and Oulebsir and Paris  
106 (1993) for Algeria. The sedimentary succession in the NI-2 borehole has been extensively studied  
107 (Oulebsir, 1992; Oulebsir and Paris, 1993, 1995; Vecoli et al., 1995; Mélou et al., 1999; Paris et al.,

108 2000). The stratigraphic nomenclature of the Cambrian–Ordovician of the Sahara Platform was  
109 created by oil companies for hydrocarbon exploration in this region (Vecoli, 1999). The sequence  
110 is, in stratigraphic order (Legrand, 1974; Vecoli, 1999): (1) Grès de Hassi Miribel Formation,  
111 comprising quartzites with rare intercalations of siltstones in the lowermost part, followed by  
112 quartzite-siltstone alternations containing lingulids in the upper part; (2) Grès de Bordj Nili  
113 Formation, with an alternation of quartzitic sandstones and black shales, overlain by interbedded  
114 shales, fine-grained chloritic sandstones with debris of lingulids and brachiopods; (3) Argiles d'El  
115 Gassi Formation, comprising a homogeneous interbedding of black and grey-green shales and  
116 siltstones. Based on graptolites, the El Gassi Shales have been assigned to a Tremadocian age  
117 (Blain, 1963; Legrand, 1974). The El Gassi Formation is unconformably overlain by intercalations  
118 of micaceous argillites and arenites of the Azzel Shale Mb of the Hassi Touareg Fm., which is  
119 Darriwilian in age.

120       Reviews of the literature covering palynological studies in the study area have been provided by  
121 Vecoli (1999) and Paris et al. (2000). Palynological investigations of the NI-2 succession have been  
122 carried out by Vecoli et al. (1995), Vecoli (1996, 1999, 2000), Vecoli and Playford (1997), Paris et  
123 al. (2000), Stricanne and Servais (2002), Servais et al. (2004), Vecoli and Le Hérisse (2004) and  
124 Spina (2015). Vecoli et al. (1995), Vecoli (1996) and Vecoli and Playford (1997) established a  
125 palynozonation for the NI2. Vecoli (2000) interpreted observed changes in the microphytoplankton  
126 assemblages in a palaeoenvironmental context. According to him, shallow water conditions  
127 prevailed in the Late Cambrian in the study area, followed by a general trend to open marine,  
128 offshore conditions in the early Tremadocian, which is interrupted by a regressive event at the  
129 Cambrian–Ordovician transition. As stated by Vecoli (2000), the palynomorph assemblages in the  
130 NI-2 borehole point to a proximal, shallow marine environment in the Middle Ordovician and  
131 restricted marine conditions in the latest Ordovician.

132       For the present study, 25 samples were investigated in detail, ranging from 3,095.3 m and  
133 3,017.25 m in depth, and ten revealed *Vulcanisphaera* in sufficient numbers of specimens for

134 further analysis. The investigated palynological slides are stored in the palaeontological collections  
135 of the University of Lille (UMR CNRS 8198 Evo-Eco-Paleo).

136

## 137 2.2 *Shinerton Shales, England*

138

139 The English material is derived from the Tremadocian Shinerton Shales, which crop out south  
140 and south-west of the Wrekin, in the county Shropshire of the Welsh Borderland in England. The  
141 slides used in this study are from the type locality and were also used for the stratigraphic dating  
142 determining the Tremadocian age of the Shinerton Shales, prepared by Rasul (1971, unpublished).  
143 Rasul (1976) used the same samples for emending the genus *Vulcanisphaera*.

144 Summaries of the regional geology of southern Shropshire are presented by Watts (1925),  
145 Stubblefield and Bulman (1927), Whittard (1952), and Cocks (1989). The Tremadocian sediments  
146 of the Shinerton Shale outcrops and of other localities in this region occur in half-grabens, which are  
147 interpreted as trans-tensional basins formed in response of the opening of the Rheic Ocean  
148 (Brenchley et al., 2006). The formational name Shinerton Shales has been applied to all lower  
149 Tremadocian rocks in the area (Fortey and Rushton, 2000). The lithology is characterised by  
150 relatively homogenous mudstones and shales, with more arenaceous beds close to the top.  
151 Stubblefield and Bulman (1927) established a stratigraphic subdivision for the Shinerton Shales. The  
152 sedimentary succession, comprising more than 1000 m of sediments, is composed as follows, from  
153 base to top (Stubblefield and Bulman, 1927; cf. Rasul, 1976, 1979; Fortey and Rushton, 2000; Fig.  
154 2): (D) “Zone of *Dictyonema flabelliforme*”: shales, with occasional intercalations of thin hard  
155 calcareous shales, irregular purplish or greenish patches, and cone-in-cone nodules, containing  
156 *Rhabdinopora (Dictyonema) flabelliformis*, marking the base of the Ordovician (129 m); (T)  
157 “Transition Beds”: a relatively thin transitional zone comprising shales of unknown composition  
158 (18 m); (C) “Zone of *Clonograptus tenellus*”: the important “*Clonograptus tenellus*”  
159 (= *Adelograptus hunnebergensis*) graptolite Zone, almost indistinguishable from the blue-green

160 shales of the *D. flabelliforme* Beds (341 m); (B) “Brachiopod Beds”: more nodular shales with  
161 abundant cone-in-cone concretions and frequent occurrence of large brachiopods (221 m) (S) “Zone  
162 of *Shumardia pusilla*”: the “*Shumardia pusilla*” (*S. salopiensis*) trilobite Zone, comprising well-  
163 bedded, evenly coloured blue shales with sporadically occurring cone-in-cone nodules (219 m); (A)  
164 “Arenaceous Beds”: a final arenite layer, with thick layers of hard, fine-grained, blue-grey  
165 sandstone, shifting from sandy and micaceous shales to a shale approaching the classic Shineton  
166 type (79 m).

167 A first palynological analysis in the Shineton Shales was carried out by Downie (1958), who  
168 identified a rich assemblage of organic-walled microphytoplankton. Rasul and Downie (1974) then  
169 published a study on the stratigraphic distribution of acritarchs in the Tremadocian sequence of the  
170 Shineton Shales. Rasul (1976) reinvestigated material from this locality, with a focus on  
171 *Vulcanisphaera*, leading to an emended diagnosis of the genus, and the description of four new  
172 species. A vertical distribution of different process morphologies of *Vulcanisphaera* species  
173 throughout the succession is presented therein (Rasul, 1976, text-figure 1).

174 Five samples from the Shineton Shales locality were studied, derived from the *Dictyonema*  
175 *flabelliforme*, the *Clonograptus tenellus* and the Brachiopod Beds. The investigated slides are part  
176 of the original material of Rasul (1971, 1976, 1979) that is stored in the palynological collections of  
177 the University of Sheffield, UK.

178

### 179 2.3 Eastern Alborz Mountains, Iran

180

181 The Iranian samples are from a Tremadocian to Floian succession of the Ghelli area in the  
182 western part of Kuh-e-Saluk, located between Bojnourd in the NE and Jajarm in the SW. The study  
183 locality is part of the Kopet-Dagh region in the northeastern Alborz Range. The Alborz Mountains  
184 stretch parallel to the southern margin of the Caspian Sea from Azerbaijan to the Aladagh  
185 Mountains in the northern parts of Khorasan Province.

186 The lower Palaeozoic in the Alborz Mountains is traditionally subdivided into (in ascending  
187 stratigraphic order), the Middle to Upper Cambrian Mila Formation, the Lower Ordovician  
188 Lashkarak Formation, the Middle to Upper Ordovician Ghelli Formation, and the Silurian Niur  
189 Formation (Ghavidel-Syooki, 2000; 2001; Ghavidel-Syooki and Vecoli, 2007; Bayet-Goll and Neto  
190 de Carvalho, 2015). However, the lithostratigraphic subdivision of this area is currently under  
191 revision (Ghobadi Pour et al., 2011; Geyer et al., 2014; Jahangir et al., 2015). Therefore, an  
192 assignment of the Tremadocian material to any existing formal lithostratigraphic unit is avoided  
193 herein.

194 Based on conodont data, Jahangir et al. (2015) supposed a cold water depositional environment  
195 during the Furongian, indicating that it was already located in temperate latitudes in the Late  
196 Cambrian. A study on the chitinozoan faunas of the north-eastern Alborz Range (Ghavidel-Syooki  
197 and Winchester-Seeto, 2002) shows a close affinity to Gondwanan faunas in the Late Ordovician.  
198 Ghavidel-Syooki and Vecoli (2007) describe a position in intermediate latitudes for northeastern  
199 Iran during the latest Ordovician and Silurian.

200 In the present study 16 rock samples from a Tremadocian to Floian succession of the Ghelli  
201 locality have been investigated in detail. The investigated palynological slides as well as the rock  
202 samples and residues from this location are stored in the palaeontological collections of the Faculty  
203 of Earth Science of the Kharazmi University in Tehran, Iran.

## 204

## 205

## 206 *2.4 Morphological criteria relevant in the diagnosis of Vulcanisphaera*

### 207

### 208 *2.4.1 Parameters used for differentiation of the genus Vulcanisphaera and its species in literature*

209 The review of the literature allows determining the diagnostical characteristics and the  
210 importance of the morphological parameters used by the different authors with regard to the  
211 diagnoses of the species and the genus, permitting a validation of each species of the genus  
212 *Vulcanisphaera*. The following characteristics appear to be essential in determination within the

213 genus: diameter of the vesicle, shape of the processes and their bifurcations, shape of the base,  
214 number of processes per base, and presence or absence of polygonal fields. Other parameters, such  
215 as geometry and width of the polygonal fields and thickness of the wall, can be regarded negligible  
216 or superfluous. On this basis, the affinities of all described species to the genus were assessed in  
217 order to verify or reject their attribution, with reclassifications of discarded species being proposed,  
218 and to synonymise species names. Diagnoses for the genus and the remaining species were  
219 emended to fully comprise the morphological variability.

220

#### 221 *2.4.2 Morphometric measurements*

222 Six parameters have been defined based on the essential morphological characteristics of  
223 *Vulcanisphaera* according to the literature. As quantitative parameters, the vesicle diameter, the  
224 process length, and the width of the process base have been measured. The process length is not  
225 always easy to evaluate, since processes might be broken, and their length can vary on the same  
226 specimen. Therefore, the length of the longest and most representative process of each specimen  
227 was chosen as a reliable measure, done from the base to the tip. Additionally, two semi-quantitative  
228 parameters were determined: the shape of the processes (Fig. 3), and the number of processes per  
229 process base, averaged in case of varying numbers on the same specimen. Nine different process  
230 shapes were defined in order to create a categorisation to which each specimen can be assigned.  
231 Finally, one qualitative parameter, i.e. the presence or absence of polygonal fields on the vesicle  
232 surface, has been recorded.

233 Each palynological slide was observed using a ZEISS Axio Imager A2 optical microscope  
234 equipped with a ZEISS Planapochromat 63x objective and a ZEISS AxioCam ERc5s microscope  
235 camera. All biometric measurements and morphological definitions were carried out on a total of  
236 757 specimens (354 from Algeria, 262 specimens from England, and 141 from Iran) with the  
237 software ZEISS AxioVision LE. The measurements were done with an accuracy of 0.01 µm.

238 A linear discriminant analysis (LDA) based on the morphometric measurements was carried out  
239 using the software PAST (Hammer et al., 2001; Hammer and Harper, 2006).

240

241

### 242 **3 The genus *Vulcanisphaera***

243

#### 244 *3.1 Historical overview*

245

246 *Vulcanisphaera* was first erected by Deunff (1961) in Cambrian–Ordovician boundary strata of  
247 the Algerian Sahara, with the description of its type species *V. africana* Deunff (1961) and a second  
248 species, *V. nebulosa* Deunff (1961). According to this initial diagnosis, the genus was characterised  
249 by a spheroidal shell with more or less pronounced conical irregularities, which possess tufts of  
250 several (2-5) processes on top. The original description included colour as a differential  
251 characteristic. Although not stated in this description, the name is derived from the volcano-like  
252 shape of the process base with the processes on top. After the initial erection of the genus, it was  
253 subsequently found in the Middle Cambrian to Tremadocian successions of all palaeocontinents.

254 Eisenack et al. (1973) reassigned *Baltisphaeridium tuberatum* (Downie, 1958) Martin, 1973 to  
255 *Vulcanisphaera*, creating the new combination *V. tuberata*, as the species shows “broad outward  
256 swellings” from which the processes arise. A later transfer to *Goniosphaeridium* by Welsch (1986a)  
257 was rejected by Sarjeant and Stancliffe (1994) who reassigned it back to *Vulcanisphaera*.

258 In the same work, Eisenack et al. (1973) proposed the new combination *V. lophophora*,  
259 originally described as *Baltisphaeridium lophophorum* Eisenack 1959.

260 Based on investigations of material from the Lower Ordovician of the Montagne Noire in  
261 France, Martin (1973) described the new species *Vulcanisphaera gorgo*, and questionably assigned  
262 another new species, *V.?* *mougnoana* (as *V.?* *mougnoanum*), to this genus. The doubt in the latter  
263 assignment arose due to the appearance of single processes (along with tufts of two or three),  
264 whereas the original genus diagnosis states the number of processes per base as 2 to 5.

265 Jardiné et al. (1974) described the new species *V. capillata* and *V. simplex* in material from the  
266 Algerian Sahara. Although a distribution of the processes in polygonal fields is visible in the  
267 holotype of *V. capillata*, this characteristic is not mentioned in the description. Polygonal fields in  
268 this species are first described by Martin in Martin and Dean, 1981 in a study on Tremadocian  
269 material from Random Island, eastern Newfoundland, Canada. The description of *V. capillata* once  
270 again states a number of one to three processes, and therefore does not meet the original diagnosis  
271 of the genus.

272 The genus was further discussed and an emendation was proposed by Rasul (1976) in a study of  
273 material from the Tremadocian of the Shineton Shales in the Wrekin District, formerly belonging to  
274 Shropshire, England, including the description of four new species. This emendation includes forms  
275 with variable processes and variable vesicle shapes, and excludes references to colour, as this  
276 represents mostly a result of geological processes. However, the number of processes per base is  
277 still stated as two to five, although single processes are visible in several pictured specimens of the  
278 newly described *V. britannica* (Rasul, 1976: pl. 1; figs. 2, 15, 16). The study even includes  
279 specimens of the also therein described *V. imparilis* that show no processes on top of the bases at all  
280 (Rasul, 1976: pl. 1; figs. 4, 6, 12). Therefore, according to both, the original diagnosis of Deunff  
281 (1961) and the emendation by Rasul (1976), the species *V. mougnoana* Martin, 1973 and *V.*  
282 *capillata* Jardiné et al., 1974 would still not meet the diagnostic criteria allowing them to be  
283 included within the genus, since they show, along with tufts of two to three, single isolated  
284 processes.

285 Volkova (1990) described a new genus, *Raphesphaera*, with two new species, *R. obsoleta* and  
286 *R. spinulifera*, and re-assigned *V. turbata* to this genus. Another species, *R. striatula*, was described  
287 by Volkova (in Volkova and Sivertseva, 1991). She states a close similarity between *R. striatula*  
288 and *Vulcanisphaera* due to the bundled process distribution, but justifies the creation of a new  
289 genus by the lack of polygonal fields in *Vulcanisphaera*, and the apparently missing conical base of  
290 the processes. Instead, the processes rise from the corners of the polygonal fields. Parsons and



291 Anderson (2000) assigned all species of *Raphesphaera* to *Vulcanisphaera* on the basis of the  
292 observations of Martin (*in* Martin and Dean, 1988), showing that the type species of  
293 *Vulcanisphaera* – *V. africana* – appears to have, also, a polygonal pattern on the vesicle surface,  
294 albeit weakly developed, which is one of the main diagnostic features of the genus *Raphesphaera*  
295 (Martin *in* Martin and Dean, 1988; Parsons and Anderson, 2000). Żylińska et al. (2006) further  
296 reflect upon this problem, questioning the generic assignment of *V. turbata*, *V. spinulifera* and *V.*  
297 *obsoleta*, as their observed specimens do also not always show the conical process bases, and  
298 propose further detailed taxonomic studies (Żylińska et al., 2006). Considering the genus diagnosis  
299 by Deunff (1961) and the emendation by Rasul (1976), the argument of polygonal fields as a  
300 diagnostic feature contradicting an assessment to the genus *Vulcanisphaera* is quite true, as  
301 mentioned above. However, following the observations of Martin (*in* Martin and Dean, 1988), and  
302 the presence of intermediate forms between *V. africana* and *V. turbata*, as will be later referred to in  
303 more detail, we consider that this problem justifies the need for a new emendation of the genus  
304 *Vulcanisphaera*, rather than the creation of a new genus. The same applies for the argument of the  
305 absence of conical processes. Here, it should be noted that conical process bases can, indeed, be  
306 observed in specimens of species of *Vulcanisphaera* bearing a polygonal tabulation, such as the  
307 holotypes of *V. mougnoana* Martin 1973, *V. capillata* Jardiné et al., 1974, and *V. turbata* Martin *in*  
308 Martin and Dean, 1981, although not as pronounced as in other species, especially regarding  
309 isolated processes. However, the first descriptions of several species of *Vulcanisphaera* with  
310 polygonal patterns mention the existence of process bases. The diagnosis of *V. capillata* Jardiné et  
311 al., 1974 refers to “slightly marked or even non-existent conical” bases, while for *V. turbata* “low,  
312 dark protuberances” (Martin *in* Martin and Dean, 1981) are described, and Martin (1973) recognises  
313 broad bases even in isolated processes *V. mougnoana*. Moreover, it can be assumed that the ridges  
314 of the polygonal fields themselves somewhat obscure the process bases.

315 Parsons (1986) described a new species, *V. disjunctospinata*, but it was never validly published.  
316 It also shows a polygonal pattern, but only single isolated processes and no tufts of processes.

317 Volkova (1999b) erected the genus *Undosisphaera*, with the single species, *U. pilosiuscula*.  
318 Like *Vulcanisphaera*, the genus displays conical process bases bearing clusters of numerous  
319 secondary processes. The higher number of processes per base was stated as the reason for the  
320 creation of this new genus, rather than including the species in *Vulcanisphaera*. However, this  
321 criterion is considered insufficient herein. This issue will be further discussed in 3.3.3. *Species*  
322 *retained in this study*.

323 A new species named *V. danilovae* is mentioned in an abstract for a symposium (Paalits and  
324 Heuse, 1998) for Cambrian-Ordovician boundary beds in the Moscow Basin, but has not been  
325 validly published after.

326 The name “*V. tuberculata* (Downie) Eis.” appears in Olaru and Lazar (2005). This is certainly a  
327 mistake, as no such species has been described, and it possibly refers to *V. tuberata* (Downie 1958)  
328 Eisenack et al., 1973. Likewise, the name “*V. spinulosa*”, mentioned in Jachowicz-Zdanowska  
329 (2011), was probably meant to be *V. spinulifera*, as indicated by the shown plates.

330 In regard of the forementioned shortcomings of the existing genus diagnoses by Deunff (1961)  
331 and Rasul (1976), namely the exclusion of single isolated processes and process bases without any  
332 processes, as well as the lack of criteria allowing for a polygonal pattern of the vesicle surface, a  
333 new emendation is evidently needed, and is presented herein.

334

### 335 3.2 Systematic palaeontology

336

337 Group *Incertae Sedis* ACRITARCHA Evitt, 1963

338 Genus *Vulcanisphaera* Deunff, 1961 emend. Rasul, 1976 emend. nov.

339 Junior Synonym: *Raphesphaera* Volkova, 1990, p. 78-80.

340

341 *Type species: Vulcanisphaera africana* Deunff, 1961, by original designation.

342        *Original diagnosis* by Deunff (1961): “Generally pale yellow or light brown body, spheroidal.  
343        The surface is bumpy in an irregular way with minuscule conical irregularities. These little  
344        extensions possess on top a tuft of more or less long, divergent or anastomosed processes in  
345        numbers of 2 to 5. The genus groups a certain number of individuals possessing always the same  
346        crateriform ornamentation, more or less pronounced. The processes differ, however, in length,  
347        thickness, and density.” (new translation)

348        *Emended diagnosis* by Rasul (1976): “Body spherical to ellipsoidal in outline, sometimes  
349        polygonal. Body wall has conical projections (processes) which sometimes are separated into  
350        hollow conical primary processes with flat or crater-like top and secondary processes; the latter  
351        arise from edge of primary process top like tuft of branches, which vary from two to five in number.  
352        These secondary processes may be slender, tapering, or curved, with tips sometimes bifurcated or  
353        ramified into numerous filamentous threads. Processes may be solid, erect or curved, short or long,  
354        body wall smooth to punctate.”

355        *Emended diagnosis* (new emendation): Vesicle spherical to ellipsoidal, sometimes polygonal  
356        outline, seemingly one-layered. Vesicle surface smooth, punctuate or granulate, bearing more or  
357        less pronounced conical projections or primary processes (process bases), with flat to crateriform  
358        top, on which are single isolated processes, or tufts of two to seven secondary processes. Secondary  
359        processes may be slender, tapering, or curved, with tips sometimes bifurcated or ramified into a  
360        number of short to long filamentous branches. Secondary processes solid, erect or curved, more or  
361        less long. Processes (primary and secondary) may be solid or hollow, with communication of  
362        internal cavities of processes and central body when hollow. Vesicle surface may possess a  
363        polygonal pattern due to more or less pronounced low ridges, with the processes located at the  
364        points of their convergence. The ridges may be smooth or ornamented with small needle-like  
365        structures.

366        *Discussion:* The original description of the genus *Vulcanisphaera* by Deunff (1961) from  
367        material of the Algerian Sahara established several diagnostic characteristics important for the

368 determination of the genus, such as a (more or less) spherical vesicle, conical irregularities with  
369 tufts of several more or less long processes, but also includes colour as a parameter for  
370 identification. While investigating new material from England, Rasul (1976) proposed an  
371 emendation of the genus, correcting and completing the diagnosis. The new description excluded  
372 references to colour, and integrated a greater morphological variability of the vesicle and the  
373 processes. Furthermore the structure of the processes was described in greater detail, having a  
374 conical or crater-shaped protuberance, herein called process base, bearing on top a set of more or  
375 less filamentous single or bifurcated processes that vary in length. However, both Deunff (1961)  
376 and Rasul (1976) stated the number of processes per base as varying between 2 and 5, whereas  
377 several of the species described in literature, i.e. *V. mougnoana* Martin, 1973, *V. capillata* Jardiné  
378 et al., 1974 or *V. turbata* Martin in Martin and Dean, 1981, show simple and isolated processes.  
379 Therefore it is necessary to integrate a greater variability of the number of processes per base in the  
380 diagnosis of the genus *Vulcanisphaera*. Furthermore, it is very clear that certain species of the  
381 genus present a very particular arrangement of processes on the surface, seemingly distributed  
382 around polygonal structures, mostly confined to the point of convergence of such structures. Martin  
383 (in Martin and Dean, 1988) points out that even the holotype of the type species *V. africana* Deunff,  
384 1961 shows a polygonal pattern. Neither Deunff (1961) nor Rasul (1976) refer to these polygonal  
385 fields. Several authors regarded this character as an argument of differentiation between several  
386 species, or even genera, e.g. Jardiné et al., 1974; Martin in Martin and Dean, 1981, 1988; Volkova,  
387 1990; and Volkova and Sivertseva, 1991. Therefore, the diagnosis must include the mentioning of  
388 polygonal fields, as it is unavoidable for some species.

389 On specimens bearing both tufts of multiple processes and single processes, the latter ones  
390 appear to be thicker than the processes in tufts. This might lead to the assumption of the forming of  
391 process tufts by splitting of a thicker single process, with the process base being the unsplit base  
392 of this process. This can be observed in all three species that are retained herein.

393        *Comparison of Vulcanisphaera with other taxa*: Several authors point out a close resemblance  
394 between *Vulcanisphaera* Deunff, 1961 and *Cristallinium* Vanguetaine, 1978, indicating a probable  
395 connection between these genera, justifying a proposal of a plexus. In the original diagnosis of  
396 *Cristallinium* (Vanguetaine, 1978) the ridges dividing the vesicle surface into polygonal fields are  
397 described as being densely ornamented with elements of reduced size, such as granules, cones or  
398 spines. Prominent processes and process bases do not appear at the points of convergence of the  
399 ridges. Ornamented ridges are, indeed, also described for species of *Vulcanisphaera*: *V. obsoleta*  
400 (Volkova, 1990) Parsons and Anderson, 2000 (originally described as *Raphesphaera obsoleta*), and  
401 *V. cantabrica* Palacios, 2015, both herein considered as junior synonyms of *V. mougnoana* Martin,  
402 1973 comb. nov., with the ridges bearing needle-like structures.

403        Martin (*in* Martin and Dean, 1988) mentioned a resemblance of *V. lanugo* (also considered a  
404 junior synonym of *V. mougnoana* herein) with *Cristallinium cambriense* (Martin *in* Martin and  
405 Dean, 1981) Martin *in* Martin and Dean, 1988, when specimens of the former are corroded, so the  
406 ornamentation is abraded and the ridges are altered. Likewise, Palacios (2015) recognised  
407 similarities between specimens of *V. cantabrica* (*V. mougnoana* Martin 1973 comb. nov. herein)  
408 with ornamented suture lines and *C. cambriense*, and noted the location of processes on the  
409 intersections of the plates and the uneven distribution of the ornamentation as differential  
410 characteristics.

411        A particularly great similarity to *Vulcanisphaera* is apparent in the species *Cristallinium*  
412 *randomense* (Martin *in* Martin and Dean, 1981) Martin *in* Martin and Dean, 1988. Indeed, the  
413 original diagnosis of this species mentions small conical bases supporting one to three processes  
414 (Martin *in* Martin and Dean, 1981). The emendation of *C. randomense* (Martin *in* Martin and Dean,  
415 1988) even described the species as representing a transition between the genera *Cristallinium* and  
416 *Vulcanisphaera* on the basis of the similar process grouping and ornamentation. Therefore, the only  
417 characteristic allowing a differentiation between the two genera seems to be the different  
418 distribution of processes. Vanguetaine (2002) re-examined the holotype of *C. randomense* (Martin

419 *in* Martin and Dean, 1981) Martin *in* Martin and Dean, 1988 and other figured specimens, and  
420 recognised certain similarities with species of *Vulcanisphaera*. He mentioned several problems with  
421 the diagnosis of the genus *Cristallinium* Vanguetaine, 1978, especially the different preservational  
422 states leading to different species diagnosis (Vanguetaine, 2002). However, no emended diagnosis  
423 was provided therein.

424 Downie (1982) noticed a close resemblance of *Retisphaeridium* Staplin, Jansonius and Pocock,  
425 1965 to *Cristallinium*, and Martin (*in* Martin and Dean, 1988) described difficulties in  
426 distinguishing the two genera when the preservation of the specimen is not good, as  
427 *Retisphaeridium* differs only by having a smooth vesicle with ribs that diminish or disappear on the  
428 equatorial margin. In the same work it is stated that corroded specimens of *Vulcanisphaera lanugo*  
429 (*V. mougnoana* herein) resemble *Retisphaeridium dichamerum* Staplin, Jansonius and Pocock,  
430 1965, *R. howellii* Martin *in* Martin and Dean, 1983 and *Cristallinium cambriense* (Martin *in* Martin  
431 and Dean, 1981) Martin *in* Martin and Dean, 1988.

432 The original diagnosis for the genus *Timofeevia* by Vanguetaine (1978) mentioned specific  
433 kinds of processes that might be simple, bifurcated or branched, are hollow or partially hollow and  
434 that are communicating freely with the central cavity of the vesicle. As in *Vulcanisphaera*  
435 *mougnoana* Martin, 1973 comb. nov. herein, the processes are confined mostly to where the ridges  
436 between the polygonal fields converge. Specimens of *Timofeevia* bearing simple processes or  
437 processes in which the distal ramifications are abraded, closely resemble specimens of *V.*  
438 *mougnoana* that show mainly single processes, but differ in having hollow rather than solid  
439 processes. Hollow processes, which communicate with the central cavity, do appear in  
440 *Vulcanisphaera simplex* Rasul, 1976 comb. nov. herein, but this species shows no polygonal pattern  
441 on the vesicle. *V. mougnoana*, and, to a lesser extent, some specimens of *V. africana* Deunff, 1961  
442 emend. nov. herein, display polygonal fields, and single, isolated processes that can appear in both  
443 species, but the processes are solid and clearly not communicating with the central cavity.  
444 Furthermore, *Timofeevia* bears no process bases, and the processes are exclusively single, isolated.

445 In addition, in samples bearing both, *Timofeevia* and *Vulcanisphaera*, distinct size differences are  
446 observable, with specimens of the former being significantly smaller than those of the latter.

447 Identification problems between *Timofeevia* and *Cristallinium* are also commonly described  
448 (Palacios et al., 2009; Palacios, 2015). It is noteworthy that Parsons (1986) described in her master's  
449 thesis a new species of *Vulcanisphaera* with a polygonal pattern, *V. disjunctospinata* nom. nud.,  
450 which differs from *V. mougnoana* by bearing exclusively simple single isolated processes, and with  
451 a slight serration of the tops of the ridges separating the polygonal fields, similar to but not as  
452 distinct as in *Cristallinium*. Although not representing published results, but well illustrated  
453 (Parsons, 1986, pl. 9; figs. 5-8; pl. 10; figs. 2, 3), this shows that specimens of *Vulcanisphaera* can  
454 be found with features that are considered typical of both genera, *Timofeevia* (exclusively isolated  
455 processes) and *Cristallinium* (dented ridges). Accordingly, the boundaries of these three genera are  
456 rather unclear. Indeed, in the same work, Parsons (1986) discusses the problems of distinguishing  
457 these three genera, and noticed that “*Vulcanisphaera* appears to integrate with the genus  
458 *Cristallinium*” (Parsons, 1986, p. 114). It should be noted that all three genera have a similar  
459 biostratigraphic distribution. Within the extent of this study no emended diagnoses for  
460 *Cristallinium*, *Retisphaeridium* or *Timofeevia* will be provided but, given the forementioned  
461 similarities, an acritarch plexus containing *Vulcanisphaera* and these three genera is proposed.  
462 Future studies are needed to solve the evident taxonomic problems in this plexus.

463

### 464 3.3 The species of *Vulcanisphaera*

465

#### 466 3.3.1 List of species described in literature

467

468 1961 *Vulcanisphaera africana* Deunff

469 1961 *V. nebulosa* Deunff

470 1967 *V. frequens* Górká

- 471 1973 *V. gorgo* Martin
- 472 1973 *V.?* *mouguoana* Martin (as *V. mouguoanum*)
- 473 1973 *V. lophophora* (Eisenack 1959) Eisenack et al.
- 474 1973 *V. tuberata* (Downie 1958) Eisenack et al.
- 475 1974 *V. capillata* Jardiné et al.
- 476 1974 *V. simplex* Jardiné et al.
- 477 1975 *V. flagellum* Martin
- 478 1976 *V. britannica* Rasul
- 479 1976 *V. cirrita* Rasul
- 480 1976 *V. imparilis* Rasul
- 481 1976 *V. pila* Rasul
- 482 1977 *V. ferosa* Fombella
- 483 1978 *V. microspinosa* Tynni nom. nud. (as *V. microspinosum*)
- 484 1981 *V. nova* Pöthe de Baldis
- 485 1981 *V. turbata* Martin (in Martin and Dean)
- 486 1986 *V. disjunctospinata* Parsons nom. nud.
- 487 1986 *V. rigitisa* Yin
- 488 1988 *V. lanugo* by Martin (in Martin and Dean)
- 489 1991 *V. minor* Uutela and Tynni
- 490 1997 *V. ancliforme* (Fombella 1978) Sarjeant and Vavrdová
- 491 1997 *V. elliptica* (Cramer and Díez 1977) Sarjeant and Vavrdová
- 492 1997 *V.?* *eodigitata* (Fombella 1978) Sarjeant and Vavrdová
- 493 1997 *V. eopirifera* (Fombella 1978) Sarjeant and Vavrdová
- 494 1997 *V. multipugiunculata* (Cramer and Díez 1977) Sarjeant and Vavrdová
- 495 1998 *V. danilovae* Paalits and Heuse nom. nud.
- 496 1998 *V. phacelosa* Yuan and Hofmann



- 497 2000 *V. obsoleta* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.  
498 2000 *V. spinulifera* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.  
499 2000 *V. striatula* Volkova in Volkova and Sivertseva 1991 comb. nov. Parsons and Anderson, p.  
500 70.  
501 2001 *V. pseudofaveolata* (Fridrichsone 1971) Zang  
502 2015 *V. cantabrica* Palacios

503

### 504 3.3.2 Species excluded from the genus *Vulcanisphaera*

505 Several species assigned to *Vulcanisphaera* show neither the former nor the new diagnostic  
506 criteria of this genus, and can, therefore, be excluded. First attributed to the genus *Baltisphaeridium*,  
507 *Vulcanisphaera lophophora* (Eisenack 1959) Eisenack et al., 1973 shows numerous processes (at  
508 least 10) grouped in tufts, directly on the vesicle surface. Although the overall appearance of this  
509 species is similar to the genus *Vulcanisphaera*, it must be noted that one of the main characteristics  
510 is the presence of processes grouped at the top of one single base. Moreover, it is described for the  
511 Silurian and is, therefore, considerably younger than other species of *Vulcanisphaera*, which are no  
512 longer represented after the Ordovician. These criteria go against maintaining this species within the  
513 genus *Vulcanisphaera*, and which is most probably related to the genus *Baltisphaeridium*.

514 The species *V. tuberata* (Downie, 1958) Eisenack et al., 1973 was described in the Shineton  
515 Shale Formation in Great Britain. It shows single processes on top of what appears to be structures  
516 similar to the process bases of *Vulcanisphaera*. The species was originally described as  
517 *Hystrichosphaeridium tuberatum* Downie, 1958, and subsequently assigned to *Baltisphaeridium*  
518 (Downie and Sarjeant, 1965) and *Acanthodiacrodium* (Martin, 1973). The reassignment to  
519 *Vulcanisphaera* was based on the “broad outward swellings” from which the processes arise.  
520 Welsch (1986a) transferred the species later to *Goniosphaeridium*, because of the absence of  
521 grouped processes on the process bases and the free communication of the process and vesicle  
522 cavities. This new combination was rejected by Sarjeant and Stancliffe (1994) who reassigned it

523 again to *Vulcanisphaera*, stating the same reason that was given by Eisenack et al. (1973). Martin  
524 (1973) justified its transfer to *Acanthodiacrodium* with the bipolar arrangement of the processes.  
525 Indeed the general shape of its body seems to be divided into two parts and is therefore  
526 diacromorph, contrary to the acanthomorph to polygonomorph *Vulcanisphaera*. This species is  
527 herein assumed to be related to the genus *Acanthodiacrodium*.

528 *V. ferrosa* Fombella 1977 shows numerous simple, flagelliform processes, located on bulbous,  
529 hollow bases. As the very long vesicle is clearly diacromorph, the affiliation of this species to  
530 *Vulcanisphaera* is rejected herein. Similarly to *V. tuberata*, this species is probably related to the  
531 genus *Acanthodiacrodium*.

532 The species *V. microspinosa* Tynni, 1978 (as *V. microspinosum*) has not been validly published,  
533 as no holotype was appointed. It shows short process bases that are distributed very densely on the  
534 vesicle surface, with four to seven very short processes. Its overall appearance, and especially the  
535 high number of processes on the vesicle, point against an affinity to *Vulcanisphaera*. The species is  
536 very rarely observed, and only little information is provided, so an affinity of *V. microspinosa* to the  
537 genus *Vulcanisphaera* cannot be confirmed. This species might be related to one of the two genera  
538 *Baltisphaeridium* and *Lophosphaeridium*.

539 *V. nova* Pöthe de Baldis, 1981 does not show conical bases on the vesicle surface. Furthermore,  
540 the species appears at the end of the Silurian, and is therefore, similar to *V. lophophora*,  
541 considerably younger than the other species of *Vulcanisphaera*. An affinity to the genus  
542 *Vulcanisphaera* cannot be admitted. This species is possibly related to the genus *Baltisphaeridium*.

543 Yin (1986) described *V. rigentisa* in Cambrian-Ordovician boundary beds of Hunjiang, Jilin,  
544 China. The species mostly bears single processes which are significantly thicker than in other  
545 species of *Vulcanisphaera*, and which are not supported by a process base. It should be noted that  
546 the author compared this species to *V. mougnoanum* because of several similarities, i.e. a thin  
547 vesicle wall and simple or branched processes that are not supported by a conical base. However,

548 the forementioned reasons and the overall appearance contradict an affinity to *Vulcanisphaera*. We  
549 propose a re-assignment to *Baltisphaeridium*.

550 *V. minor* Uutela and Tynni, 1991 was described in Middle Ordovician material from Estonia.  
551 With a diameter of 10 to 12  $\mu\text{m}$  the species has a significantly smaller vesicle as other species in the  
552 genus, hence the name. Although the description does not mention process bases, the pictured  
553 holotype shows numerous densely distributed similar structures with small protuberances. Given  
554 the density and appearance of these structures, and only one picture and few information provided,  
555 the affinity to *Vulcanisphaera* is contradicted herein. It should be noted that the species seems to be  
556 very similar to *V. microspinosa* Tynni, 1978, and might, likewise, be related to *Baltisphaeridium* or  
557 *Lophosphaeridium*.

558 Sarjeant and Vavrdová (1997) published a comprehensive taxonomical revision of the genus  
559 *Multiplicisphaeridium*, including the reassignment of five species to *Vulcanisphaera*, erecting the  
560 new combinations *V. ancliforme* (Fombella, 1978) Sarjeant and Vavrdová, 1997, *V. elliptica*  
561 (Cramer and Díez, 1977) Sarjeant and Vavrdová, 1997, *V.? eodigitata* (Fombella, 1978) Sarjeant  
562 and Vavrdová, 1997, *V. eopirifera* (Fombella, 1978) Sarjeant and Vavrdová, 1997, and *V.*  
563 *multiugiunculata* (Cramer and Díez, 1977) Sarjeant and Vavrdová, 1997. *V. multiugiunculata*  
564 was subsequently transferred to *Ammonidium* by Rubinstein et al. (1999). The other reassignments  
565 of Sarjeant and Vavrdová (1997) are contradicted herein. Although the original description of *V.?*  
566 *eodigitata* (Fombella, 1978) Sarjeant and Vavrdová, 1997 (as *Multiplicisphaeridium eodigitatum*)  
567 includes diagnostic characteristics of *Vulcanisphaera*, such as a process base ending in two or three  
568 spines, an affinity to this genus cannot be confirmed herein. But the general process morphology  
569 differs from that of *Vulcanisphaera*, with a very broad (8 – 16  $\mu\text{m}$ ) columnar base and secondary  
570 branching of the processes on top of these. The diameter of the vesicle is very large (64  $\mu\text{m}$ )  
571 compared to the sizes known from species of *Vulcanisphaera*. Moreover, as already mentioned by  
572 Sarjeant and Vavrdová (1997) as a reason for the uncertainty of the assignment to the genus, the  
573 state of preservation of the holotype (Fombella, 1978, pl. 1, fig. 4) is poor. Aside from the spherical

574 vesicle, the shape of the processes of *V. eopirifera* (Fombella, 1978) Sarjeant and Vavrdová, 1997,  
575 described as clavate or baculate, with bi- or trifurcate pinnae at the distal ends (Fombella, 1978), are  
576 stated as the reason for the reassignment to *Vulcanisphaera*. The pictured holotype (Fombella,  
577 1978, pl. 3, fig. 20) shows rather baculate processes, with widened distal ends, and very small  
578 pinnae, which seem to not appear in tufts. Therefore, an affinity to *Vulcanisphaera* is contradicted  
579 herein. *Multiplicisphaeridium ellipticum* Cramer and Díez, 1977 has been reassigned to  
580 *Vulcanisphaera* on the basis of the “short, stout and broad-based, hollow and distally palmate”  
581 processes. The vesicle has a very oval shape and the processes are quite dissimilar with any other  
582 specimen of *Vulcanisphaera*. They have thick cylindrical stems and show distal palmate branching  
583 into numerous denticulate pinnae, and no process base with single or several processes on top. The  
584 species was first described under the genus *Multiplicisphaeridium* by Cramer and Díez (1977). It  
585 may be more appropriate to reclassify this species under its original name *Multiplicisphaeridium*  
586 *ellipticum*. Lastly, the filling of the processes and bases of the pinnae “with what appears to be  
587 secondary wall material” (Cramer and Díez, 1977) can be considered another argument against  
588 maintenance within the genus *Vulcanisphaera*, as nothing comparable has been described for this  
589 genus. The reassignment of *Multiplicisphaeridium ancliforme* Fombella, 1978 to *Vulcanisphaera*  
590 was due to the essentially conical shape of the processes and the tufts of filiform spines at their  
591 distal ends (Sarjeant and Vavrdová, 1997). Although stated as subspherical to polygonal, the  
592 pictured holotype has a very polygonal shape, due to the wide “process bases”, and appears to be  
593 herkomorph, with very high ridges between the processes dividing the vesicle surface into  
594 polygonal fields. The conical structure of the processes seems to be caused by the curvature of these  
595 ridges. The processes are moreover described as being columnar in the upper part. This species is  
596 probably related to *Timofeevia* Vanguetaine, 1978, as it meets well the original diagnosis of this  
597 genus.

598 The Neoproterozoic *V. phacelosa* Yuan and Hofmann, 1998, which was described with only one  
599 single specimen found, shows indeed grouped processes, but the number of processes within these

600 is much higher (10-15) than in other species of *Vulcanisphaera* and no process bases appear.  
601 Moreover, *V. phacelosa* differs by having an extremely large vesicle size (ca. 140 µm) and a  
602 Precambrian distribution. Therefore this species cannot be maintained within the genus  
603 *Vulcanisphaera*.

604 On the basis of grouped processes on a common base, Zang (2001) re-assigned the Early  
605 Cambrian *Baltisphaeridium pseudofaveolatum* Fridrichsone, 1971 to *Vulcanisphaera*, creating the  
606 new combination *V. pseudofaveolata*. Because of the general appearance of the processes, which  
607 seem to occur mostly single isolated (cf. Zang et al., 2007; fig. 14, I-L), and the age, which is  
608 notably older than that of the other species, an affinity to *Vulcanisphaera* is rejected herein.

609

### 610 3.3.3 Species retained in this study

611

612 *Vulcanisphaera africana* Deunff, 1961 emend. nov.

613 (Plate I, 6–16)

614

615 1958 *Hystriospheridium* sp. Downie, p. 340, pl. 16, fig. 10

616 \* 1961 *Vulcanisphaera africanum* Deunff, p. 42; pl. 2, figs. 1, 2; holotype figs. 1, 2.

617 1961 *V. nebulosa* Deunff, p. 42; pl. 2, fig. 3.

618 1961 *V. cf. nebulosa* Deunff, pl. 2, fig. 5.

619 1967 *V. frequens* Górka, p. 4: pl. 1, figs. 10–11, 1–2; holotype pl. 1, 10–11.

620 1973 *V. gorgo* Martin, p. 12; pl. 2, figs. 1, 4; holotype figs. 1, 4.

621 1975 *V. sp.* Martin, p. 9; pl. I, figs. 2, 4; pl. IV, fig. 9.

622 1976 *V. cirrita* Rasul, p. 480-481; pl. 1, fig. 3.

623 1976 *V. pila* Rasul, p. 481.; text-figure 1: 3; pl. 1, fig. 10.

624 1992 *V. aff. africana* Paalits, pl. 4, fig. 6.

625 2006 *Stelliferidium* sp. Aráoz and Vergel, pl. (“figura”) 6, L.

626 *Holotype*: Deunff, 1961, pl. 2, fig. 1, 2.

627 *Original diagnosis* (translated from Deunff, 1961): Shell light brown of 40 to 45  $\mu\text{m}$  spherical,  
628 possessing on the surface small cones carrying processes about 10  $\mu\text{m}$  height, grouped by three, and  
629 whose ends are finely branched.

630 *Emended diagnosis*: More or less spherical to subspherical vesicle outline; smooth surface;  
631 small solid more or less conical bases, bearing at their distal ends tufts of two to five processes, or  
632 more rarely a single isolated process; processes are of variable length, solid, tapering, erect or  
633 curved, with simple, bi-, trifurcated or finely branched distal ends, sometimes forming numerous  
634 anastomosing, filamentous threads; isolated processes usually have a broader base than those  
635 grouped in tufts.

636 *Dimensions*: (311 specimens measured). Vesicle diameter: 20  $\mu\text{m}$  (39.7  $\mu\text{m}$ ) 60  $\mu\text{m}$ . Process  
637 length: 2  $\mu\text{m}$  (10.47  $\mu\text{m}$ ) 24  $\mu\text{m}$ . Width of process bases: 0.5  $\mu\text{m}$  (2.54  $\mu\text{m}$ ) 4.9  $\mu\text{m}$ .

638 *Comparison*: *Vulcanisphaera africana* differs from *V. mougnoana* in not displaying well  
639 defined ridges between the processes which create a distinct pattern of polygonal fields on the  
640 vesicle surface. *V. simplex* differs from *V. africana* in having hollow processes, with the process  
641 and vesicle cavities freely communicating, and in having a smaller average vesicle size.

642 *Discussion*: Deunff (1961) erected the genus *Vulcanisphaera* with the description of two  
643 species: the type species *V. africana* and *V. nebulosa*. The difference between the two species lies in  
644 the different types of their processes, with those of *V. africana* having finely branched distal ends  
645 and those of *V. nebulosa* displaying short curved processes. The curvature of the processes is  
646 considered herein as insignificant, since the processes are flexible. With all transitional process  
647 shapes evidently existent, as also observed in the material investigated in the present study, a  
648 maintenance of *V. nebulosa* as a separate species must be rejected.

649 The species *V. frequens* Górká, 1967 can be considered identical to *V. nebulosa*. Martin (1973)  
650 states that this species differs from *V. africana* by more distant and unbranched processes and the  
651 ornamentation of the central body. In the original diagnoses of *V. africana* and *V. nebulosa* the

652 surface texture is not mentioned, therefore this characteristic cannot be used to differentiate between  
653 these species.

654 Similarly, the diagnosis of *V. gorgo* Martin, 1973 does not provide any new differential features.  
655 The processes are described as being curved and divided in fine coalescent strips.

656 Several authors, i.e. Elouad-Debbaij (1988), Martin *in* Martin and Dean (1981) and Molyneux  
657 (1999) already considered *V. cirrita* as a junior synonym of *V. africana*, as the only difference  
658 between the two species is, according to Rasul (1976), the slightly shorter appendages in *V.*  
659 *africana*, a criterion that must be regarded insufficient to justify maintaining both species.

660 *V. pila* was erected by Rasul (1976) based on “short, solid, pillar-like processes” (Rasul, 1976,  
661 p. 481), which differ from the long and distally bifurcated processes of *V. africana* and hollow  
662 simple processes *V. frequens*. It needs to be pointed out that the diagnosis of *V. frequens* does not  
663 mention hollow processes, and the pictured specimens rather indicate solid ones. Further, the  
664 argument of process shape and length is negligible due to aforementioned reasons that all transitions  
665 are evidently existent.

666 *Remarks:* Transitional forms between *V. turbata* Martin (*in* Martin and Dean, 1981) and *V.*  
667 *africana* Deunff, 1961, have already been observed by Martin (*in* Martin and Dean, 1988) in the  
668 Upper Cambrian of Manuels River New Foundland, Canada, as well as by Young et al. (1994) in  
669 the Upper Cambrian of St Tudwal's Peninsula in Great Britain. Within the present study, transitions  
670 between *V. africana* and *V. mougnoana* were also found in the material of the Algerian Sahara.  
671 Martin (*in* Martin and Dean, 1988) notes that on *V. africana*, a vesicle tabulation (polygonal fields)  
672 can be recognised; a characteristic that is more pronouncedly developed in *V. turbata* even though it  
673 is generally not very obvious. Infact, according to the author, the holotype of *V. africana* of Deunff  
674 (1961; pl. 2, figs. 1, 2) shows a discrete polygonal pattern. Apart from the more obvious vesicle  
675 tabulation, a lower number of tufts of generally shorter and proximally stouter processes of *V.*  
676 *turbata* are mentioned as distinguishing characteristics (Martin *in* Martin and Dean, 1988). *V.*  
677 *turbata* is herein considered a junior synonym of *V. mougnoana*, therefore still remains as a species



678 separate from *V. africana*. Although transitional forms obviously exist, the statistical analyses (see  
679 below) point to two separate species. Moreover, the distinctly pronounced tabulation, which is  
680 diagnostic for *V. mougnoana*, certainly provides information; e.g. it can be regarded as a response  
681 to changing environmental conditions, as is discussed later, that would be lost by merging the two  
682 species together.

683

684

685 *Vulcanisphaera mougnoana* (Martin, 1973) emend. nov.

686 (Plate I, Figs. 1-5)

687

688 \* 1973 *Vulcanisphaera ? mougnoanum* Martin, p. 13; pl. II, figs. 2, 8, 9; holotype fig. 8.

689 1974 *V. capillata* Jardiné et al., p. 119; pl. II, fig. 8.

690 1980 *V. cf. africana* Volkova, pl. on p. 54, fig. 6.

691 1980 *V. sp. 1* Volkova, pl. on p. 54, fig. 10

692 1981 *V. turbata* Martin (*in* Martin and Dean), p. 23; text-fig. 6; pl. 1, figs. 2–4; holotype fig. 2,  
693 text-fig. 6.

694 1983 *V. aff. capillata* Volkova, pl. 1, fig. 11.

695 1983 *Cristallinium* sp. Volkova, pl. 2, fig. 3, 5.

696 1988 *Vulcanisphaera lanugo* by Martin (*in* Martin and Dean), p. 42 pl. 18, figs. 7, 9–12, 14–17,  
697 holotype fig. 12.

698 1990 *Raphesphaera obsoleta* Volkova, p.79; pl. 8, figs. 11, 12; holotype fig. 11.

699 1990 *R. spinulifera* Volkova, p. 79-80; pl. 8, figs. 7, 8, 15; holotype fig. 7.

700 1990 *R. turbata* Martin (*in* Martin and Dean, 1981) Volkova comb. nov.

701 1990 *Vulcanisphaera* sp. Volkova, pl. XIII, figs. 4, 5.

702 1991 *R. striatula* Volkova *in* Volkova and Sivertseva, p. 121; pl. (“Рис.”) 1, figs. i, l, v (*u, л, в*);  
703 holotype: i, l (*u, л*).



704 1996 *V. nebulosa* Deunff 1961 Ghavidel-Syooki (incorrect identification)  
705 1999a “Gen. et sp. nov. № 2” Volkova; pl. IV, fig. 8.  
706 1999b *Undosisphaera pilosiuscula* Volkova; p. 75; pl. (“таблице”) VIII, fig.1, 2, 6; holotype  
707 fig. 1  
708 2000 *V. obsoleta* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.  
709 2000 *V. spinulifera* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.  
710 2000 *V. striatula* Volkova in Volkova and Sivertseva, 1991 comb. nov. Parsons and Anderson,  
711 p. 70.  
712 2006 *Timofeevia* cf. *T. microretis* Aráoz and Vergel, pl. (“figura”) 5, K.  
713 2011 *V.* sp. Jachowicz-Zdanowska, p. 256-257, pl. (“fig.”) 10, fig. J.  
714 2015 *V. cantabrica* Palacios, pp. 100, 103; pl. XV, figs. 1–6; holotype fig. 1.  
715 *Holotype*: Martin, 1973, pl. II, fig. 8.  
716 *Original diagnosis* (translated from Martin, 1973): Central body globular with a diameter of 45  
717 to 62  $\mu\text{m}$ . Appendages in a number of sixty to eighty and of a length of 11 to 18  $\mu\text{m}$ . Conical shape  
718 with single or finely branched distal end. In a polygonal and often hexagonal arrangement, they are  
719 isolated or grouped by two or three on the same specimen. Isolated appendages have a broad base of  
720 1.5 to 2  $\mu\text{m}$ ; those grouped are thinner, the width of their base is 0.5 to 1  $\mu\text{m}$ .  
721 *Emended diagnosis*: More or less spherical to ellipsoidal vesicle, sometimes slightly polygonal  
722 in outline; psilate to granulate surface; small solid conical process bases with either a simple single  
723 tapering solid process or tufts of two to numerous solid processes; processes are of variable length,  
724 solid, tapering, erect or curved, with simple, bi-, trifurcated or finely branched distal ends; isolated  
725 appendages usually have a broader base than those grouped in tufts; thin ridges between processes  
726 forming a polygonal structure on the vesicle surface with the processes appearing where these  
727 ridges merge, with smooth or slightly dented tops.  
728 *Dimensions*: (280 specimens measured). Vesicle diameter: 30  $\mu\text{m}$  (43.75  $\mu\text{m}$ ) 60  $\mu\text{m}$ . Process  
729 length: 1.24  $\mu\text{m}$  (11  $\mu\text{m}$ ) 20.36  $\mu\text{m}$ . Width of process bases: 0.8  $\mu\text{m}$  (1.7  $\mu\text{m}$ ) 3.8  $\mu\text{m}$ .

730        *Comparison: Vulcanisphaera mougnoana* differs from *V. africana* and *V. simplex* in displaying  
731 well defined ridges between the processes which create a distinct pattern of polygonal fields on the  
732 vesicle surface. *V. simplex* differs from *V. mougnoana* in having hollow processes, with the process  
733 and vesicle cavities freely communicating. While the same types of processes in *V. africana* and *V.*  
734 *mougnoana* occur, *V. mougnoana* generally seems to tend to the simpler process shapes, with more  
735 complex ramifications only rarely occurring. Single isolated processes are commonly observed in *V.*  
736 *mougnoana*, while they are very uncommon in *V. africana*. The average vesicle size is clearly  
737 larger in *V. mougnoana* than in *V. simplex*, but only slightly larger than in *V. africana*.

738        *Discussion:* Martin (1973) attributed the species *V.? mougnoana* to the genus *Vulcanisphaera*  
739 with doubt, as the original description of *Vulcanisphaera* by Deunff (1961) states a number of two  
740 to five processes on each protuberance, whether *V.? mougnoana* shows single isolated processes.  
741 However, the description of *V. capillata* by Jardiné et al. (1974) includes single isolated processes  
742 as well, which are also clearly visible in the holotype. Interestingly, this description, different to the  
743 one of *V.? mougnoana*, does not include a polygonal tabulation, although this characteristic is  
744 visible in the holotype. Aside from that, the descriptions are almost identical, therefore certainly  
745 refer to synonymous species. The emended diagnosis allows to clarify this problem.

746        Within the first description of *V. turbata* Martin (*in* Martin and Dean 1981) discussed the  
747 differences between *V. turbata* and *V.? mougnoana* (as *V. mougnoanum*), namely the minimum  
748 number of two processes on each protuberance, a greater development of anastomosing threads  
749 from the processes, and granulation of the vesicle wall. Again, single isolated processes are  
750 mentioned (Martin *in* Martin and Dean, 1981).

751        In her master's thesis Parsons (1986) described the new species *V. disjunctospinata* (nom. nud.),  
752 which differs from *V. mougnoana* by bearing exclusively single isolated processes, and mentioned a  
753 slight serration of the tops of the ridges separating the polygonal fields.

754        The description of *V. lanugo* by Martin (*in* Martin and Dean, 1988), as also mentioned therein in  
755 the comparison of the two species, differs from *V. turbata* in a smaller vesicle size (14-35 µm) and

756 less developed and more fragile ornamentation. The processes are stated to occur, as in *V. turbata*,  
757 in groups of two to three, but are of somewhat smaller length (4-8  $\mu\text{m}$ , max 12  $\mu\text{m}$  vs. 6-20  $\mu\text{m}$ ).  
758 These differences are herein regarded as to insignificant to justify the maintenance of a separate  
759 species.

760 Volkova (1990) described a new genus, *Raphesphaera*, with two new species, *R. obsoleta*, and  
761 *R. spinulifera*, and reassigned *Vulcanisphaera turbata* to this genus. The distinction between the  
762 two genera was based on the polygonal field pattern, which is not described in the original genus  
763 diagnosis of *Vulcanisphaera*, and the apparently missing individual bases for the tufts of processes  
764 in *Raphesphaera*, which is considered as a diagnostic characteristic of *Vulcanisphaera*. Another  
765 species of this genus, *R. striatula*, was described by Volkova (*in* Volkova and Sivertseva, 1991).  
766 Parsons and Anderson (2000) considered *Raphesphaera* as a junior synonym of *Vulcanisphaera*,  
767 therefore reassigned all its species to this genus. This reclassification is justified by observations of  
768 Martin (*in* Martin and Dean, 1988), according to which *V. africana* shows a faint polygonal pattern  
769 that is even visible in the holotype of Deunff (1961). Moreover, the original diagnosis of *V. turbata*  
770 does indeed include the description of process bases (as “low, dark protuberances”), which are also  
771 clearly visible in the pictured specimens (Martin *in* Martin and Dean, 1981).

772 According to Volkova (1990), *V. spinulifera* differs from *V. turbata* only by its shorter  
773 appendages. This difference is regarded insignificant herein and cannot justify a specific separation.  
774 The original description of *V. obsoleta* (as *Raphesphaera obsoleta*; Volkova, 1990) mentions  
775 needles on the ridges between the polygonal fields as the characteristic to differentiate it from other  
776 species. This feature, indeed, has not been described within other species of *Vulcanisphaera*, but in  
777 species of other genera. The subject of intergeneric similarities is discussed in part 3.2. *Systematic*  
778 *palaeontology*. Aside from this the diagnosis is similar to the forementioned species which are  
779 considered synonymous to *V. mougnoana* in the present study. Transitional forms between *V.*  
780 *spinulifera* and *V. turbata* have been observed by Żylińska et al. (2006) in the Furongian of Poland.

781 *V. striatula* shows, according to its original diagnosis (as *Raphesphaera striatula*), two types of  
782 ridges on the vesicle surface: straight and curved ones (Volkova and Sivertseva, 1991). Each time  
783 two straight ridges with a groove in between divide the polygonal fields, and curved ridges run from  
784 the corners of the fields towards the center. This feature is indeed not described for other species of  
785 *Vulcanisphaera*. However, as not many pictures are provided to substantiate a sufficient difference  
786 in the arrangement of the ridges, it is proposed herein to include *V. striatula* in the emended species  
787 *V. mougnoana*. Once again, the mentioning in the description of thickened conical process bases,  
788 whose absence was stated as one of the reasons for the creation of a separate genus, *Raphesphaera*,  
789 is remarkable. In addition, it should be noted that single processes are included in the diagnosis of  
790 *V. striatula*.

791 Volkova (1999b) erected the new genus *Undosisphaera*, with a single species, *U. pilosiuscula*,  
792 in lower Tremadocian material from the Moscow Syncline. In her description she stated close  
793 similarities to *Vulcanisphaera* and *Raphesphaera*, as all three taxa display conical process bases,  
794 but she pointed to the different process number as the reason for generic separation. While  
795 according to Volkova (1999b), *Vulcanisphaera* and *Raphesphaera* show clusters of two to five  
796 processes, *Undosisphaera* has “numerous fine unbranched hairs” (Volkova, 1999b, p. 75). Indeed,  
797 the number of processes per process base is clearly higher than 5, but this characteristic is  
798 considered herein as not sufficient to justify the creation of a separate genus. The specimens of  
799 *Undosisphaera* shown in the plate (Volkova, 1999b, pl. VIII, 1, 2, 6) display simple tapering  
800 processes that are also described for *Vulcanisphaera*. Therefore, only the number of processes  
801 differs, which is an insignificant differentiation criterion. In comparison with *Raphesphaera*,  
802 Volkova (1999b) mentions the polygonal plates of this genus as a differentiating character.  
803 However, the pictured specimens seem to have a surface structure similar to that of *R. striatula*  
804 (which is considered herein a junior synonym of *V. mougnoana*) shown in the plates of Volkova  
805 and Sivertseva (1991: pl. 1, fig. *u, л, в*). Particularly the holotype of *U. pilosiuscula* (Volkova,  
806 1999b: pl. VIII, fig. 1) shows a prominent ornamentation with straight ridges in between the process

807 bases, dividing the vesicle surface into polygonal fields, and sinuous ridges running from the  
808 process bases into the fields, very much resembling the surface pattern described and pictured for *R.*  
809 *striatula*. Due to the great morphological similarities of the two genera, the genus *Undosisphaera* is  
810 considered herein a junior synonym of *Vulcanisphaera*. Based on the four specimens shown in  
811 plates (Volkova 1999a: pl. IV, fig. 8; Volkova, 1999b: pl. 1, figs. *u, л, e*), with to date no further  
812 occurrences described and pictured, *U. pilosiuscula* is assumed to be a junior synonym of *V.*  
813 *mouignoana* due to the aforementioned similarities with *R. striatula* in regard to surface structures.

814 The description of *V. cantabrica* Palacios, 2015, based on Furongian material from Spain, does  
815 not provide any new characteristics that would justify maintaining it as a separate species. The  
816 greatest difference here is the smaller length of the processes (1.5–2.5  $\mu\text{m}$ ). In comparing *V.*  
817 *cantabrica* to *V. lanugo*, Palacios (2015) mentioned the smaller vesicle diameter, a thinner wall, and  
818 longer and more delicate processes of *V. lanugo* as differential characteristics, but also recognised a  
819 great similarity between the two species, when specimens of *V. lanugo* have lost their processes  
820 (Palacios, 2015). Therein, he also reassigned several specimens, which were formerly described as  
821 *V. lanugo* (Palacios et al., 2006, 2012; Palacios, 2008), to *V. cantabrica*.

822 As mentioned before, transitions between *V. turbata* Martin (*in* Martin and Dean, 1981) and *V.*  
823 *africana* Deunff, 1961, have been already observed by Martin (*in* Martin and Dean, 1988), and  
824 Young et al. (1994) in Upper Cambrian strata of Newfoundland, Canada, and Wales, Great Britain.

825

826 *Vulcanisphaera simplex* (Jardiné et al., 1974) emend. nov.

827 (Plate II, 1-16)

828

829 \* 1974 *Vulcanisphaera simplex* Jardiné et al., pl. II, 7.

830 1975 *V. flagellum* Martin, p. 8-9; pl. I, fig. 16; pl. III, fig. 14; pl. IV, figs. 13, 21, 31; holotype,  
831 pl. IV, fig. 13, 21.

832 1976 *V. imparilis* Rasul, p. 481-482; pl. 1, figs. 4-6, 12; holotype: pl. 1, fig. 6.

833 1976 *V. britannica* Rasul, p. 482, 484; pl. 1, figs. 2, 7-9, 13-16; holotype: pl. 1, fig. 7.

834 1979 *V. imparila* Rasul, p. 69, 70; text fig. 3.

835 *Holotype*: Jardiné et al., 1974, pl. II, 7.

836 *Original diagnosis* (translated from Jardiné et al., 1974): Spherical vesicle with almost  
837 polygonal outline due to the strong expansion of the process bases; complex appendages with  
838 conical base, ending in a tuft of two to four fine branches, rather short, with a simple end or  
839 bifurcated in tenuous elements. Body diameter: 30-50  $\mu\text{m}$ ; height of the undivided process base  
840 (“basal cone”): 3-10  $\mu\text{m}$ ; length of branches: 3-7  $\mu\text{m}$ .

841 *Emended diagnosis*: Spherical to polygonal vesicle outline; smooth vesicle surface; processes  
842 may be short tuberculate, evocate, clavate, or echinate, with rounded, pointed, flat or crateriform  
843 ends, or more or less long, single simple tapering, or bi- to polyfurcating processes on the same  
844 specimen, forming a conical or cylindrical process base (primary process) surmounted by two to  
845 five tapering secondary processes; secondary processes may be simple, acicular, flexuous, more or  
846 less curved, with simple or bifurcated ends; process surface may be smooth, granulate, or bearing  
847 short spines; processes including hollow bases communicating with the vesicle cavity.

848 *Dimensions*: (280 specimens measured). Vesicle diameter: 18  $\mu\text{m}$  (26.7  $\mu\text{m}$ ) 45.47  $\mu\text{m}$ . Process  
849 length: 1.27  $\mu\text{m}$  (8  $\mu\text{m}$ ) 20  $\mu\text{m}$ . Width of process bases: 1.0  $\mu\text{m}$  (2.7  $\mu\text{m}$ ) 5.1  $\mu\text{m}$ .

850 *Comparison*: *V. simplex* Jardiné et al., 1974 differs from *V. africana* and *V. mougnoana* Martin,  
851 1973 by having more pronounced, higher process bases, hollow processes and process bases with  
852 communicating internal cavities of the processes and the central body, no appearance of complex  
853 process branching except furcating tips, and an exclusively psilate surface of the central body. It  
854 furthermore differs from *V. mougnoana* Martin, 1973 by not showing a polygonal pattern on its  
855 surface. Moreover, the average vesicle diameter of *V. simplex* is noticeably smaller than of the other  
856 two species.

857 *Discussion*: The species diagnosis of *Vulcanisphaera flagellum* Martin, 1975 differs only  
858 slightly from that of *V. simplex* Jardiné et al., 1974, by having a higher number of processes on the

859 bases (2 to 7 vs. 2 to 4), a smaller vesicle size (22-32  $\mu\text{m}$  vs. 30-50  $\mu\text{m}$ ) and more developed  
860 crateriform protuberances. These differences must therefore reasonably be considered a widening of  
861 the diagnosis of *V. simplex*, rather than a justification for a creation of a new species. With *V.*  
862 *britannica* Rasul (1976) described a new species with a fairly broad range of morphologies,  
863 including 4 varieties, therein called *Forma 1* to *4*. The descriptions showed strong similarities with  
864 several other formerly described species of *Vulcanisphaera*, with *V. britannica Forma 2 sensu*  
865 Rasul (1976) conforming well to *V. simplex* Jardiné et al., (1974). Moczyłowska and Stockfors  
866 (2004) mentioned the high morphological variability of the processes and overall habit of the  
867 vesicle of *V. britannica*, calling the species a “waste basket”. They regarded the changing  
868 morphology as clearly stratigraphically related, as the appearance of morphological innovations are  
869 recorded successively in the studied section, with a trend to a more simplified morphology, with  
870 longer, more straight and less branching processes. Within the same publication, Rasul (1976)  
871 described another relatively variable species, *V. imparilis* Rasul, 1976, likewise with four varieties,  
872 called *Forma 1* to *4*, differing mostly in the process form. The description and appearance of *V.*  
873 *imparilis Forma 4* is matching well *V. flagellum* Martin, 1975 and shows no new characteristics  
874 justifying the maintenance of a separate species. The other three varieties show clear similarities  
875 with *V. britannica* Rasul, 1976, especially *Forma 2 sensu* Rasul, 1976, differing only in the process  
876 shape, as recognised by Rasul (1976) therein. These observations strongly point to a single, highly  
877 morphologically variable species. With *V. simplex* being the first described species in this plexus,  
878 its diagnosis is emended herein to include the characteristics of the latter described species  
879 considered as junior synonyms.

880

### 881 3.4 Statistical analysis

882

883 The results of the linear discriminant analysis (LDA), based on the biometric data of 756  
884 specimens of the investigated samples, show a good discrimination between the three species as



885 defined in the new classification scheme. Of the six used parameters, vesicle diameter and process  
886 shape have been revealed as the most important characters for differentiation between the classes.  
887 The three classes shown in the scatter plot, which are corresponding to the three emended species of  
888 *Vulcanisphaera*, are well separated, indicating that the new classification scheme is robust. The *V.*  
889 *africana* class includes 311 specimens, the *V. mougnoana* class 278, and the *V. simplex* class 167.  
890 Based on the given data the algorithm predicted 335 specimens belonging to *V. africana* and 254 to  
891 *V. mougnoana*, therefore assigning, respectively, 27 and 3 specimens, to the wrong species. All 167  
892 specimens of *V. simplex* were correctly predicted. In total, 96 % of the specimens were correctly  
893 classified.

894 While *Vulcanisphaera simplex* is clearly separated from the other two species, there is a slight  
895 overlapping of the groups of *V. africana* and *V. mougnoana* (Fig. 4). This is caused by transitional  
896 specimens in between the two species, which are also recognised in the literature (Martin and Dean,  
897 1988; Young et al., 1994). Nevertheless, the classes representing these two species are well  
898 separated, substantiating the maintaining of both species.

899

## 900 **4 Biostratigraphy and palaeogeography of *Vulcanisphaera***

901

### 902 *4.1. Biostratigraphy*

903

904 The stratigraphic distribution of the different species of *Vulcanisphaera* as revised herein is  
905 reported in Figure 5. Only occurrences with precise stratigraphic assignments are included.

906 The stratigraphic distribution of the genus *Vulcanisphaera* (Fig. 5) extends from the Drumian  
907 (Miaolingian) in the middle Cambrian to at least the Floian in the Early Ordovician, with only a few  
908 occurrences described in younger material, up to the late Middle Ordovician (Darriwilian). Fang  
909 (1986) reported *V. africana* in the Hungshihyen Formation in Yunnan, China, which is correlating  
910 to the Floian to Dapingian. Only two occurrences of *V. africana* are recorded in Darriwilian



911 material, in North Wales (Booth, 1979) and in Cumbria, England (Arthurton and Wadge, 1981).  
912 Moreover, Booth (1979) includes occurrences in the Arenig of the Lake District in Great Britain,  
913 without a more detailed stratigraphic assignment. Additionally, occurrences of *Vulcanisphaera*  
914 without species level definition are described for the lower Arenig (Floian) of Wales and Cumbria  
915 in Great Britain (Molyneux and Dorning, 1989; Molyneux, 1990), in the upper Arenig (Dapingian  
916 or Darriwilian) of Cumbria (Arthurton and Wadge, 1981), the middle Arenig of the Jujuy Province  
917 in Argentina (Vergel et al., 2002), and in Arenigian material from Sardinia, Italy (Pittau Demelia  
918 and Del Rio, 1982). Given the rarity of records of *Vulcanisphaera* from this age, the presence of the  
919 genus in the Floian and younger strata awaits new data to be confirmed. Reworking has to be taken  
920 into consideration. Arthurton and Wadge (1981), for instance, noted the presence of many species  
921 similar to Tremadocian forms from Saint Petersburg, Russia, and North Africa in their material  
922 from the Arenig and Llanvirn of Cumbria, England. The appearance of *Vulcanisphaera* in the  
923 Upper Ordovician, as described by He and Yin (1993; as *V. cf. aff. mougnoana*) in material from  
924 North China and by Legault (1982) in Newfoundland, Canada, as well as in Upper Ordovician to  
925 Silurian material in India (Sinha et al., 1996a, 1996b) is highly questionable and represents  
926 probably either reworked material or wrong taxon determination. The pictured specimen of He and  
927 Yin (1993; pl. III, fig. 11) does not resemble *Vulcanisphaera*.

928 One record of *V. africana* exists for the Middle Cambrian (Volkova, 1980) and several others  
929 with a vague stratigraphic assignment of middle to late Cambrian (Martin, 1980; Ghavidel-Syooki,  
930 1993; Ribecai and Vanguetaine, 1993; Brück and Vanguetaine, 2004). The species appears with  
931 certainty in the Furongian (Jiangshanian) *Parabolina spinulosa* trilobite Biozone (Martin in Martin  
932 and Dean, 1988; Parsons and Anderson, 2000; Żylińska et al., 2006; Jachowicz-Zdanowska, 2011).  
933 It needs to be pointed out that transitions between *V. turbata* (*V. mougnoana* herein) and *V. africana*  
934 are described in older strata (*Olenus* trilobite Biozone; Martin in Martin and Dean, 1988; Young et  
935 al., 1994), possibly indicating an evolutionary tendency towards loss of an underlying sutural  
936 pattern. Records of *V. africana* extend to the *Didymograptus artus* (“*D. bifidus*”) Biozone in the

937 Darriwilian (Booth, 1979; cf. Arthurton and Wadge, 1981).

938 The earliest records of *V. mougnoana* (as *V. lanugo*) are described in peri-Gondwanan strata for  
939 the *Tomagnostus fissus*, *Ptychagnostus atavus* and *Paradoxides hicksi* biozones (Martin in Martin  
940 and Dean, 1988; Vanguetaine and Brück, 2008; Palacios et al. 2012) within the *Paradoxides*  
941 *paradoxissimus* Superzone, therefore of Drumian (Miaolingian) age. In the Baltic realm the species  
942 is found in material as old as the upper part of the *Paradoxides forchhammeri* (*Lejopyge laevigata*)  
943 Biozone in the Guzhanguan (Volkova, 1990). The youngest appearances of *V. mougnoana* are  
944 described for the late Tremadocian to early Floian (Molyneux and Rushton, 1988; Molyneux and  
945 Dorning, 1989).

946 No occurrence of *V. simplex* is described in material older than the latest Cambrian. In  
947 accordance with Moczyłowska and Stockfors (2004), the first appearance of *V. simplex* is most  
948 probably in the uppermost Cambrian *Acerocare* zone (cf. Moczyłowska et al., 2004; Jachowicz-  
949 Zdanowska, 2011). Apart from this, the species seems to be confined to the Tremadocian.  
950 Molyneux and Dorning (1989) recorded occurrences from the uppermost Tremadocian–lowermost  
951 Floian ‘Login Beds’ in Wales, which have no independent age control. As mentioned before,  
952 occurrences of *V. simplex* in the Upper Ordovician (Sinha et al., 1996b) are most probably  
953 erroneous.

954 For the Laurentian realm very few of occurrences of *Vulcanisphaera* appear in literature. *V.*  
955 *mougnoana* (as *V. turbata*) and *V.* sp. are described in Furongian material of Arkansas and  
956 Missouri, USA (Wood and Stephenson, 1989; 1990), and *V.* sp. in the Furongian of the Quebec  
957 region, Canada (Lavoie et al., 2003). The rarity of records of *Vulcanisphaera* from Laurentia rather  
958 reflects a lack of studies from this region than it indicates a genuine absence of the genus from the  
959 palaeocontinent.

960 Based on the results of this study and earlier investigations by Vecoli (1996, 1999) for the NI-2  
961 borehole, and Rasul and Downie (1974) and Rasul (1976, 1979), the stratigraphic distribution of the  
962 different species of *Vulcanisphaera* can be assessed for the three study localities. As the first

963 species, *V. mougnoana* appears in the lowermost part of the Bordj Nili Fm. (Furongian). The  
964 stratigraphic range of this species does not exceed the lower part of the El Gassi Fm., Tremadocian.  
965 Occurrences of *V. africana* are also recorded for the Furongian of the Bordj Nili Fm., but the  
966 species appears later than *V. mougnoana*. The stratigraphic distribution of *V. africana* extends to the  
967 upper part of the Tremadocian El Gassi Formation. *V. simplex* does not appear before the  
968 Tremadocian, with questionable occurrences in the uppermost part of the Bordj Nili Fm. and the  
969 lower El Gassi Fm., and some occurrences in the middle to uppermost El Gassi Fm.

970 In the Shineton Shales outcrops no occurrences of *V. mougnoana* are recorded, whereas *V.*  
971 *africana* appears throughout the entire Tremadocian succession, as does *V. simplex*, with the  
972 exception of the uppermost part.

973 All three species appear in the Tremadocian of the Ghelli outcrop in Iran. *V. africana* is present  
974 in all samples from LG1 to LG12, except LG8. *V. simplex* is only found in three samples, LG4,  
975 LG7, and LG14. *V. mougnoana* appears in the samples LG2, LG8 and LG12 to LG29, exceeding  
976 the distribution of *V. africana* and *V. simplex* in this locality.

977

#### 978 4.2 Palaeobiogeography

979

980 All available data from the literature are used to plot the palaeobiogeographic distribution of  
981 *Vulcanisphaera* on global palaeogeographic reconstructions based on the PALAEOMAP project of  
982 Scotese (2016), using the software GPlates (Boyden et al., 2011) (Fig. 6). Slight changes were  
983 applied to the given reconstructions in order to have the North Kara Terrane *sensu* Lorenz et al.  
984 (2007) separated from Siberia, as occurrences of *Vulcanisphaera* are recorded in Severnaya  
985 Zemlya, Russia. Only those occurrences with relatively precise and robust information regarding  
986 the time interval and geographical position are considered in this study. In accordance with the  
987 stratigraphic distribution, two time intervals, the Furongian and the Tremadocian, were chosen to  
988 show changes in the global palaeogeographic distribution of the different species of

989 *Vulcanisphaera*. The palaeogeographic reconstructions showing the occurrence distribution are  
990 illustrated in Mollweide projection maps (Fig. 6), created with the software QGIS (QGIS  
991 Development Team, 2019).

992 It appears that the genus has a very widespread, rather cosmopolitan distribution from the late  
993 Cambrian to the Early Ordovician, appearing at the margins of Gondwana, Avalonia, Baltica, the  
994 North Kara Terrane and Laurentia (Wood and Stephenson, 1989; 1990). The few occurrences  
995 recorded for Laurentia are possibly simply due to the scarcity of palynological investigations, but  
996 palaeogeography might have played a role. Although all occurrences of *Vulcanisphaera* are  
997 restricted to the southern hemisphere, mostly due to the continental configuration, the genus  
998 appears across a wide range of palaeolatitudes. By applying models for palaeoclimate zones based  
999 on sedimentological indicators (Boucot et al., 2013) on the palaeobiogeographical distribution maps  
1000 some statements can be made regarding the palaeoecology of the genus. The fact that most  
1001 occurrences are located between 90°S and 30°S, with a latitudinal distribution confined northward  
1002 by the warm waters of the tropic belt, probably indicates that the genus generally preferred cold-  
1003 temperate to warm-temperate sea waters. It is noteworthy that the northernmost occurrences are  
1004 recorded from the western margin of Gondwana, in today's Iran (Ghavidel-Syooki, 1993, 1994,  
1005 1995, 1997, 1998, 2000, 2006; Mehrjerdi, 2001; Ghavidel-Syooki and Vecoli, 2008; this study).  
1006 This might be due to the proposed upwelling zone in this region (Servais et al., 2014), bringing  
1007 colder, denser, nutrient-rich waters up from the deeper ocean.

1008 While the palaeogeographic distribution of *V. africana* does not change pronouncedly through  
1009 time, obvious changes are visible in regard of *V. simplex* and *V. mougnoana*. The first only appears  
1010 sporadically in the latest Furongian and becomes widely distributed during the Tremadocian, and  
1011 the geographical distribution of the latter is decreasing over time: after being cosmopolitan during  
1012 the late Cambrian, it is only found throughout the southern peri-Gondwana realm and Baltica in the  
1013 Tremadocian.

1014

1015 4.2.1 *Gondwana*

1016 *Vulcanisphaera africana* is known from the Furongian to the Tremadocian of Iran (Ghavidel-  
1017 Syooki, 1993; 1994; 1995; 1997; 1998; 2000; 2001; 2006; Mehrjerdi, 2001; Ghavidel-Syooki and  
1018 Vecoli, 2008), Tunisia (Vecoli et al., 1999; Tongiorgi and Di Milia, 1999), Algeria (Deunff, 1961;  
1019 Combaz, 1967; Jardiné et al., 1974; Baudelot et al., 1981; Vecoli et al., 1995; 1999; Vecoli, 1996),  
1020 Iraq (Baban and Lawa, 2016), Italy (Pittau, 1985; Di Milia et al., 1993; Ribecai et al., 2005),  
1021 Argentina (e.g. Bultynck and Martin, 1982; Rubinstein, 1993; 1997; 2003; Rubinstein et al., 1999;  
1022 2003; Aráoz and Vergel, 2001; 2006; Vergel et al., 2002; Aráoz, 2002; Aceñolaza et al., 2003), and  
1023 appears in Furongian material of Bolivia (Vergel et al., 2013), and in the Tremadocian of Libya  
1024 (Deunff and Massa, 1975), Morocco (Elouad Debbaj, 1988; Nowak et al., 2015), France (e.g.,  
1025 Rauscher, 1971; 1973; Martin, 1973; Eisenack et al., 1976; Baudelot and Bessiere, 1977; Fournier-  
1026 Vinas, 1978; Cocchio, 1981; 1982; Baudelot and Fournier-Vinas, 1984), Czech Republic  
1027 (Vavrdová, 1976) and Germany (Reitz, 1991). Few occurrences of *V. mougnoana* are described in  
1028 the Miaolingian, i.e. in Spain (Palacios, 2015), Algeria (Vecoli et al., 2008), and Iran (Ghavidel-  
1029 Syooki and Vecoli, 2008). While the species becomes widely distributed during the Furongian, with  
1030 occurrences in Iran (Ghavidel-Syooki, 2006; Ghavidel-Syooki and Vecoli, 2008, Iraq (Baban and  
1031 Lawa, 2016), Libya (Albani et al., 1991; Tawadros et al., 2001), Tunisia (Vecoli et al., 1999),  
1032 Algeria (Vecoli et al., 1995; 1999; Vecoli, 1996), Italy (e.g., Di Milia, 1991; Di Milia et al., 1993;  
1033 Ribecai et al., 2005), Spain (Albani et al., 2006; Palacios, 2015), Bolivia (Vergel et al., 2013) and  
1034 Argentina (Aráoz and Vergel, 2006; Vergel et al., 2013), its distribution is notably more limited in  
1035 the Tremadocian, with findings in Algeria (Díez and Cramer, 1974; Jardiné et al., 1974; Vecoli et  
1036 al., 1995; Vecoli, 1996), France (Martin, 1973) and Argentina (Aráoz, 2002; Vergel et al., 2002;  
1037 Aceñolaza et al., 2003; Aráoz and Vergel, 2006). Occurrences of *V. simplex* are described for  
1038 Cambrian–Ordovician boundary strata in Iraq (Baban and Lawa, 2016), Spain (Fombella, 1979;  
1039 Fombella Blanco et al., 1993) and the Tremadocian of Iran (Ghavidel-Syooki, 2000, 2001;  
1040 Mehrjerdi, 2001; present study), Tunisia (Vecoli et al., 1999), Algeria (Jardiné et al., 1974; Vecoli

1041 et al., 1995, 1999; Vecoli, 1996; Vecoli and Playford, 1997), possibly Morocco (Elouad Debbaj,  
1042 1988), France (Baudelot and Fournier-Vinas, 1984), Italy (Pittau, 1985; Di Milia et al., 1993),  
1043 Germany (Reitz, 1991), and Argentina (Aceñolaza et al., 2003).

1044

#### 1045 4.2.2 Avalonia

1046 Occurrences of *V. africana* are recorded from the Furongian to Tremadocian of Newfoundland  
1047 (Dean and Martin, 1978; Martin, 1980; Martin in Martin and Dean, 1981, 1988; Parsons and  
1048 Anderson, 1986, 2000; Molyneux et al., 1996; Vanguetaine, 2002) and Belgium (Martin, 1969;  
1049 1973; 1975; Eisenack et al., 1973; Vanguetaine, 1973; 1978; 1991; Herbosch et al., 1991; Ribecai  
1050 and Vanguetaine, 1993) and in the Tremadocian of England (Booth, 1979; Molyneux and Rushton,  
1051 1984, 1988; Molyneux et al., 1996) and Wales (Tappin and Downie, 1978; Booth, 1979; Molyneux  
1052 and Dorning, 1989). *V. mougnoana* appears from the Miaoulingian to Furongian of Ireland (Brück  
1053 and Vanguetaine, 2004; Vanguetaine and Brück, 2008), Nova Scotia in Canada (Palacios et al.,  
1054 2009, 2012), from the Miaoulingian to Tremadocian of Newfoundland in Canada (Dean and Martin,  
1055 1978; Martin, 1980, 1982; Martin and Dean, 1981, 1988; Parsons and Anderson, 1986, 1996, 2000;  
1056 Volkova, 1990; Molyneux et al., 1996), in the Furongian of Belgium (Vanguetaine, 1986, 1992,  
1057 2002; Ribecai and Vanguetaine, 1993) and Wales (Young et al., 1994) and in Lower Ordovician  
1058 successions of England (Molyneux and Rushton, 1988). While *V. simplex* is not described for  
1059 Cambrian strata of Avalonia, it is recorded from the Tremadocian to Floian of England (Rasul,  
1060 1976, 1979; Molyneux and Rushton, 1984; Molyneux and Dorning, 1989) and the Tremadocian of  
1061 Belgium (Martin, 1975; André et al., 1991; Herbosch et al., 1991; Vanguetaine, 2008).

1062

#### 1063 4.2.3 Baltica

1064 Apart from one record in the Miaoulingian of the Moscow Basin (Volkova, 1980), *V. africana* is  
1065 described for the Furongian of Norway (Welsch 1986a, 1986b), from the Furongian to Tremadocian  
1066 of Sweden (Tongiorgi et al., 1988; Di Milia et al., 1989; Tongiorgi and Ribecai, 1990; Ribecai and

1067 Tongiorgi, 1997), the Baltic region (Yankauskas and Paškevičienė, 1972; Yankauskas 1976;  
1068 Kheinsalu et al., 1990; Paalits, 1992, 1995; Mens et al., 1997), the Holy Cross Mountains in Poland  
1069 (Górka, 1967, 1969; Żylińska et al., 2006) and Kolguev Island (Moczydłowska and Stockfors,  
1070 2004), the Moscow Basin (Aristova, 1980a) and the Kostroma region (Aristova, 1980b) in Russia,  
1071 and the Tremadocian of the Carpathian Foredeep Basin in Ukraine and Poland (Jachowicz-  
1072 Zdanowska, 2011). *V. mougnoana* appears from the Miaolingian to Tremadocian of the Carpathian  
1073 Foredeep Basin in Ukraine and Poland (Jachowicz-Zdanowska, 2011), the Furongian of the  
1074 Yaroslavl Oblast in Russia (Volkova, 1990) and the Holy Cross Mountains in Poland (Żylińska et  
1075 al., 2006), and from the Furongian to Tremadocian of Estonia (Volkova and Mens, 1988; Mens et  
1076 al., 1989, 1993; Volkova, 1989a, b, 1990; Paalits, 1992, 1995; Volkova and Sivertseva, 1991), the  
1077 Leningrad region (Volkova and Sivertseva, 1991) and the Moscow region in Russia (Volkova,  
1078 1996, 1999a, b). Records of *V. simplex* exist for the uppermost Cambrian of Poland (Jachowicz  
1079 Zdanowska, 2011), from the uppermost Cambrian to Tremadocian of Kolguev Island in Russia  
1080 (Moczydłowska and Stockfors 2004), in the Tremadocian of the Arkhangelsk Oblast (Volkova,  
1081 1995), the Moscow region (Aristova, 1980a; Volkova, 1999a) and the Saint Petersburg region  
1082 (Volkova, 1989c, 1993, 1995) in Russia, and Estonia (Volkova, 1989c, 1993, 1995; Paalits, 1995).

1083

#### 1084 4.2.4 North Kara Terrane

1085 *V. mougnoana* (as *V. turbata*) and *V. sp.* appear in Furongian material from October Revolution  
1086 Island of the Severnaya Zemlya Archipelago in the Arctic of Russia (Raevskaya and Golubkova,  
1087 2006). Palaeogeographically this locality is considered as belonging to a separate (micro-)plate  
1088 ('North Kara Terrane'; Metoelkin et al., 2000; Cocks and Torsvik, 2005, 2006; Lorenz et al., 2007),  
1089 which merged with Baltica in the Late Ordovician (Torsvik and Cocks, 2013).

1090

#### 1091 4.2.5 Laurentia



1092 The coverage of studies regarding acritarch material from Laurentia is rather poor. Therefore,  
1093 the fossil record is fairly sparse. *V. africana* is found in uppermost Cambrian to Tremadocian  
1094 successions of Alberta, Canada (Martin, 1992, 1993 [cf. aff.]; Molyneux et al., 1996) as well as in  
1095 reworked material from the Carboniferous of the County Clare in Ireland (Clayton et al., 1980). *V.*  
1096 *mouguoana* appears in the Furongian of Arkansas and Missouri, U.S.A. (Wood and Stephenson,  
1097 1989, 1990).

1098

1099

## 1100 **5 Discussion**

1101

1102 The results of the revision of the acritarch genus *Vulcanisphaera* shows a high intraspecific  
1103 variability of morphologies. In particular the process shape and length is highly variable in all of the  
1104 three species. Within this work, these observations are assumed to be related to ecophenotypism.  
1105 However, this interpretation remains only a hypothesis for now, as our data basis does not allow  
1106 testing if a correlation between morphology and palaeoecological parameters exists. The  
1107 sedimentology of the studied sections in the Algerian Sahara, in the Alborz (Iran) and in Shropshire  
1108 (England), has not been sufficiently investigated for this purpose. Rasul (1976) shows that the  
1109 process shapes of *V. simplex* in the Shineton Shales seem to change gradually through the  
1110 succession (text-figure 1; cf. Moczydłowska and Stockfors, 2004), which might be a response to a  
1111 changing environment. Analogies in fossil and modern dinoflagellates exist (e.g. Servais et al.,  
1112 2004). Cultural experiments with living dinoflagellates as well as observations of surface sediments  
1113 show a relationship between several morphological characteristics of dinoflagellate resting cysts  
1114 and environmental factors (e.g. Kokinos and Anderson, 1995; Dale, 1996; Ellegaard, 2000; Mertens  
1115 et al., 2009). Within these studies, variations in process length and vesicle diameter of dinoflagellate  
1116 resting cysts in response to variations of water temperatures and salinities were observed.  
1117 Considering that many acritarchs, such as *Vulcanisphaera*, are interpreted as resting cysts of  
1118 dinoflagellate-like organisms, it is reasonable to interpret the observed intraspecific morphological



1119 variations in *Vulcanisphaera* as reflecting a changing palaeoenvironments, possibly, in analogy to  
1120 modern dinoflagellate cysts, changing salinity and/or temperature. However, bringing a final  
1121 conclusion in this matter is out of the scope of this study.

1122 The great morphological variability of *Vulcanisphaera* and its relation to morphologically  
1123 similar taxa (such as *Cristallinium* and *Timofeevia*) show that the classification of acritarchs into  
1124 morphological large groups, such as plexi, should be discussed in the future.

1125

1126

## 1127 **6 Conclusions**

1128

1129 (1) The revision of the important Late Cambrian to Early Ordovician acritarch genus  
1130 *Vulcanisphaera* Deunff, 1961 shows that only three of the 32 described species can be maintained  
1131 within the genus: *V. africana* Deunff, 1961, *V. nougnoana* Martin, 1973 and *V. simplex* Jardiné et  
1132 al., 1974. Based on a comprehensive reinvestigation of the literature eleven species were found to  
1133 not show the diagnostic criteria for maintaining them within the genus *Vulcanisphaera*. The  
1134 remaining species are here considered junior synonyms of the three species validated in this study.

1135 (2) This new classification scheme has been tested and validated by quantitative multivariate  
1136 analyses of morphometric measurements of abundant material from three different localities in  
1137 Algeria, Great Britain and Iran.

1138 (3) The stratigraphic distribution of *Vulcanisphaera* extends from the Middle Cambrian Series 3  
1139 to the Floian (Early Ordovician), with questionable occurrences in younger material. *V. mougnoana*  
1140 appears in the Drumian, with its youngest occurrences described in Tremadocian to Floian  
1141 boundary strata. *V. africana* occurs with certainty in the Jiangshanian, and is present from the  
1142 Furongian to the Darriwilian (Middle Ordovician). Occurrences of *V. simplex* are known from the  
1143 latest Cambrian *Acerocare* zone and the Tremadocian (Lower Ordovician).

1144 (4) Regarding the palaeobiogeography of the genus, *Vulcanisphaera* shows a rather  
1145 cosmopolitan distribution, covering a wide range of latitudes, with occurrences described from all

1146 major palaeocontinents except Siberia, from which data are absent so far. Nevertheless, according  
1147 to the available data, the genus is restricted to the southern hemisphere and seems to show a  
1148 preference to warm-temperate to cold-temperate waters.

1149 (5) Morphological similarities between the genera *Vulcanisphaera* and *Timofeevia*  
1150 Vanguetaine, 1978, *Cristallinium* Vanguetaine, 1978 and *Retisphaeridium* Staplin, Jansonius and  
1151 Pocock, 1965 are recognised and need to be further clarified in future studies.

1152

1153

#### 1154 **Acknowledgments**

1155 D.M.K. acknowledges the Ecole Doctorale ED 104 (Sciences de la Matière, du Rayonnement et de  
1156 l'Environnement), University of Lille, for financial support in the frame of his PhD study. The  
1157 authors thank Charlie Wellman for the provision of samples from the collection of S. Rasul  
1158 (University of Sheffield). We acknowledge two anonymous referees for the valuable suggestions  
1159 that greatly improved the manuscript. This work is a contribution to the IGCP 653 'The Great  
1160 Ordovician Biodiversification Event.' (<http://www.igcp653.org/>).

1161

#### 1162 **References**

1163

1164 Aceñolaza, G.F., Aráoz, L., Vergel, M.D.M., Tortello, M.F., Nieva, S.M., 2003. Paleontology and  
1165 biostratigraphy of the Lower Ordovician strata cropping out at the Abra de Zenta (Cordillera  
1166 Oriental, Jujuy and Salta provinces), NW Argentina. In: Albanesi, G.L., Beresi, M.S., Peralta,  
1167 S.H. (Eds.), Ordovician from the Andes: Proceedings of the International Symposium on the  
1168 Ordovician System. Serie Correlación Geológica 17. Instituto Superior de Correlación  
1169 Geológica (INSUGEO), San Juan, Argentina, pp. 23–28.

1170 Albani, R., Massa, D., Tongiorgi, M., 1991. Palynostratigraphy (Acritarchs) of some Cambrian  
1171 Beds from the Rhadames (Ghadamis) Basin (western Libya-southern Tunisia). Bollettino della  
1172 Società Paleontologica Italiana 30, 255–280.

- 1173 Albani, R., Bagnoli, G., Bernárdez, E., Gutiérrez-Marco, J.C., Ribecai, C. 2006. Late Cambrian  
1174 acritarchs from the “Túnel Ordovícico del Fabar”, Cantabrian Zone, N Spain. Review of  
1175 Palaeobotany and Palynology 139, 41–52.
- 1176 Albani, R., Bagnoli, G., Ribecai, C., Raevskaya, E., 2007. Late Cambrian acritarch *Lusatia*:  
1177 Taxonomy, palaeogeography, and biostratigraphic implications. Acta Paleontologica Polonica  
1178 52 (4), 809–818.
- 1179 André, L., Herbosch, A., Louwey, S., Servais, T., Grootel, G. Van, Vanguetstaine, M., Verniers, J.,  
1180 1991. Guidebook to the excursion on the stratigraphy and Magmatic Roc of the Brabant Massif,  
1181 Belgium. Annales de la Société Géologique de Belgique 114, 283–323.
- 1182 Aráoz, L., 2002. Palinología de los niveles inferiores de la Formación Santa Rosita, en el Abra de  
1183 Zenta, provincias de Salta y Jujuy, República Argentina. Seminario Inédito. Facultad de  
1184 Ciencias Naturales e I.M.L, Universidad Nacional de Tucumán, Tucumán, Argentina, p. 187.
- 1185 Aráoz, L., Vergel, M.d.M., 2001. Acritarcos del Ordovícico Inferior (Formación Santa Rosita) en el  
1186 Abra de Zenta, Cordillera Oriental, Argentina. V Jornadas de Comunicaciones. Facultad de  
1187 Ciencias Naturales e I.M.L, Universidad Nacional de Tucumán (Serie Monográfica y Didáctica.  
1188 41), Tucumán, Argentina, p. 55.
- 1189 Aráoz, L., Vergel, M.d.M., 2006. Palinología de la transición Cambro-Ordovícica en Quebrada de  
1190 Moya, Cordillera Oriental, Argentina. Revista Brasileira de Paleontologia 9 (1), 1–8.
- 1191 Aristova, K.E., 1980a. Etalonnnye kompleksy Mikrfossiliiy Ordovika i Silura Moskovskoy Sineklizy.  
1192 Palynology in USSR: Articles of the Soviet palynologists for the 5th International Palynological  
1193 Conference in Cambridge. Akademiya Nauk SSSR, Leningrad, Russia, pp. 47–49. (in Russian)
- 1194 Aristova, K.E., 1980b. Akritarckhi pogramichnykh sloev tremadokskogo i arenigskogo yarusov  
1195 Moskovskoj sineklizy. In: Byvsheva, T.V. (Ed.), Palinologicheskie issledovaniya Proterozoya i  
1196 Fanerozoya neftegazonoshykh provintsyj. Trudy Vsesoyuznogo Neftyanogo Nauchno-  
1197 Issledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI), Leningrad, Russia, 217, pp. 10–  
1198 18. (in Russian)

- 1199 Arthurton, R.S., Wadge, A.J., 1981. Ordovician and Silurian. In: Arthurton, R.S., Wadge, A.J.  
1200 (Eds.), *Geology of the Country around Penrith*. Geological Survey of Great Britain (Memoirs,  
1201 Sheet - New Series), London, U.K., pp. 4–21.
- 1202 Baban, D.H., Lawa, F.A., 2016. Palynological and stratigraphical evidences on the Age of the  
1203 outcropped Khabour Formation near Chalki Nasara Village, Kurdistan Region, northern Iraq.  
1204 *JZS Special Issue, GeoKurdistan II*, 293–318.
- 1205 Baudelot, S., Bessiere, G., 1977. Données palynostratigraphiques sur le Paleozoique Inferieur du  
1206 Massif de Mouthoumet (Hautes Corbieres,Aude). *Annales de la Société Géologique du Nord*,  
1207 97, 21–25.
- 1208 Baudelot, S., Fournier-Vinas, C., 1984. Bassins Paleozoiques Caches sous l'Aquitaine-Etude  
1209 micropaleontologique de Carottes Prelevees a l'Occasion de Forages Petroliers. In: *Geologie  
1210 Profonde de la France - Program of deep geology of France first phase of investigation - 1983-  
1211 1984*, Documents du Bureau des Recherches Géologiques et Minières 81 (7), 1–11.
- 1212 Baudelot, S., Bouillin, J.-P., Durand-Delga, M., 1981. Decouverte d'ordovicien Inferieur Date par  
1213 Acritarches dans l'Ouest de la Pitite Dabylie (Algerie); Consequences structurales. *Comptes  
1214 Rendus de l'Académie des Sciences, Série II*, 293, 611–614.
- 1215 Bayet-Goll, A., Neto de Carvalho, C., 2015. Ichnology and sedimentology of a tide-influenced delta  
1216 in the Ordovician from the northeastern Alborz range of Iran (Kopet Dagh region). *Lethaia* 49,  
1217 327-350.
- 1218 Blain, M., 1963. Découverte de la zone à Dictyonema flabelliforme Eichwald dans l'Ordovicien  
1219 inférieur du Sahara algérien septentional. *Bulletin de la Société Géologique de France* 5 (7),  
1220 1105–1112.
- 1221 Booth, G.A., 1979. Lower Ordovician Acritarchs from successions in England and North Wales.  
1222 Ph.D. thesis, Department of Geology, University of Sheffield, England.
- 1223 Boucot, A.J., Chen Xu, Scotese, C.R., Morley, R.J., 2013. *Phanerozoic Paleoclimate: An Atlas of  
1224 Lithologic Indicators of Climate*. Society for Sedimentary Geology (SEPM Concepts in

- 1225 Sedimentology and Paleontology 11), Tulsa (OK).
- 1226 Boyden, J.A., Müller, R.D., Gurnis, M., Torsvik, T.H., Clark, J.A., Turner, M., Ivey-Law, H.,  
1227 Watson, R.J., Cannon, J.S., 2011. Next-generation plate-tectonic reconstructions using Gplates.  
1228 In: Keller, G.R., Baru, C. (Eds.), Geoinformatics: Cyberinfrastructure for the Solid Earth.  
1229 Cambridge University Press, Cambridge, pp. 95–114.
- 1230 Brenchley, P.J., Rushton, A.W.A., Howells, M., Cave, R., 2006. Cambrian and Ordovician: the  
1231 early Palaeozoic tectonostratigraphic evolution of the Welsh Basin, Midland and Monian  
1232 Terranes of Eastern Avalonia. In: Brenchley, P.J., Rawson, P.F. (Eds.), The Geology of England  
1233 and Wales, 2nd edition. Geological Society of London, London, pp. 25–74.
- 1234 Brocke, R., Fatka, O., Molyneux, S.G., Servais, T., 1995. First appearance data of selected Early  
1235 Ordovician acritarch taxa from Peri-Gondwana. In: Cooper, J.D., Droser, M.L., Finney, S.C.  
1236 (Eds.), Ordovician Odyssey: Short Papers for the 7<sup>th</sup> International Symposium on the  
1237 Ordovician System. Pacific Section – Society for Sedimentary Geology (PS-SEPM), Fullerton  
1238 (CA), USA, pp. 473–476.
- 1239 Brocke, R., Fatka, O., Servais, T., 1997. A review of the Ordovician acritarchs *Aureotesta* and  
1240 *Marrocanium*. Annales de la Société Géologique de Belgique 120 (1), 1–21.
- 1241 Brück, P.M., Vanguetaine, M., 2004. Acritarchs from the Lower Palaeozoic succession on the  
1242 south County Wexford coast, Ireland: new age constraints for the Cullenstown Formation and  
1243 the Cahore and Ribband Groups. Geological Journal 39(2), 199–224.
- 1244 Bultynck, P., Martin, F., 1982. Conodontes et Acritarches de l'Ordovicien Inferieur et Acritarches  
1245 du Silurian Inferieur de la Partie Septentrional de la Cordillere Argentine. Bulletin de l'Institut  
1246 Royal des Sciences Naturelles de Belgique 53 (4), 1–21.
- 1247 Clayton, G., Johnston, I.S., Smith, D.G., 1980. Micropalaeontology of a Courceyan (Carboniferous)  
1248 borehole section from Ballyvergin, County Clare, Ireland. Journal of Earth Sciences 3(1), 81–  
1249 100.

- 1250 Cocchio, A.M., 1981. Microflores des Series du Paleozoique Inferieur du Massif de Mouthoumet  
1251 (Corbieres, Aude). Ph.D. thesis, Université Paul-Sabatier, Toulouse, France.
- 1252 Cocchio, A.M., 1982. Donnees nouvelles sur les Acritarches du Tremadoc et de l'Arenig dans le  
1253 Massif de Mouthoumet (Corbieres, France). *Revue de Micropaléontologie* 25 (1), 26–36.
- 1254 Cocks, L.R.M., 1989. The geology of South Shropshire. *Proceedings of the Geologists' Association*,  
1255 100 (4), 505–519.
- 1256 Cocks, L.R.M., Torsvik, T.H., 2005. Baltica from the late Precambrian to mid-Palaeozoic times: the  
1257 gain and loss of a terrane's identity. *Earth-Science Reviews* 72, 39–66.
- 1258 Cocks, L.R.M., Torsvik, T.H., 2006. European geography in a global context from the Vendian to  
1259 the end of the Palaeozoic. *In: Gee, D.G., Stephenson, R.A. (Eds.), European Lithosphere*  
1260 *Dynamics. Geological Society, Memoirs 32. Geological Society, London, UK, pp. 83–95.*
- 1261 Combaz, A., 1967. Un microbios du Trémadocien dans un sondage d'Hassi-Messaoud. *Actes de la*  
1262 *Société linéenne de Bordeaux* 104, série B. 29, 1–26.
- 1263 Cramer, F.H., Díez, M.d.C.R., 1977. Late Arenigian (Ordovician) acritarchs from Cis-Saharan  
1264 Morocco. *Micropaleontology* 23 (3), 339–360.
- 1265 Dale, B., 1996. Dinoflagellate cyst ecology: modelling and geological applications. *In: Jansonius,*  
1266 *J., McGregor, D.C. (Eds.), Palynology: Principles and Applications, Vol. 3. American*  
1267 *Association of Stratigraphic Palynologists Foundation, Dallas (TX), USA, pp. 1249–1275.*
- 1268 Dean, W.T., Martin, F., 1978. Lower Ordovician acritarchs and trilobites from Bell Island, eastern  
1269 Newfoundland. *Geological Survey of Canada Bulletin* 284, 35.
- 1270 Deunff, J., 1961. Un microplancton à Hystrichosphères dans le Trémadoc du Sahara. *Revue de*  
1271 *Micropaléontologie* 4 (1), 37–52.
- 1272 Deunff, J., Massa, D., 1975 Palynologie et stratigraphie du Cambro-Ordovicien (Libye nord-  
1273 occidentale). *Comptes Rendus de l'Académie des Sciences Paris, Série D*, 281, 21-24.
- 1274 Di Milia, A., 1991. Upper Cambrian acritarchs from the Solanas Sandstone Formation, Central  
1275 Sardinia, Italy. *Bollettino della Società Paleontologica Italiana* 30 (2), 127–152.

- 1276 Di Milia, A., Ribecai, C., Tongiorgi, M., 1989. Late Cambrian acritarchs from the Peltura  
1277 scarabaeoides Trilobite Zone at Degerhamn (Oland, Sweden). *Palaeontographia Italica* 76, 1–56.
- 1278 Di Milia, A., Tongiorgi, M., Albani, R., 1993. Acritarch findings in Early Paleozoic, low-grade  
1279 metasediments of Sardinia (Italy): A review. *Revista Española de Paleontología* 8 (2), 170–176.
- 1280 Díez, M.d.C.R., Cramer, F.H., 1974. Range chart of selected Lower Paleozoic acritarch Taxa.  
1281 *Review of Palaeobotany and Palynology* 18 (1), 155–170.
- 1282 Downie, C., 1958. An assemblage of microplankton from the Shineton Shales (Tremadocian).  
1283 *Proceedings of the Yorkshire Geological Society* 31 (4/ 12), 331–350.
- 1284 Downie, C., 1982. Lower Cambrian acritarchs from Scotland, Norway, Greenland and Canada.  
1285 *Transactions of the Royal Society of Edinburgh, Earth Sciences* 72, 245–266.
- 1286 Downie, C., Sarjeant, W.A.S., 1965. Bibliography and index of fossil dinoflagellates and acritarchs.  
1287 *Geological Society of America, Memoir* 94, 1–180.
- 1288 Eisenack, A., 1959. Neotypen baltischer Silur-Hystrichosphären und neue Arten. *Palaeontographica*  
1289 112A, 193–211.
- 1290 Eisenack, A., Cramer, F.H., Díez, M.d.C.R., 1973. Katalog der fossilen Dinoflagellaten,  
1291 Hystrichosphären und verwandten Mikrofossilien, Band III, Acritarcha 1. Teil. E.  
1292 Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.
- 1293 Eisenack, A., Cramer, F.H., Díez, M.d.C.R., 1976. Katalog der fossilen Dinoflagellaten,  
1294 Hystrichosphären und verwandten Mikrofossilien, Band IV, Acritarcha 2. Teil. E.  
1295 Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.
- 1296 Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing  
1297 salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and*  
1298 *Palynology* 109, 65–81.
- 1299 Elouad-Debbaij, Z., 1988. Acritarches et Chitinozoaires du Trémadoc de l'Anti-Atlas central  
1300 (Maroc). *Revue de Micropaléontologie* 31 (2), 85–128.
- 1301 Evitt, W.R., 1963. A discussion and proposals concerning fossil dinoflagellates, Hystrichospheres,

- 1302 and acritarchs. II. Proceedings of the Indian National Science Academy 49 (3), 298–302.
- 1303 Fang, X., 1986. Ordovician micropaleoflora in Kunming-Luquan Region, Yunnan Province, and its  
1304 stratigraphical significance. Professional Papers on Stratigraphy and Palaeontology 16, 125–  
1305 172. (in Chinese, with English abstract)
- 1306 Fatka, O., Brocke, R., 1999. Morphologic variability in two populations of *Arbusculidium*  
1307 *filamentosum* (Vavrdová 1965) Vavrdová 1972. Palynology 23, 153–180.
- 1308 Fatka, O., Brocke, R., 2008. Morphologic variability in Lower Palaeozoic acritarchs: Importance  
1309 for acritarch systematics. Acta Musei Nationalis Pragae – Series B – Historia Naturalis 64 (2-4),  
1310 97–107.
- 1311 Fatka, O., Molyneux, S.G., Servais, T., 1997. The Ordovician acritarch *Frankea*: some critical  
1312 remarks. Geobios 30 (3), 321–326.
- 1313 Fombella, M.A., 1977. Acritarcos de edad Cámbrico Medio – Inferior de la Provincia de León,  
1314 España. Revista Española de Micropaleontología 9 (1), 115–124.
- 1315 Fombella, M.A., 1978. Acritarcos de la Formacion Oville, edad Cámbrico Medio-Tremadoc,  
1316 Provincia de León, España. Palinología, Número extraordinario 1, 245–261.
- 1317 Fombella, M.A., 1979. Palinología de la Formación Oville al norte y sur de la Cordillera  
1318 Cantábrica, España. Palinología 1, 1–17.
- 1319 Fombella Blanco, M.A., Valencia Barrera, R.M., Fernández González, D., Cachán Santos, L.J.,  
1320 1993. Diferencias de composición en las asociaciones de acritarcos de seis localidades de la  
1321 Formación Oville (No de España). Edad Cámbrico Medio-Tremadoc Inferior. Revista Española  
1322 de Paleontología 8 (2), 221–235.
- 1323 Fortey, R.A., Rushton, A.W.A., 2000. Welsh Borderland. In: Fortey, R. A., Harper, D.A.T.,  
1324 Ingham, J.K., Owen, A.W. Parkes, M.A., Rushton, A.W.A., Woodcock, N.H. (Eds.), A revised  
1325 correlation of Ordovician Rocks in the British Isles. Geological Society of London (Special  
1326 Reports 24), London, UK, pp. 25–28.



- 1327 Fournier-Vinas, C., 1978. Acritarches Cambro-Ordoviciens des Monts de Lacaune (Nord de la  
1328 Montagne Noire, France). *Palinologiá*, Número extraordinario 1, 263–271.
- 1329 Fridrichsone, A.I., 1971. Akritarkhi *Baltisphaeridium* i gistrikhosfery(?) iz kembriiskikh otlozhenii  
1330 Latvii. In: *Paleontologiya i Stratigrafiya Pribaltiki i Belorussii*, sbornik III. Lithuanian Science  
1331 Research, Geological Survey Institute, Vilnius, 3, 5–22.
- 1332 Geyer, G., Bayet-Goll, A., Wilmsen, M., Mahboubi, A., Moussavi-Harami, R., 2014.  
1333 Lithostratigraphic revision of the middle Cambrian (Series 3) and upper Cambrian (Furongian)  
1334 in northern and central Iran. *Newsletters on Stratigraphy* 47, 21–59.
- 1335 Ghavidel-Syooki, M., 1993. Palynological study of Paleozoic sediments of the Chal-i-Sheh area,  
1336 southwestern Iran. *Journal of Sciences Islamic Republic of Iran* 4(1), 32–46.
- 1337 Ghavidel-Syooki, M., 1994. Biostratigraphy and paleo-biogeography of some Paleozoic rocks at  
1338 Zagros and Alborz Mountains. *Geological Survey of Iran, Treatise on the Geology of Iran* 18,  
1339 1–168.
- 1340 Ghavidel-Syooki, M., 1995. Palynostratigraphy and palaeogeography of a Palaeozoic sequence in  
1341 the Hassanakdar area, Central Alborz Range, Northern Iran. *Review of Palaeobotany and*  
1342 *Palynology* 86, 1, 91–109.
- 1343 Ghavidel-Syooki, M., 1996. Palynostratigraphy and paleobiogeography of the Lower Paleozoic  
1344 sequence in the northeastern Alborz range (Kopet-Dagh region) of Iran. In: Goodman, D.K.,  
1345 Clarke, R.T. (eds), *Proceedings of the IX International Palynological Congress*, Houston, TX.  
1346 American Association of Stratigraphic Palynologists Foundation, pp. 17–35.
- 1347 Ghavidel-Syooki, M., 1997. Acritarch biostratigraphy of the Palaeozoic rock units in the Zagros  
1348 Basin, Southern Iran. In: Fatka, O., Servais, T. (Eds.), *Acritarcha in Praha*. Proceedings of the  
1349 International Meeting and Workshop of the Acritarch Subcommittee of the Commission  
1350 Internationale de microflore du Paleozoique (CIMP), 1996, Prague, Czech Republic. Univerzita  
1351 Karlova, Prague (*Acta Universitatis Carolinae, Geologica* 40, 3–4), pp. 385–411.

- 1352 Ghavidel-Syooki, M., 1998. Acritarch biostratigraphy and palaeogeography of Lower Palaeozoic  
1353 rock units at Southwestern Kashmar City, Central Iran. Programme and Abstracts for the CIMP  
1354 Symposium and Workshops in Pisa, Italy. Università degli Studi di Pisa, Dipartimento di  
1355 Scienze della Terra, Pisa, Italy, pp. 13-14.
- 1356 Ghavidel-Syooki, M., 2000. Palynostratigraphy and palaeobiogeography of Lower Paleozoic strata  
1357 in the Ghelli area, northeastern Alborz Range of Iran (Kopet-Dagh Region). Iranian Journal of  
1358 Science and Technology 11 (4), 305–318.
- 1359 Ghavidel-Syooki, M., 2001. Palynostratigraphy and paleobiogeography of the Lower Paleozoic  
1360 sequence in the northeastern Alborz Range (Kopet-Dagh Region) of Iran. In: Goodman, D.K.,  
1361 Clarke, R.T. (Eds.), Proceeding of the IX International Palynological Congress, 1996, Houston  
1362 (TX), USA. American Association of Stratigraphic Palynologists Foundation, Dallas (TX),  
1363 USA, pp. 17–35.
- 1364 Ghavidel-Syooki, M., 2006. Palynostratigraphy and palaeogeography of the Cambro-Ordovician  
1365 strata in southwest of Shahrud City (Kuh-e-Kharbash, near Deh-Molla), Central Alborz Range,  
1366 northern Iran. Review of Palaeobotany and Palynology 139, 81–95.
- 1367 Ghavidel-Syooki, Vecoli, 2007. Latest Ordovician–early Silurian chitinozoans from the eastern  
1368 Alborz Mountain Rangem Kopet–Dagh region, northeastern Iran: biostratigraphy and  
1369 palaeobiogeography. Review of Palaeobotany and Palynology 145, 173–192.
- 1370 Ghavidel-Syooki, M., Vecoli, M., 2008. Palynostratigraphy of Middle Cambrian to lowermost  
1371 Ordovician stratal sequences in the High Zagros Mountains, southern Iran: Regional  
1372 stratigraphic implications, and palaeobiogeographic significance. Review of Palaeobotany and  
1373 Palynology 150, 97–114.
- 1374 Ghavidel-Syooli, M., Winchester-Seeto, T., 2002. Ghavidel-Syooki, M. et al. (2002) Biostratigraphy  
1375 and palaeogeography of Late Ordovician chitinozoans from the northeastern Alborz Range, Iran  
1376 Review of Palaeobotany and Palynology 118(4), 77–99.
- 1377 Ghobadi Pour, M., Kebriaee-Zadeh, M.R., Popov, L.E., 2011. Early Ordovician (Tremadocian)

1378 brachiopods from the Eastern Alborz Mountains, Iran. *Estonian Journal of Earth Sciences* 60,  
1379 65–82.

1380 Górká, H., 1967. Quelques nouveaux acritarches des silexites du Trémadocien supérieur de la  
1381 région de Kielce (Montagne de Ste. Croix, Pologne). *Cahiers de Micropaléontologie, Série 1* 6;  
1382 Archives originales, Centre de documentation; Centre National de la Recherche Scientifique,  
1383 France 441, 1–8.

1384 Górká, H., 1969. Microorganismes de l'Ordovicien de Pologne. *Palaeontologia Polonica* 22, 1–102.

1385 Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: palaeontological statistics software package  
1386 for education and data analysis. *Palaeontologia Electronica* 4, 1–9.

1387 Hammer, O., Harper, D.A.T., 2006. *Paleontological data analysis*. Oxford: Blackwell Publishing.

1388 He, S.-C., Yin, L.-M., 1993. Late Ordovician acritarchs from the Changwu Formation of Jiangshan,  
1389 Zhejiang, China. *Acta Palaeontologica Sinica (Gushengwu Xuebao)* 32 (5), 611–633. (in  
1390 Chinese, with English summary)

1391 Herbosch, A., Vanguetstaine, M., Degardin, J.M., Dejonghe, L., Fagel, N., Servais, T., 1991. Etude  
1392 lithostratigraphique, biostratigraphique et sédimentologique du Sondage de Lessines (Bord  
1393 Meridional du Massif du Brabant, Belgique). *Annales de la Société Géologique de Belgique* 114  
1394 (1), 195–212.

1395 Jachowicz-Zdanowska, M., 2011. Cambrian organic microfossils at the border area of the East- and  
1396 West-European Platforms (SE Poland and Western Ukraine). *Annales Societatis Geologorum*  
1397 *Poloniae* 81, 241–267.

1398 Jahangir, H., Ghobadi Pour, M., Ashuri, A., Amini, A., 2015. Terminal Cambrian and Early  
1399 Ordovician (Tremadocian) conodonts from Eastern Alborz, north-central Iran. *Alcheringa: An*  
1400 *Australian Journal of Palaeontology* 40(2), 219–243.

1401 Jardiné, S., Combaz, A., Magloire, L., Peniguel, G., Vachey, G., 1974. Distribution stratigraphique  
1402 des acritarches dans le Paléozoïque du Sahara Algérien. *Review of Palaeobotany and*  
1403 *Palynology* 18 (1), 99–129.

- 1404 Kheinsalu, K., Viira, V., Paalits, I., 1990. Pogranichnye Kembro-Ordovikskie otlozheniya Razreza  
1405 Saka Ii v Severo-Vostochnoi Estonii. Eesti NSV Teaduste Akadeemia Toimetised, Geologia  
1406 40 (1), 8–15. (in Russian)
- 1407 Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the  
1408 marine dinoflagellate *Lingulodinium polyedrum* (= *L. machaerophorum*). Palynology 19, 143–  
1409 166.
- 1410 Lavoie, D., Burden, E., Lebel, D., 2003. Stratigraphic framework for the Cambrian-Ordovician rift  
1411 and passive margin successions from southern Quebec to western Newfoundland. Canadian  
1412 Journal of Earth Sciences 40, (2), 177–205.
- 1413 Legault, J.A., 1982. First report of Ordovician, (Caradoc-Ashgill) palynomorphs from Orphan  
1414 Knoll, Labrador Sea. Paleontologicheskii Zhurnal (Paleontological Journal) 19 (9), 1851–1856.
- 1415 Legrand, P., 1974. Résultats récents sur le problème de la limite Cambrien-Ordovicien au Sahara  
1416 algérien septentrional. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 64 (1–2),  
1417 159–180.
- 1418 Legrand, P., 1985. Lower Palaeozoic rocks of Algeria. In: Holland, C.H. (Ed.), Lower Palaeozoic of  
1419 North-Western and West Central Africa (Lower Palaeozoic Rocks of the World, 4). John Wiley  
1420 and Sons Ltd., New York, USA, pp. 5–90.
- 1421 Le Hérissé, A., 1989. Acritarches et kystes d'algues prasinophycees du Silurien de Gotland, Suede.  
1422 Palaeontographia Italica 76, 57-302.
- 1423 Li, J., Servais, T., Yan, K., 2014. The Ordovician acritarch genus *Rhopaliophora*: Biostratigraphy,  
1424 palaeobiogeography and palaeoecology. Review of Palaeobotany and Palynology 208, 1–24.
- 1425 Lorenz, H., Männik, P., Gee, D., Proskurnin, V., 2007. Geology of the Severnaya Zemlya  
1426 Archipelago and the North Kara Terrane in the Russian high Arctic. International Journal of  
1427 Earth Sciences (Geologische Rundschau) 97, 519–547.

- 1428 Martin, F., 1969. Les Acritarches de l'Ordovicien et du Silurien belges. Détermination et valeur  
1429 stratigraphique. Institut royal des sciences naturelles de Belgique, Mémoire 160, 1–175. (Cover  
1430 date 1968, but issue date 1969)
- 1431 Martin, F., 1973. Les acritarches de l'Ordovicien Inferieur de la Montagne Noire (Herault, France).  
1432 Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 48, (10), 1–61. (cover date  
1433 1972, but issue date 1973)
- 1434 Martin, F., 1975. Acritarches du Cambro-Ordovicien du Massif Brabant, Belgique. Bulletin de  
1435 l'Institut Royal des Sciences Naturelles de Belgique 51, (1), 1–38.
- 1436 Martin, F., 1980. Middle and Upper Cambrian and Lower Ordovician acritarchs from Random  
1437 Island, eastern Newfoundland. Abstracts of the 5<sup>th</sup> International Palynological Conference,  
1438 Cambridge, U.K., p. 251.
- 1439 Martin, F., 1982. Some aspects of late Cambrian and early Ordovician acritarchs. In: Bassettm  
1440 M.G., Dean, W.T., (eds), The Cambrian – Ordovician boundary: sections, fossil distributions,  
1441 and correlations. National Museum of Wales, Geological Series No. 3, Cardiff, 227 pp.
- 1442 Martin, F. 1992. Uppermost Cambrian and Lower Ordovician acritarchs and Lower Ordovician  
1443 chitinozoans from Wilcox Pass, Alberta. Geological Survey of Canada, Bulletin 420, 1–57.
- 1444 Martin, F. 1993. Acritarchs: a reiew. Biological Reviews of the Cambridge Philosophical Society  
1445 68(4), 475–538.
- 1446 Martin, F., Dean, W.T., 1981. Middle and Upper Cambrian and Lower Ordovician acritarchs from  
1447 Random Island, Eastern Newfoundland. Geological Survey of Canada, Bulletin 43 pp.
- 1448 Martin, F., Dean, W.T., 1983. Late Early Cambrian and early Middle Cambrian acritarchs from  
1449 Manuels River, eastern Newfoundland. Current Research, Part B, Geological Survey of Canada,  
1450 Paper 83-1B, 353–363.
- 1451 Martin, F., Dean, W.T., 1988. Middle and Upper Cambrian acritarch and Trilobite zonation at  
1452 Manuels River and Random Island, eastern Newfoundland. Geological Survey of Canada,  
1453 Bulletin, 91 pp.

- 1454 Massa, D., 1988. Paléozoïque de Libye Occidentale : Stratigraphie et Paléogéographie. Ph.D. thesis,  
1455 University of Nice, France.
- 1456 Mehrjerdi, H., 2001. Palynostratigraphy and palaeobiogeography of a Lower Palaeozoic sequence  
1457 in the type-section of Shirgesht Formation, Northern Tabas City, East-Central Iran. Iranian  
1458 International Journal of Science 2 (2), 129–153.
- 1459 Mélou, M., Oulebsir, L., Paris, F., 1999. Brachiopodes et chitinozoaires ordoviciens dans le NE du  
1460 Sahara Algérien: Implications stratigraphiques et paléogéographiques. Geobios 32 (6), 823–839.
- 1461 Mens, K.A., Viive, V., Paalits, I., Puura, I., 1989. Cambrian-Ordovician boundary Beds at  
1462 Maekalda, Tallinn, North Estonia. Eesti NSV Teaduste Akadeemia Toimetised, Geologia 38,  
1463 (3), 101–111.
- 1464 Mens, K.A., Viira, V., Paalits, I., Puura, I., 1993. Biostratigrafiya verkhnego Kembriya Estonii.  
1465 Eesti NSV Teaduste Akadeemia Toimetised, Geologia 42. 148–159. (in Russian)
- 1466 Mens, K.A., Paalits, I., Puura, I., 1997. Upper Cambrian acritarchs from the basal conglomerate of  
1467 the Kallavere Formation on the Pakri Peninsula, northwestern Estonia. In: Fatka, O., Servais, T.  
1468 (Eds.), Acritarcha in Praha. Proceedings of the International Meeting and Workshop of the  
1469 Acritarch Subcommittee of the Commission Internationale de microflore du Paleozoique  
1470 (CIMP), 1996, Prague, Czech Republic. Univerzita Karlova, Prague (Acta Universitatis  
1471 Carolinae, Geologica 40, 3–4), 531–543.
- 1472 Mertens K.N., Ribeiro, S., Bouimetarhan, I., Caner, H., Combourieu-Nebout, N., Dale, B., De  
1473 Vernal, A., Ellegaard, M., Filipova, M., Godhe, A., Goubert, E., Grøsfjeld, K., Holzwarth, U.,  
1474 Kotthoff, U., Leroy, S.A.G., Londeix, L., Marret, F., Matsuoka, K., Mudie, P.J., Naudts, L.,  
1475 Peña-Manjarrez, J.L., Persson, A., Popescu, S.-M., Pospelova, V., Sangiorgi, F., van der Meer  
1476 M.T.J., Vink, A., Zonneveld, K.A.F., Vercauteren, D., Vlassenbroeck, J., Louwye, S., 2009.  
1477 Process length variations in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in  
1478 surface sediments: Investigation its potential as salinity proxy. Marine Micropalaeontology 70,  
1479 54–69.

- 1480 Metoelkin, D.V., Kazansky, A.Y., Vernikovsky, V.A., Gee, D., Torsvik, T.H., 2000. Pervyye  
1481 paleomagnitnyye dannyye po rannemu paleozoyu arhipelaga Severnaya Zemlya i ikh  
1482 geodinamicheskaya interpretatsiya. *Geologiya i Geofizika* 41 (12), 1816–1820. (in Russian)
- 1483 Moczyłowska, M., Stockfors, M., 2004. Acritarchs from the Cambrian-Ordovician Boundary  
1484 Interval on Kolguev Island, Arctic Russia. *Palynology* 28, 15–73.
- 1485 Moczyłowska, M., Popov, L., Stockfors, M., 2004. Upper Cambrian-Ordovician successions  
1486 overlying Timanian complexes: new evidence of acritarchs and brachiopods from Kolguev Island,  
1487 Arctic Russia. *Geobios* 37, 239–251.
- 1488 Molyneux, S.G., 1990. Advances and problems in Ordovician palynology in England and Wales.  
1489 *Journal of the Geological Society, London* 147 (4), 615–618.
- 1490 Molyneux, S.G., 1999. A reassessment of Manx Group acritarchs, Isle of Man. Geological Society,  
1491 London, Special Publications 160, 23–32.
- 1492 Molyneux, S.G., Dorning, K.J., 1989. Acritarch dating of Latest Tremadoc - Earliest Arenig (Early  
1493 Ordovician) sediments in the Carmarthen District, South Wales. *Geological Magazine* 126 (6),  
1494 707–714.
- 1495 Molyneux, S.G., Rushton, A.W.A., 1984. Discovery of Tremadoc rocks in the Lake District.  
1496 *Proceedings of the Yorkshire Geological Society* 45 (1), 123–127.
- 1497 Molyneux, S.G., Rushton, A.W.A., 1988. The age of the Watch Hill Grits, (Ordovician), English  
1498 Lake District; Structural and palaeogeographical implications. *Transactions of the Royal Society  
1499 of Edinburgh. Earth Sciences* 79, 43–69.
- 1500 Molyneux, S.G., Le Hérissé, A., Wicander, R., 1996. Paleozoic phytoplankton. In: Jansonius, J.,  
1501 Mcgregor, D.C. (Eds.), *Principles and Applications. Applications. American Association of  
1502 Stratigraphic Palynologists, Dallas (TX), USA*, pp. 493–529.
- 1503 Navidi-Izad, N., Hashemi, H., Regnier, S., Kroeck, D., Yan, K., Servais, T., 2020. Revision of the  
1504 Middle–Upper Ordovician acritarch genus *Orthosphaeridium* Eisenack 1968 nov. emend.  
1505 *Review of Palaeobotany and Palynology* 273.

- 1506 Nowak, H., Akodad, M., Lefebvre, B., Servais, T., 2015. Discovery of the messaoudensis-trifidum  
1507 acritarch assemblage (upper Tremadocian-lower Floian, Lower Ordovician) in the subsurface of  
1508 Morocco. *Estonian Journal of Earth Sciences* 64, (1), 80–83.
- 1509 Olaru, L., Lazar, A., 2005. New data on typical acritarch assemblage from the Upper Formation  
1510 (TG-4) from Tulghes Group, Balan Area, Eastern Carpathians (Romania). *Analele Științifice ale*  
1511 *Universității “Al. I. Cuza” Iași, Geologie* LI, 77–96.
- 1512 Oulebsir, L., 1992. Chitinozoaires et palynomorphes dans l'Ordovicien du Sahara algérien :  
1513 biostratigraphie et approche des paléoenvironnements. Ph.D. thesis, University of Rennes I,  
1514 Rennes, France.
- 1515 Oulebsir, L., Paris, F., 1993. Nouvelles espèces de chitinozoaires dans l'Ordovicien inférieur et  
1516 moyen du sud-est du Sahara algérien. *Revue de Micropaléontologie* 36 (3), 269–292.
- 1517 Oulebsir, L., Paris, F., 1995. Chitinozoaires ordoviciens du Sahara algérien : biostratigraphie et  
1518 affinités paléogéographiques. *Review of Palaeobotany and Palynology* 86, 49–68.
- 1519 Paalits, I., 1992. Upper Cambrian acritarchs from boring core M-72 of North Estonia. *Proceedings*  
1520 *of the Estonian Academy of Sciences, Geology* 41 (1), 29–37.
- 1521 Paalits, I., 1995. Acritarchs from the Cambrian–Ordovician boundary beds at Tõnismägi, Tallin,  
1522 North Estonia. *Proceedings of the Estonian Academy of Sciences, Geology* 44 (2), 87–96.
- 1523 Paalits, I., Heuse, T., 1998. Late Cambrian and Early Ordovician organic-walled microfossils from  
1524 Well Danilov-7 (Moscow Syncline, East European Platform). *CIMP Symposium and*  
1525 *Workshops in Pisa, Italy. CIMP Newsletter* 55, 18.
- 1526 Palacios, T., 2008. Middle Cambrian acritarchs zones in the Oville Formation and their correlation  
1527 with trilobite zones in the Cantabrian Mountains, Northern Spain. In: Rábano, I., Gozalo, R.,  
1528 García Bellido, D. (eds), *Advances in trilobite researchs 9. Cuadernos del Museo Geominero,*  
1529 *Instituto Geológico y Minero de España, Madrid*, pp. 289–295.
- 1530 Palacios, T., 2015. Acritarch assemblages from the Oville and Barrios Formations, northern Spain:  
1531 A pilot proposal of a middle Cambrian (Series 3) acritarch biozonation in northwestern



- 1532 Gondwana. *Review of Palaeobotany and Palynology* 219, 71–105.
- 1533 Palacios, T., Jensen, S., Apalategui, O., 2006. Biostratigrafía de acritarcos en el Cámbrico Inferior y  
1534 Medio del margen septentrional de Gondwana (Área de Zafra, Suroeste de la Península Ibérica).  
1535 In: Fernández-Martínez, E. (Ed.), Libro de Resúmenes, XXII Jornadas de la Sociedad Española  
1536 de Paleontología. Universidad de León Secretariado de Publicaciones, León, Spain, pp. 156–  
1537 161.
- 1538 Palacios, T., Jensen, S., Barr, S.M., White, C.E., 2009. Acritarchs from the MacLean Brook  
1539 Formation, southeastern Cape Breton Island, Nova Scotia, Canada: New data on Middle  
1540 Cambrian-Lower Furongian acritarch zonation. *Palaeogeography, Palaeoclimatology,*  
1541 *Palaeoecology* 273, 123–141.
- 1542 Palacios, T., Jensen, S., White, C.E., Barr, S.M., 2012. Cambrian acritarchs from the Bourinot belt,  
1543 Cape Breton Island, Nova Scotia: Age and stratigraphic implications. *Canadian Journal of Earth*  
1544 *Sciences* 49 (1), 289–307.
- 1545 Paris, F., Bourahrouh, A., Le Hérisse, A., 2000. The effects of the final stages of the Late  
1546 Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well  
1547 NI-2 (NE Algerian Sahara). *Review of Palaeobotany and Palynology* 113, 87–104.
- 1548 Parsons, M.G., 1986. The Middle Cambrian, Upper Cambrian, and lower Tremadoc acritarchs of  
1549 Random Island, Trinity Bay, southeastern Newfoundland. Master of Science thesis, Department  
1550 of Biology, Memorial University of Newfoundland, Canada.
- 1551 Parsons, M.G., Anderson, M.M., 1986. Three new assemblages of acritarchs from Late Upper  
1552 Cambrian to Early Tremadocian rocks of Random Island, Trinity Bay, Eastern Newfoundland.  
1553 *Geological Society of America, Abstracts and Programs* 18 (1): abstracts of the 99<sup>th</sup> Annual  
1554 Meeting and Exposition of the Geological Society of America, San Antonio (TX), USA.  
1555 Geological Society of America, Boulder (CO), USA, p. 60.
- 1556 Parsons, M.G., Anderson, M.M., 1996. Late Cambrian acritarch assemblages from the Peltura  
1557 Scarabaeoi and *Acerocare* Trilobite zones of Random Island, South-Eastern Newfoundland. In:

- 1558 Fatka, O., Servais, T. (Eds.), *Acritarcha in Praha: Proceedings of International Meeting and*  
1559 *Workshop. Acta Universitatis Carolinae-Geologica* 40 (3-4). Univerzita Karlova, Prague, pp.  
1560 583–593.
- 1561 Parsons, M.G., Anderson, M.M., 2000. *Acritarch microfloral succession from the Late Cambrian*  
1562 *and Ordovician (Early Tremadoc) of Random Island, Eastern Newfoundland, and its*  
1563 *comparison to coeval microfloras, particularly those of the Eastern European Platform.*  
1564 *American Association of Stratigraphic Palynologists, Contributions Series* 38, 1–129.
- 1565 Pittau, P., 1985. *Tremadocian (Early Ordovician) acritarchs of the Arburese Unit, southwest*  
1566 *Sardinia (Italy). Bollettino della Società paleontologica italiana* 23 (2), 161–204. (Cover date  
1567 1984, but issue date 1985).
- 1568 Pittau Demelia, P., Del Rio, M., 1982. *Acritarchi e Loro significato stratigrafico nelle Successioni*  
1569 *Paleozoiche della Sardegna. Guida Alla Geologia del Paleozoico Sardo. Guide Geologiche*  
1570 *Regionali, Società Geologica Italiana*, 33–35.
- 1571 Pöthe de Baldis, E.D., 1981. *Paleomicroplankton y mioesporas del Ludloviano inferior de la*  
1572 *Formacion Los Espejos en el perfil los azulejitos, en la Provincia de San Juan, Republica*  
1573 *Argentina. Revista Española de Micropaleontología* 13 (2), 231–265.
- 1574 QGIS Development Team, 2019. *QGIS Geographic Information System. Open Source Geospatial*  
1575 *Foundation Project.* <http://qgis.osgeo.org>
- 1576 Raevskaya, E., Golubkova, E., 2006. *Biostratigraphical implications of Middle–Upper Cambrian*  
1577 *acritarchs from Severnaya Zemlya (high Arctic of Russia). Review of Palaeobotany and*  
1578 *Palynology* 139, 53–69.
- 1579 Rasul, S.M., 1971. *A systematic and stratigraphic study of the Tremadocian acritarchs of*  
1580 *Shropshire. Ph.D. thesis, University of Sheffield, UK.*
- 1581 Rasul, S.M., 1976. *New species of the genus Vulcanisphaera (Acritarcha) from the Tremadocian of*  
1582 *England. Micropaleontology* 22 (4), 479–484.
- 1583 Rasul, S.M., 1979. *Acritarch zonation of the Tremadoc Series of the Shineton Shales, Wrekin,*

- 1584 Shropshire, England. *Palynology* 3, 53–72.
- 1585 Rasul, S.M., Downie, C., 1974. The stratigraphic distribution of Tremadoc acritarchs in the  
1586 Shineton Shales succession, Shropshire, England. *Review of Palaeobotany and Palynology* 18  
1587 (1), 1–9.
- 1588 Rauscher, R., 1971. Acritarches du Paleozoïque inférieur de la Montagne Noire. *Bulletin du Service*  
1589 *de la carte géologique d'Alsace et de Lorraine* 24 (4), 291-296.
- 1590 Rauscher, R., 1973. Recherches micropaléontologiques et stratigraphiques dans l'Ordovicien et le  
1591 Silurien en France. Études des acritarchs, des chitinozoaires et des spores. *Sciences*  
1592 *Géologiques, Université Louis Pasteur de Strasbourg, Institut de Géologie Mémoire* 38, 1-224.
- 1593 Reitz, E., 1991. Acritarchen des Unter-Tremadoc aus dem Westlichen Frankenwald, NE-Bayern.  
1594 *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1991 (2), 97-104.
- 1595 Ribecai, C., Tongiorgi, M., 1997. *Lusatia dramatica*, a distinctive new species from the Upper  
1596 Cambrian of Oland (Sweden). *Review of Palaeobotany and Palynology* 98 (1), 27–32.
- 1597 Ribecai, C., Vanguetaine, M., 1993. Latest Middle-Late Cambrian acritarchs from Belgium and  
1598 northern France. In: Molyneux, S.G., Doring, K.J. (Eds.), *Contributions to Acritarch and*  
1599 *Chitinozoan Research. Special Papers in Palaeontology* 48. The Palaeontological Association,  
1600 Durham, UK, pp. 45–55.
- 1601 Ribecai, C., Bagnoli, G., Mazzarini, F., Musumeci, G., 2005. Paleontological evidence for Late  
1602 Cambrian in the Arburese area, SW Sardinia. *Carnets de Géologie / Notebooks on Geology,*  
1603 *Memoir* 2005/02, Abstract 08, 45–50.
- 1604 Rubinstein, C.V., 1993. Investigaciones palinológicas en el Paleozoico Inferior de Argentina.  
1605 *Zentralblatt für Geologie und Paläontologie, Teil I: Allgemeine, Angewandte, Regionale und*  
1606 *Historische Geologie* 1, 217–230.
- 1607 Rubinstein, C.V., 1997. Tremadocian acritarchs from Northwestern Argentina. *Review of*  
1608 *Palaeobotany and Palynology* 98 (1), 41–45.

- 1609 Rubinstein, C.V., 2003. Ordovician acritarchs from northwestern Argentina: new insights into the  
1610 biostratigraphy and paleoenvironmental aspects of the Central Andean Basin and Famatina. In:  
1611 Albanesi, G.L., Beresi, M.S., Peralta, S.H. (Eds.), Ordovician from the Andes. Proceedings of  
1612 the 9<sup>th</sup> International Symposium on the Ordovician System in San Juan, Argentina. Universidad  
1613 Nacional de Tucumán, Instituto Superior de Correlación Geológica (INSUGEO; Serie  
1614 Correlación Geológica 17), Tucumán, Argentina, p. 125–130.
- 1615 Rubinstein, C.V., Toro, B.A., Waisfeld, B.G., 1999. Acritarch biostratigraphy of the upper  
1616 Tremadoc-Arenig of the Eastern Cordillera, northwestern Argentina: relationships with  
1617 graptolite and trilobite faunas. *Bollettino della Società Paleontologica Italiana* 38 (2-3), 267–  
1618 286.
- 1619 Rubinstein, C.V., Mángano, M.G., Buatois, L.A., 2003. Late Cambrian acritarchs from the Santa  
1620 Rosita Formation: Implications for the Cambrian-Ordovician Boundary in the Eastern  
1621 Cordillera, northwest Argentina. *Revista Brasileira de Paleontologia* 6, 43–48.
- 1622 Sarjeant, W.A.S., Stancliffe, R.P.W., 1994. The *Micrhystridium* and *Veryhachium* Complexes  
1623 (Acritarcha: Acanthomorphae and Polygonomorphae): A Taxonomic Reconsideration.  
1624 *Micropaleontology* 40 (1), 1–77.
- 1625 Sarjeant, W.A.S., Vavrdová, M., 1997. Taxonomic reconsideration of *Multiplicisphaeridium*  
1626 Staplin, 1961 and other acritarch genera with branching processes. *GeoLines* 5, 1–53.
- 1627 Scotese, C.R., 2016. PALEOMAP PaleoAtlas for Gplates and the PaleoData Plotter Program,  
1628 PALEOMAP Project, <http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/>
- 1629 Servais, T., 1993. The Ordovician acritarch *Frankea*. In: Molyneux, S.G., Dorning, K. J. (Eds.),  
1630 Contributions to acritarch and chitinozoan research. The Palaeontological Association (Special  
1631 Papers in Palaeontology 48), Durham, UK, pp. 79–95.
- 1632 Servais, T., 1997. An annotated bibliographical review of Ordovician acritarchs. *Annales de la*  
1633 *Société Géologique de Belgique* 120 (1), 23–72.
- 1634 Servais, T., Brocke, R., Fatka, O., 1996. Variability in the Ordovician acritarch *Dicrodiacrodium*.

- 1635 Palaeontology 39 (2), 389–405.
- 1636 Servais, T., Stricanne, L., Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs  
1637 at the Cambrian–Ordovician transition in the Algerian Sahara. Palaeontology 47 (2), 395–414.
- 1638 Servais, T., Vecoli, M., Li, J., Molyneux, S.G., Raevskaya, E.G., Rubinstein, C.V., 2007. The  
1639 acritarch genus *Veryhachium* Deunff 1954: Taxonomic evaluation and first appearance.  
1640 Palynology 31, 191–203.
- 1641 Servais, T., Li, J., Molyneux, S.G., Vecoli, M., 2008. The Ordovician acritarch genus *Coryphidium*.  
1642 Revue de micropaléontologie 51, 97–120.
- 1643 Servais, T., Danelian, T., Harper, D.A.T., Munnecke, A., 2014. Possible oceanic circulation  
1644 patterns, surface water currents and upwelling zones in the Early Palaeozoic. GFF 136 (1), 229–  
1645 233.
- 1646 Sinha, H.N., Prasad, B., Srivastava, S.S., 1996a. Taxonomy of *Veryhachium* complex from the  
1647 Lower Paleozoic marine sediments of Tethyan Garhwal Himalaya, and their environmental  
1648 significance. In: Pandey, J., Azmi, R.J., Bhandari, A., Dave, A. (Eds.), Contributions to XV  
1649 Indian Colloquium on Micropaleontology and Stratigraphy. Keshava Deva Malaviya Institute of  
1650 Petroleum Exploration, Wadia Institute of Himalayan Geology, Dehradun, India, pp. 567–576.
- 1651 Sinha, H.N., Srivastava, S.S., Prasad, B., 1996b. Record of Prolific and Indubitable acritarchs from  
1652 the Lower Paleozoic strata of the Tethyan Garhwal Himalaya and age implication. Current  
1653 Science 71 (1), 24–31.
- 1654 Spina, A., 2015. Latest Ordovician (Hirnantian) miospores from the NI-2 well, Algeria, North  
1655 Africa, and their evolutionary significance. Palynology 39 (2), 205–219.
- 1656 Staplin, F., Jansonius, J., Pocock, S.A.J., 1965. Evaluation of some Acritarchous Hystrichosphere  
1657 Genera. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 123 (2), 167–201.
- 1658 Stricanne, L., Servais, T., 2002. A statistical approach to classification of the Cambro-Ordovician  
1659 galeate acritarch plexus. Review of Palaeobotany and Palynology 118, 239–259.
- 1660

- 1661 Stubblefield, C.J., Bulman, O.M.B., 1927. The Shineton Shales of the Wrekin District: with notes  
1662 on their development in other parts of Shropshire and Herefordshire. *Quarterly Journal of the*  
1663 *Geological Society* 83 (1-5), 96–146.
- 1664 Tappin, D. R., Downie, C., 1978. New Tramadoc strata at outcrop in the Bristol Channel. *Journal of*  
1665 *the Geological Society, London* 135, 321.
- 1666 Tawadros, E., Rasul, S.M., Elzaroug, R., 2001. Petrography and palynology of quartzites in the  
1667 Sirte Basin, central Libya. *Journal of African Earth Sciences* 32 (3), 373–390.
- 1668 Tongiorgi, M., Di Milia, A., 1999. Differentiation and spread of the Baltic Acritarch Province  
1669 (Arenig-Llanvirn). *Bollettino della Società Paleontologica Italiana* 38 (2-3), 297–312.
- 1670 Tongiorgi, M., Ribecai, C., 1990. Comunità Fitoplanctoniche (Acritarchi) del Cambriano Termilae -  
1671 Tremadocian Di Oland (Svezia). *Bollettino della Società Paleontologica Italiana* 29 (1), 77–88.
- 1672 Tongiorgi, M., Di Milia, A., Stouge, S., Bagnoli, G., 1988. Acritarchs from the Upper Cambrian-  
1673 Lower Tremadocian section of Degerham Road at Oeland, Sweden. Abstracts of the 7<sup>th</sup>  
1674 International Palynological Congress, Brisbane, Australia. p. 164.
- 1675 Torsvik, T.H., Cocks, L.R.M., 2013. New global palaeogeographical reconstructions for the Early  
1676 Palaeozoic and their generation. In: Harper, D.A.T., Servais, T. (eds), *Early Palaeozoic*  
1677 *Biogeography and Palaeogeography*. Geological Society of London, Memoirs 38, London, pp.  
1678 5–24.
- 1679 Tynni, R., 1978. Lower Cambrian fossils and acritarchs in the sedimentary rocks of Soderfjarden,  
1680 Western Finland. *Geological Survey of Finland, Bulletin* 297, 39–81.
- 1681 Uutela, A., Tynni, R., 1991. Ordovician acritarchs from the Rapla borehole, Estonia. *Geological*  
1682 *Survey of Finland, Bulletin* 353, 1–135.
- 1683 Vanguetaine, M., 1973. The Late Cambrian age of the Upper RN2B from the Stavelot area. In:  
1684 Vozzhennikova, T.F., Timofeev, T.B. (Eds.), *Mikrofossilii Drevneishikh Otlozhenii*.  
1685 *Proceedings of the 3rd International Palynological Conference, 1971, Novosibirsk, Russia*.  
1686 Nauka, Moscow, Russia, p. 31.

- 1687 Vanguestaine, M., 1978. Critères palynostratigraphiques conduisant a la reconnaissance d'un pli  
1688 couche revinien dans le sondage de Grand-Halleux. Annales de la Société géologique de  
1689 Belgique 100, 249-276. (Cover date 1977, but issue date of 1978).
- 1690 Vanguestaine, M., 1986. Progres recents de la stratigraphie par Acritarches du Cambro-Ordovicien  
1691 d'Ardenne, d'Irlande, d'Angleterre, du Pays de Galles et de Terre-Neuve Orientale. Annales de la  
1692 Société Géologique du Nord 105, 65–76.
- 1693 Vanguestaine, M., 1991. Datation par acritarches des couches Cambro-Tremadociennes les plus  
1694 profondes du sondage de Lessines (bord méridional du Massif de Brabant, Belgique). Annales  
1695 de la Société Géologique de Belgique 114 (1), 213–231.
- 1696 Vanguestaine, M., 1992. Biostratigraphie par Acritarches du Cambro-Ordovicien de Belgique et des  
1697 Regions limitrophes : Synthese et perspectives d'Avenir. Annales de la Société Géologique de  
1698 Belgique 115 (1), 1–18.
- 1699 Vanguestaine, M., 2002. The Late Cambrian acritarch *Cristallinium randomense*: morphology,  
1700 taxonomy and stratigraphical extension. Review of Palaeobotany and Palynology 118, 269–285.
- 1701 Vanguestaine, M., 2008. Early and Middle Ordovician acritarchs of the Senne-Sennette river  
1702 valleys (Brabant Massif, Belgium) and their stratigraphic implications. Geologica Belgica 11, 3–  
1703 24.
- 1704 Vanguestaine, M., Brück, P.M., 2008. A Middle and Late Cambrian age for the Booley Bay  
1705 Formation, County Wexford, Ireland: New acritarch data and its implications. Revue de  
1706 micropaléontologie 51, 67–95.
- 1707 Vavrdová, M., 1976. Mechanismus excystace u rane paleozoických akritarch. Casopis pro  
1708 Mineralogii a Geologii 21 (1), 55–64.
- 1709 Vecoli, M., 1996. Stratigraphic significance of acritarchs in Cambro-Ordovician boundary strata,  
1710 Hassi R'mel area, Algerian Sahara. Bollettino della Societa Paleontologica Italiana 35 (1), 3–58.
- 1711 Vecoli, M., 1999. Cambro-Ordovician palynostratigraphy (acritarchs and prasinophytes) of the  
1712 Hassi-R'Mel area and northern Rhadames Basin, North Africa. Palaeontographia Italica 86, 1–

- 1713 112.
- 1714 Vecoli, M., 2000. Palaeoenvironmental interpretation of microphytoplankton diversity trends in the  
1715 Cambrian–Ordovician of the northern Sahara Platform. *Palaeogeography, Palaeoclimatology,*  
1716 *Palaeoecology* 160, 329–346.
- 1717 Vecoli, M., Le Hérisse, A., 2004. Biostratigraphy, taxonomic diversity and patterns of  
1718 morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton) from  
1719 the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes.  
1720 *Earth-Science Reviews* 67, 267–311.
- 1721 Vecoli, M., Playford, G., 1997. Stratigraphically significant acritarchs in uppermost Cambrian to  
1722 basal Ordovician strata of Northwestern Algeria. *Grana* 36 (1), 17–28.
- 1723 Vecoli, M., Albani, R., Ghomari, A., Massa, D., Tongiorgi, M., 1995. Précisions sur la limite  
1724 Cambrien-Ordovicien au Sahara Algérien (Secteur de Hassi-Rmel). *Comptes Rendus de*  
1725 *l'Académie des Sciences – Series IIA – Earth and Planetary Science* 320, 515–522.
- 1726 Vecoli, M., Tongiorgi, M., Abdesselam-Rouighi, F.-F., Benzarti, R., Massa, D., 1999.  
1727 Palynostratigraphy of Upper Cambrian-upper Ordovician intracratonic clastic sequences, North  
1728 Africa. *Bollettino della Società Paleontologica Italiana* 38 (3), 331–341.
- 1729 Vecoli, M., Videt, B., Paris, F., 2008. First biostratigraphic (palynological) dating of Middle and  
1730 Late Cambrian strata in the subsurface of northwestern Algeria, North Africa: Implications for  
1731 regional stratigraphy. *Review of Palaeobotany and Palynology* 149, 57–62.
- 1732 Vergel, M.d.M., Aráoz, L., Rubinstein, C.V., 2002. Palinomorfos Ordovícicos de Argentina: Una  
1733 visión integradora. In: Aceñolaza, G.F. (Ed.) *Aspects of the Ordovician System in Argentina.*  
1734 *Serie Correlación Geológica, Instituto Superior de Correlación Geológica (INSUGEO)* 16 (16),  
1735 209–224.
- 1736 Vergel, M.d.M., Aceñolaza, G.F., Aráoz, L., 2013. Palynology of the Iscayachi Formation  
1737 (Cambro-Ordovician) from the Cordillera Oriental of Southern Bolivia: New data from the  
1738 western margin of Gondwana. *Geologica Acta*, 11 (2), 167–176.



- 1739 Volkova, N.A., 1980. Akritarki srednego i verkhnego kembriya Moskovskoy sineklizy. Izvestiya  
1740 Akademii Nauk SSSR, Seriya Geologicheskaya 12, 49–57. (in Russian)
- 1741 Volkova, N.A., 1983. Akritarkhi srednego i verkhnego kembriya severo-zapada Vostochno-  
1742 Evropeiskoj Platformy. In: Papulov, G.N. (Ed.), Stratigrafiya i korrelyatsiya osadkov metodami  
1743 palinologii. Materialy IV Vsesoyuznoj Palinologicheskoy Konferentsii. Uralskij Nauchnyi  
1744 Tsent, Trudy, Akademiya Nauk SSSR, Materialy IV Vsesoyuznoi Palinogicheskoi  
1745 Konferentsii, Tyumen 1981, 13–17. (in Russian)
- 1746 Volkova, N.A., 1989a. Acritarchs from the Cambrian-Ordovician boundary sediments of northern  
1747 Estonia. International Geology Review 31 (9), 904–913.
- 1748 Volkova, N.A., 1989b. Akritarkhi pogranichnykh otlozhenij kembriya i ordovika severa Estonii.  
1749 Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya 7, 59–67. (in Russian)
- 1750 Volkova, N.A., 1989c. Akritarkhi verkhnej chasti pakerortskogo gorizonta severa Estonii i  
1751 Leningradskoj oblasti. In: Akhmetev, M.A. (Ed.) Paleofloristika i Stratigrafiya Fanerozoja.  
1752 Geologicheskij Institut, Trudy, Akademiya Nauk SSSR, Moskva, 4–16. (in Russian)
- 1753 Volkova, N.A., 1990. Akritarkhi srednego i verkhnego kembriya Vostochno-Evropeiskoj  
1754 Platformy. Geologicheskij Institut, Trudy, Akademiya Nauk SSSR, Moskva, Nauka 454, 1–116.  
1755 (in Russian, with English abstract)
- 1756 Volkova, N.A., 1993. Taksonomicheskij sostav akritarkh i klimat v rannem tremadoke Baltijskoj  
1757 fitoplanktonnoj provintsii. Stratigrafiya. Geologicheskaya Korrelyatsiya (Stratigraphy and  
1758 Geological Correlation) 1 (5), 39–44. (in Russian)
- 1759 Volkova, N.A., 1995. Akritarkhi pogranichnykh otlozhenij kembriya-ordovika Baltijskoj  
1760 fitoplanktonnoj provintsii. Stratigrafiya. Geologicheskaya Korrelyatsiya (Stratigraphy and  
1761 Geological Correlation) 3 (4), 31–43. (in Russian)
- 1762 Volkova, N.A., 1996. Kompleksy Akritarkh kembriya Moskovskoj sineklizy. Byulleten  
1763 Moskovskogo Obshchestva Ispytatelej Prirody, Otdel Geologicheskij 71 (6), 51–57. (in  
1764 Russian)

- 1765 Volkova, N.A., 1999a. Akritarkhi verkhnikh sloyev verkhnego kembriya - nizhnego tremadoka  
1766 Moskovskoj sineklizy. Stratigrafiya. Geologicheskaya Korrelyatsiya (Stratigraphy and  
1767 Geological Correlation) 7 (5), 43–55. (in Russian)
- 1768 Volkova, N.A., 1999b. Novye rody akritarkh iz nizhnego tremadoka Moskovskoj sineklizy.  
1769 Paleontologicheskij Zhurnal (Paleontological Journal) 6, 73–75. (in Russian, with English  
1770 abstract)
- 1771 Volkova, N.A., Mens, K.A., 1988. Raspredelenie akritarkh v pogranichnykh sloyakh kembriya i  
1772 ordovika razreza Sukhrumyagi (Severnaya Estoniya). Eesti NSV Teaduste Akadeemia  
1773 Toimetised, Geologia 37, 97–102. (in Russian)
- 1774 Volkova, N.A., Sivertseva, I.A., 1991. Novye akritarkhi iz tremadoka na severe Russkoy plity.  
1775 Paleontologicheskij Zhurnal (Paleontological Journal) 25 (3), 119–123. (in Russian, with  
1776 English abstract).
- 1777 Wang, W., Servais, T., Yan, K., Vecoli, M., Li, J., 2015. The Ordovician acritarch *Dactylofusa*  
1778 *velifera* Cocchio 1982: a biostratigraphical and palaeogeographical index species. Palynology  
1779 39, 125–141.
- 1780 Wang, W., Monnet, C., Servais, T., 2017. Quantitative methods used for understanding the  
1781 taxonomy of acritarchs: a case study of the Middle Ordovician genus *Frankea* Burmann 1970.  
1782 Palynology 41, 69–79.
- 1783 Watts, W.W., 1925. The geology of South Shropshire. Proceedings of the Geologists' Association  
1784 36 (4), 321–363.
- 1785 Welsch, M., 1986a. Die Acritarchen der höheren Digermul-Gruppe, Mittelkambrium bis Tremadoc,  
1786 Ost-Finnmark, Nord-Norwegen. Paläontographica Abteilung B 201 (1), 1–109.
- 1787 Welsch, M., 1986b. Palynologische Untersuchungen (Acritarchen) an kambrischen und  
1788 tremadocischen Sedimenten der Östlichen Finnmark (Norwegen). CFS. Courier  
1789 Forschungsinstitut Senckenberg 86, 27–43.

- 1790 Whittard, W.F., 1952. A Geology of South Shropshire. Proceedings of the Geologists' Association  
1791 63, 143–197.
- 1792 Wood, G.D., Stephenson, J.T., 1989. Cambrian palynomorphs from the warm-water provincial  
1793 realm, Bonnetterre and Davis Formations of Missouri and Arkansas (Reelfoot rift area);  
1794 biostratigraphy, paleoecology and thermal maturity. In: Gregg, J.M., Palmer, J.R., Kurtz, V.E.  
1795 (Eds.), Field guide to Upper Cambrian of southeastern Missouri; stratigraphy, sedimentology  
1796 and economic geology, Geological Society of America, Field Trip. Department of Geology and  
1797 Geophysics, University of Missouri, pp. 84–102.
- 1798 Wood, G.D., Stephenson, J.T., 1990. Organic-walled microfossils from the Cambrian Davis Shale  
1799 and Bonnetterre Formation, Mid-Continent United States; Integration of palynological,  
1800 geological and geophysical disciplines in the exploration of the Reelfoot Rift area. Palynology  
1801 14, 219.
- 1802 Yan, K., Servais, T., Li, J., 2010. Revision of the Ordovician acritarch genus *Ampullula* Righi  
1803 1991. Review of Palaeobotany and Palynology 163, 11–25.
- 1804 Yan, K., Li, J., Molyneux, S.G., Raevskaya, E.G., Servais, T., 2017. A review of the Ordovician  
1805 acritarch genus *Barakella* Cramer & Díez 1977. Palynology 41, 80–94.
- 1806 Yankauskas, T.V., 1976. Revision de l'age de Formations “Cambro-Ordoviciennes” des Regions  
1807 Baltiques par l'Analyse micropaleontologique (Acriarches, Chitinozoaires). Compte-Rendu  
1808 Sommaire et Bulletin de la Société Géologique de France 2, 47–49.
- 1809 Yankauskas, T.V., Paškevičienė, L., 1972. Mikropaleontologičeskaya kharakteristika Yulgazeskoi  
1810 Pachki Tremadoka Estonii. Eesti NSV Teaduste Akadeemia Toimetised, Geologia 21 (1), 92–  
1811 93. (in Russian)
- 1812 Yin, L.M., 1986. Acritarchs. In: Chen, J.Y. (Ed.), Aspects of Cambrian–Ordovician boundary in  
1813 Dayangcha, China. Contribution to Dayangcha International Conference on C/O boundary.  
1814 China Prospect Publishing House, Beijing, pp. 314–373.

- 1815 Young, T., Martin, F., Dean, W.T., Rushton, A.W.A., 1994. Cambrian stratigraphy of St.Tudwal's  
1816 Peninsula, Gwynedd, Northwest Wales. *Geological Magazine* 131 (3), 335–360.
- 1817 Yuan Xunlai, Hofmann, H.J., 1998. New microfossils from the Neoproterozoic (Sinian)  
1818 Doushantuo Formation, Wengan, Guizhou Province, southwestern China. *Alcheringa* 22, 189–  
1819 222.
- 1820 Zang, W.-L., 2001. Acritarchs. In: Alexander, E. M., Jago, J. B., Rozanov, A. Y. & Zhuravlev, A.  
1821 Y. (eds), *The Cambrian biostratigraphy of the Stansbury Basin, south Australia*. Russian  
1822 Academy of Sciences, *Transactions of the Palaeontological Institute*, 282, IAPC  
1823 Nauka/Interperiodica, Moscow, 74–85.
- 1824 Zang, W.-L., Moczyłowska, M., Jago, J.B., 2007. Early Cambrian acritarch assemblage zones in  
1825 South Australia and global correlation. *Memoirs of the Association of Australasian*  
1826 *Palaeontologists*, 33, 141–177.
- 1827 Żylińska, A., Szczepanik, Z., Salwa, S., 2006. Cambrian of the Holy Cross Mountains, Poland;  
1828 biostratigraphy of the Wiśniówka Hill succession. *Acta Geologica Polonica* 56 (4), 443–461.
- 1829

1830 Figure 1. Geographic positions of the sample localities in Algeria (A: borehole NI-2), Great Britain  
1831 (B: Shineton Shales outcrops), and Iran (C: Ghelli outcrop).

1832

1833 Figure 2. Lithostratigraphic profiles of the three sample localities, NI-2 borehole in Algeria, Ghelli  
1834 outcrop in Iran, and Shineton Shales outcrops in Great Britain with sample levels.

1835

1836 Figure 3. Categories of process shapes used in the linear discriminant analysis (LDA).

1837

1838 Figure 4. Results of the linear discriminant analysis showing three distinct classes corresponding to  
1839 the emended species of *Vulcanisphaera*. Transitional forms between *V. africana* and *V. mougnoana*  
1840 are indicated in the overlapping of the two classes.

1841

1842 Figure 5. Stratigraphic distribution of the different species of *Vulcanisphaera* discussed here in the  
1843 three main palaeogeographical domains, peri-Gondwana, Baltica and Laurentia (Fig. 5), where  
1844 occurrences of this genus are known.

1845

1846 Figure 6. Palaeobiogeographical distribution of the three species of *Vulcanisphaera* for the  
1847 Furongian (A) and the Tremadocian (B). Palaeogeographical reconstruction based on Scotese  
1848 (2016), palaeoclimate zones based on Boucot et al. (2013).

1849

1850 Plate I. **1-5:** *Vulcanisphaera mougnoana*: **1.** Ghelli locality LG27.1; EF: J64/2. **2.** NI-2 3056.9 m;  
1851 EF: Z45. **3.** NI-2 3056.9 m; EF: F36/2. **4.** NI-2 3056.9 m; EF: Y45, specimen showing both, isolated  
1852 processes (example A) and tufts of processes (example B). **5.** NI-2 3056.9 m; EF: Y34. 6-16: *V.*  
1853 *africana*: **6.** Ghelli locality LG4.2; EF: U52, specimen showing both, isolated processes (example  
1854 A) and tufts of processes (example B). **7.** Ghelli locality LG4.2; EF: X23. **8.** NI-2 3053.9 m; EF:  
1855 M41/4. **9.** NI-2, 3017.25 m; EF: P40. **10.** NI-2 3017.25 m; EF: L56/4. **11.** NI-2 3017.25 m; EF: K57.

1856 **12.** Shineton Shales B15/1; EF: R27/1. **13.** Shineton Shales C10/1; EF: K27/1. **14.** Shineton Shales  
1857 D6/1; EF: E22/2. **Fig. 15.** Shineton Shales D6/1; EF: G26/2. **16.** Shineton Shales C10/1; EF: K49.  
1858 Scale bars: 20  $\mu\text{m}$ .

1859

1860 Plate II. **1-16:** *V. simplex*. **1.** Shineton Shales, C10/1; EF: K41/1. **2.** Shineton Shales, D6/1; EF:  
1861 F34. **3.** Shineton Shales, D6/1; EF: H61/4. **4.** Shineton Shales outcrops, C10/1; EF: K41/2. **5.**  
1862 Shineton Shales, B8/1; EF: U50/3. **6.** Shineton Shales, B15/1; EF: K26. **7.** Shineton Shales, B15/1;  
1863 EF: G26. **8.** Shineton Shales, B15/1; EF: U27. **9.** Shineton Shales, B8/1; EF: M50/3. **10.** Shineton  
1864 Shales, B15/1; EF: Q26/2. **11.** Shineton Shales, C10/1; EF: Q26/4. **12.** Shineton Shales outcrops  
1865 C10/1; EF: Q27/1. **13.** Shineton Shales outcrops, B8/1; EF: T49/2. **14.** Shineton Shales B8/1; EF:  
1866 T49/2. **15.** Shineton Shales B8/1; EF: V50/1. **16.** Shineton Shales B8/1; EF: M50/4. Scale bars: 20  
1867  $\mu\text{m}$ .

1868

Figure 1

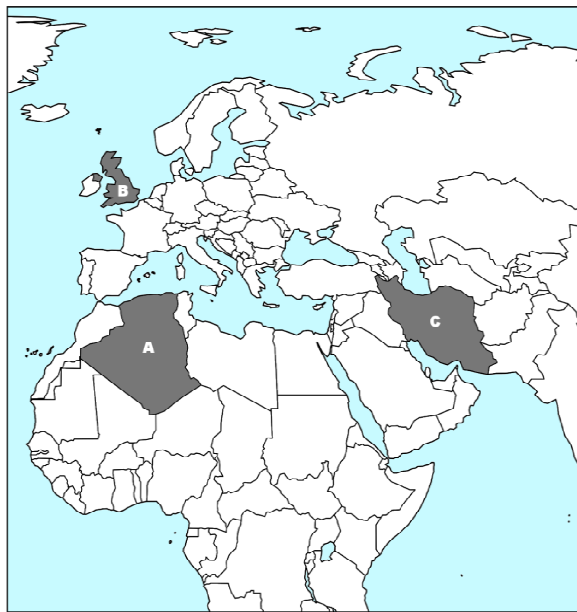
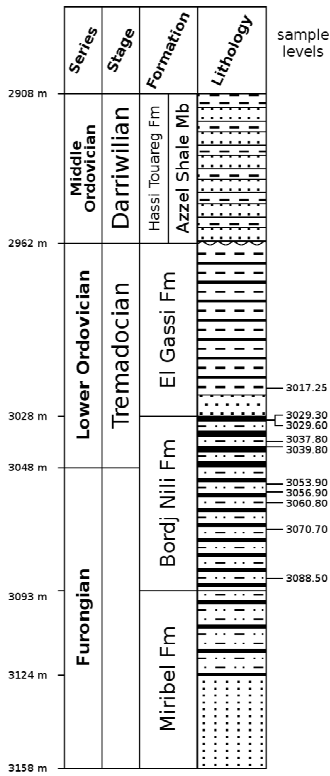
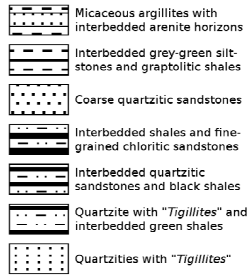
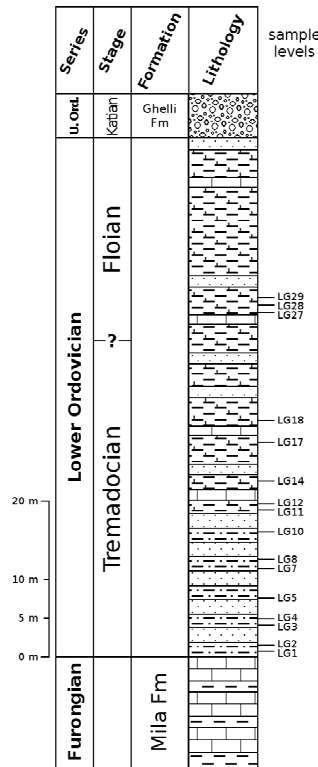
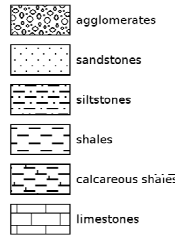


Figure 2

NI-2, Algeria



Ghelli area, Iran



Shineton Shales, Great Britain

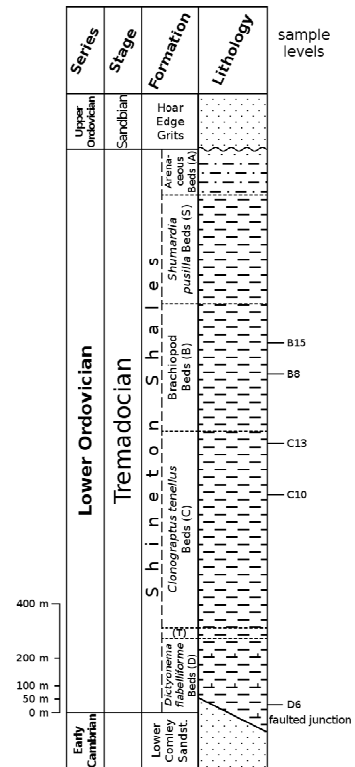
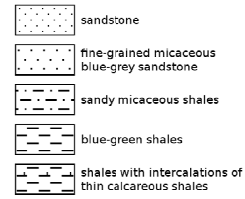




Figure 3

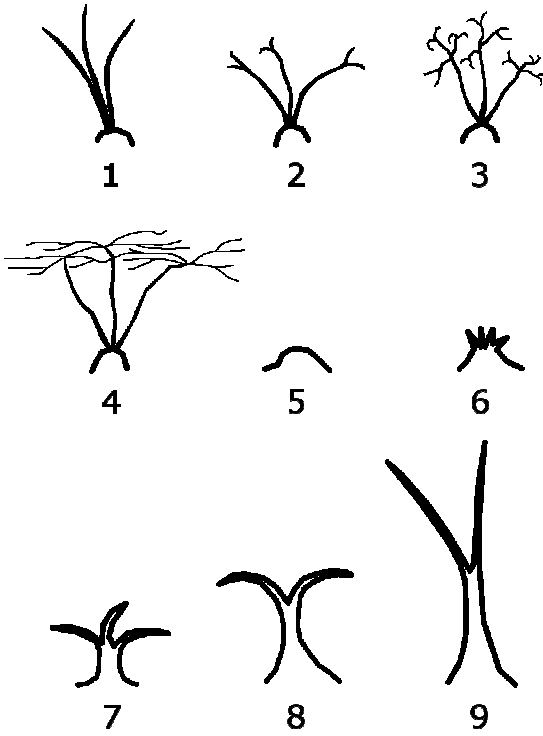


Figure 4

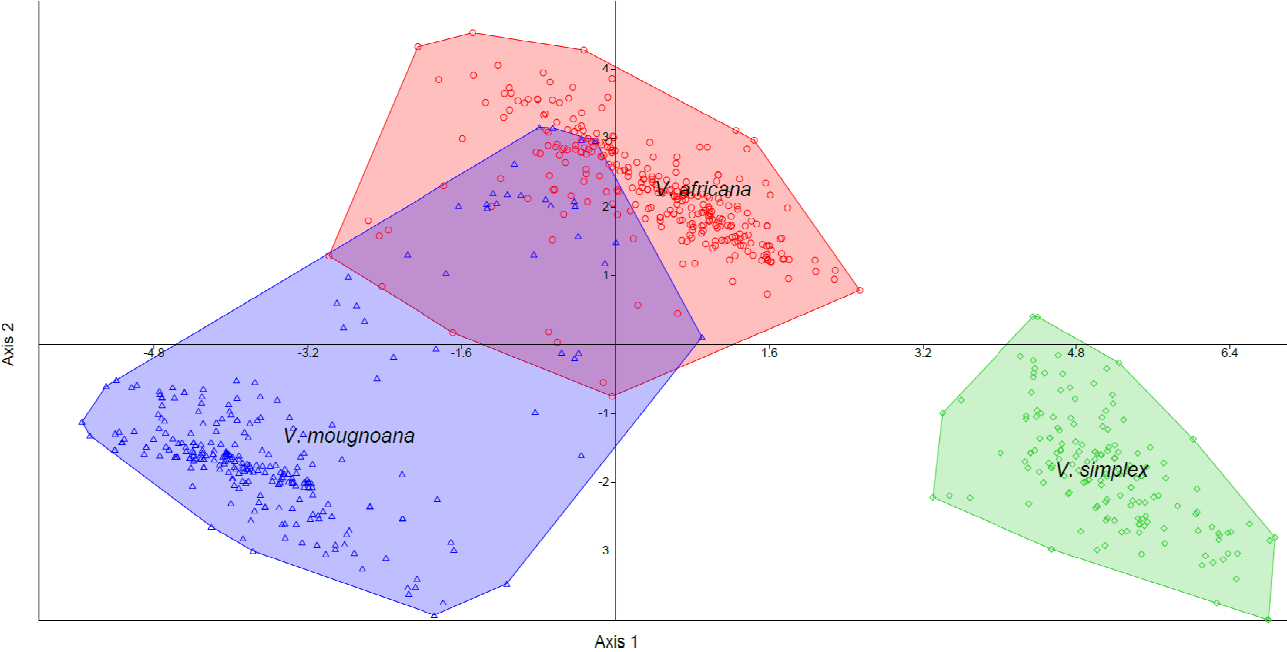




Figure 6

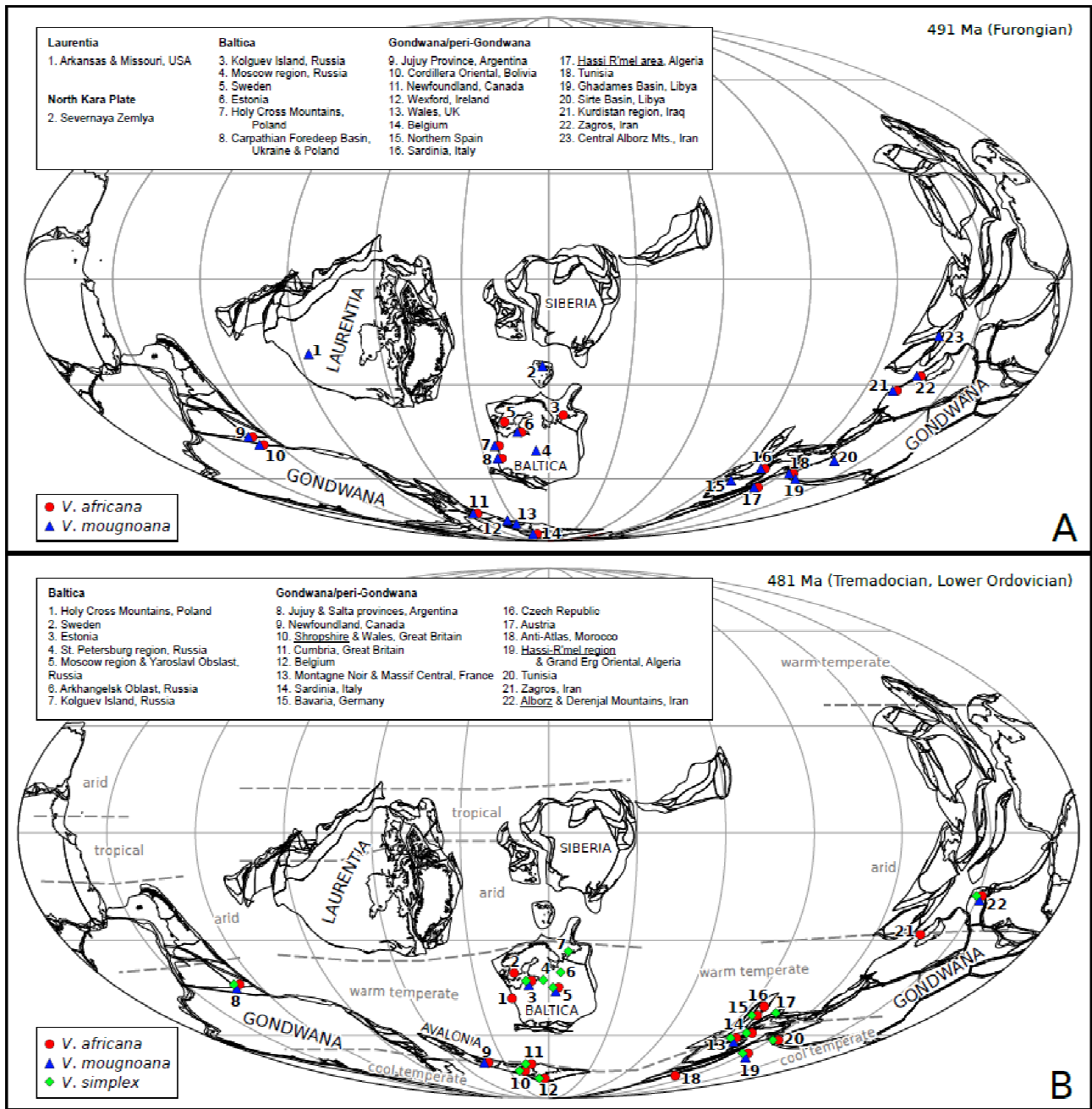




Plate I

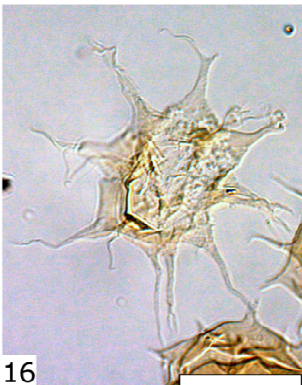
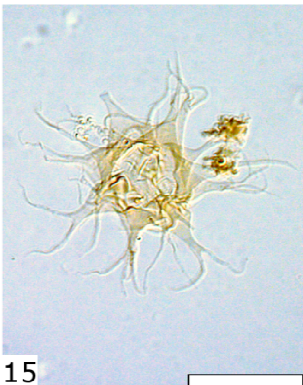
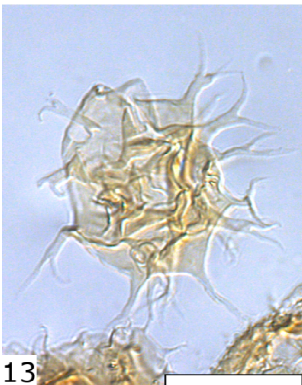
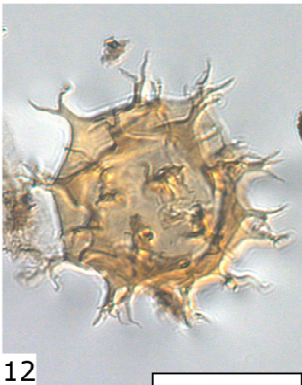
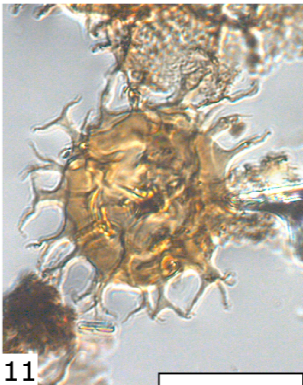
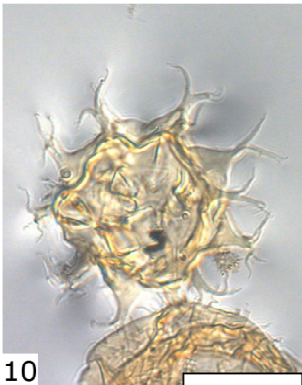
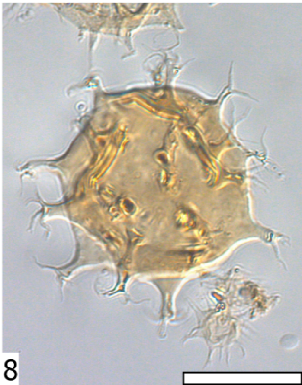
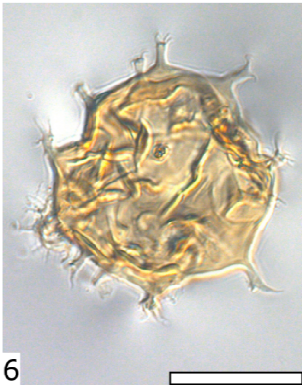
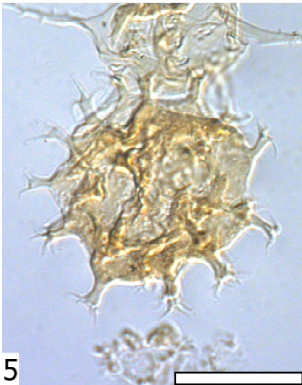
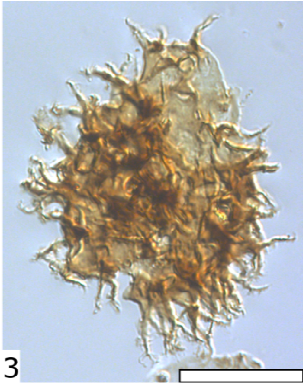
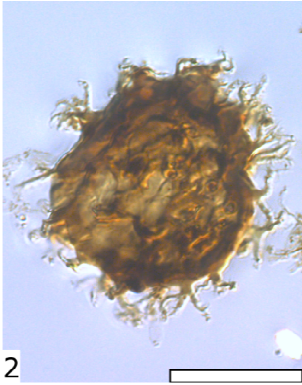
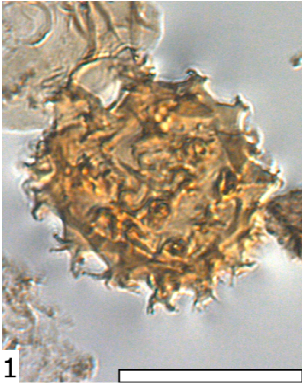
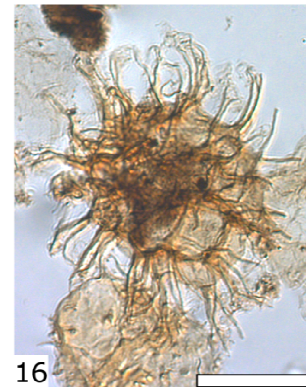
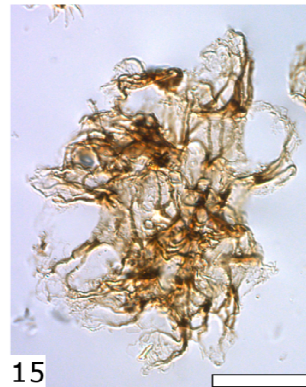
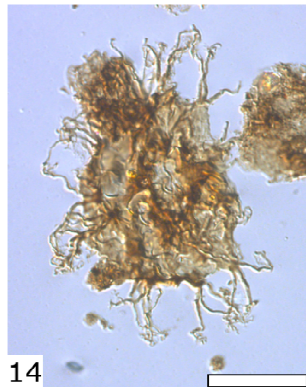
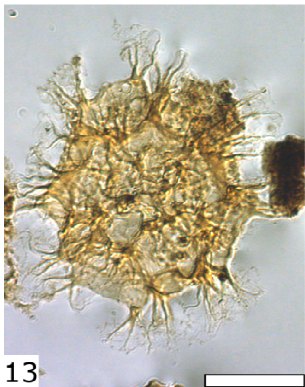
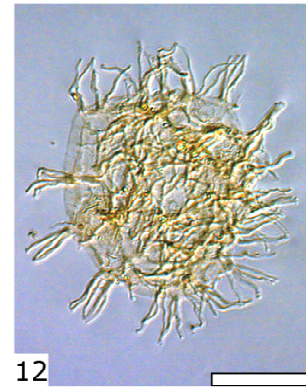
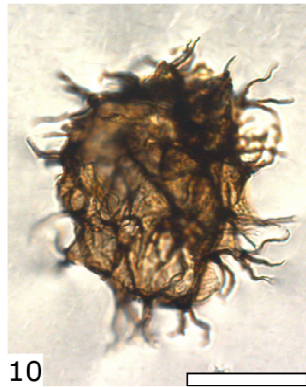
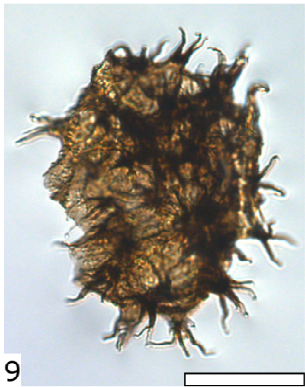
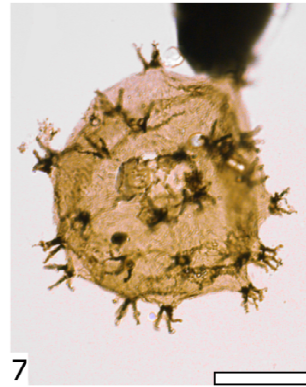
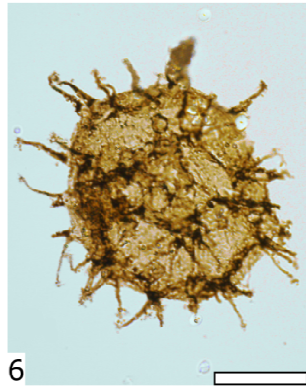
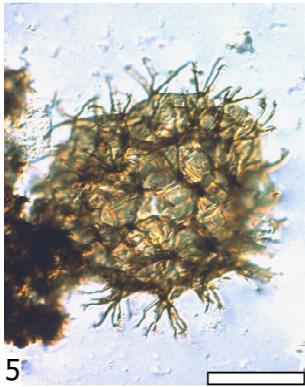
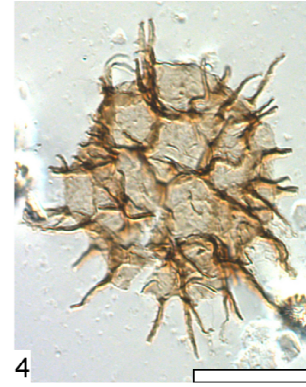
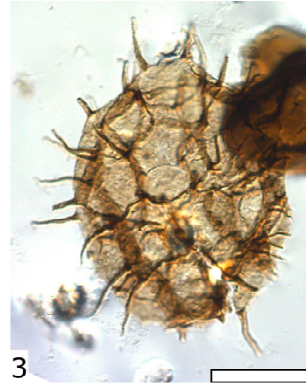
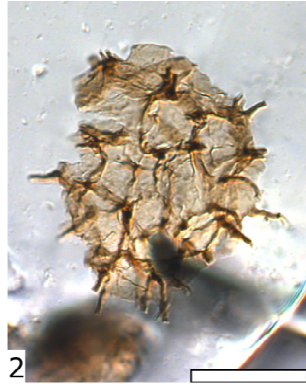
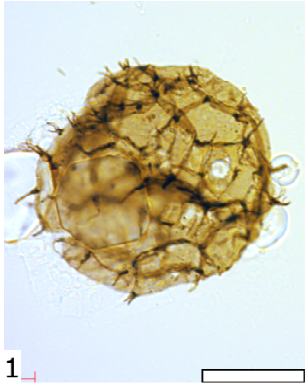




Plate II





### **Article III**

#### **Revision of the Middle–Late Ordovician acritarch genus *Orthosphaeridium* Eisenack 1968 nov. emend.**

Navid Navidi–Izad, Hossein Hashemi, Sylvie Régnier, David Kroeck, Kui Yan, Thomas Servais

Published 2020 in *Review of Palaeobotany and Palynology*.







## Revision of the Middle–Upper Ordovician acritarch genus *Orthosphaeridium* Eisenack 1968 nov. emend

Navid Navidi-Izad<sup>a,b</sup>, Hossein Hashemi<sup>a,\*</sup>, Sylvie Régnier<sup>b</sup>, David Kroeck<sup>b</sup>, Kui Yan<sup>c</sup>, Thomas Servais<sup>b</sup>

<sup>a</sup> Department of Geology, Faculty of Earth Sciences, Kharazmi University, 49 Mofatteh Avenue, 15614 Tehran, Iran

<sup>b</sup> Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

<sup>c</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, East Beijing Road 39, 210008 Nanjing, China

### ARTICLE INFO

#### Article history:

Received 17 March 2019

Received in revised form 20 August 2019

Accepted 20 October 2019

Available online 05 November 2019

#### Keywords:

Phytoplankton  
Lower Paleozoic  
Paleoecology  
Biostratigraphy  
Taxonomy

### ABSTRACT

The acritarch genus *Orthosphaeridium* Eisenack 1968 is one of the most frequently recorded acritarch taxa in the Ordovician. The taxonomy of this easily recognizable genus is revised herein based on a detailed literature review and on new investigations of palynological material from northeastern Iran and South China. The review confirms that *Baltisphaera* Burmann 1970 is a junior synonym of *Orthosphaeridium* of which the diagnosis is here emended. Over 20 species have been described in the literature, but many of them are apparently synonyms. The review indicates that the following four species can be easily differentiated: *Orthosphaeridium bispinosum* Turner 1984, *Orthosphaeridium ternatum* (Burmann 1970) Eisenack et al. 1976, *Orthosphaeridium rectangulare* (Eisenack 1963) Eisenack 1968 (type species) and *Orthosphaeridium octospinosum* Eisenack 1968. The taxonomical ranks of *Orthosphaeridium rectangulare* var. *quadricornis* Burmann 1970 and *Orthosphaeridium octospinosum* var. *insculptum* Loeblich 1970 are changed from the species to the varietal level. The review indicates that *Orthosphaeridium* first appeared in South China in the *Expansograptus hirundo* graptolite Biozone, i.e. in the early Dapingian (stage slice Dp1 and time slice 3a of the Middle Ordovician) and that it reached a global distribution during the Middle and Late Ordovician. The genus disappeared at the end of the Ordovician and has never been recorded from the Silurian. The genus is thus a stratigraphical index fossil for the Middle and Late Ordovician. *Orthosphaeridium* has been recorded from the margins of all paleocontinents and paleoecologically seems to be an eurythermic taxon.

© 2019 Elsevier B.V. All rights reserved.

### 1. Introduction

Graptolites and conodonts are traditionally two major groups of stratigraphic index fossils for the Ordovician. However, in successions where these fossils are absent, palynomorphs, such as acritarchs and chitinozoans, have a good biostratigraphic potential, including for long distance correlations in Lower Paleozoic strata. Some of the First Appearance Datums (FADs) of significant acritarch taxa have shown a great potential for the definition of Ordovician stage boundaries and long-distance correlation (Li et al., 2002; Molyneux et al., 2007; Li et al., 2010; Servais et al., 2018).

Some Ordovician acritarch taxa with biostratigraphic, but also paleogeographic, significance have been reviewed in recent years, for example, *Ampullula* (Yan et al., 2010), *Arbusculidium* (Fatka and Brocke, 1999), *Arkonina–Striatotheca* (Servais, 1997), *Aureotesta* (Brocke et al., 1997), *Barakella* (Yan et al., 2017), *Coryphidium* (Servais et al., 2008), *Dactylofusa velifera* (Wang et al., 2015), *Dicrodiacrodium* (Servais et al.,

1996), *Frankea* (Servais, 1993; Fatka et al., 1997), *Pachysphaeridium* (Ribecai and Tongiorgi, 1999), *Peteinosphaeridium*, *Liliosphaeridium* and *Cycloposphaeridium* (Playford et al., 1995), *Rhopaliophora* (Li et al., 2014), *Sacculidium* (Ribecai et al., 2002) and *Veryhachium* (Servais et al., 2007). These revisions allow precise correlations that challenge graptolite and chitinozoan biostratigraphy (Servais et al., 2018) and provide detailed biostratigraphic information from strata where other fossils are absent (e.g., Kroeck et al., 2019).

The very common Ordovician genus *Orthosphaeridium* has not been revised to date. It has first been described by Eisenack (1968) and has subsequently been recorded widely in the Ordovician, also under different names, such as *Baltisphaera* Burmann, 1970. To date, over 20 species and one infraspecific taxon have been attributed to the genus *Orthosphaeridium*. This acanthomorph acritarch is easily distinguishable due to its large vesicle, and its long, simple and hollow processes that display a distinctive plug at their base. Several species have been described on the basis of a very limited number of specimens, and many of them appear to be synonyms and need a detailed revision. The aim of the present study is thus to revise the genus *Orthosphaeridium* in detail, in terms of taxonomy and biostratigraphy.

\* Corresponding author.

E-mail address: [h.hashemi@khu.ac.ir](mailto:h.hashemi@khu.ac.ir) (H. Hashemi).

In addition, all occurrences of *Orthosphaeridium* are plotted on a paleogeographic reconstruction map to show its paleobiogeographical extension, the ecological distribution of the genus is also discussed.

## 2. Material and methods

The newly investigated material used in this study comes from a stratigraphic section in northeastern Iran, the type section for the Upper Ordovician Ghelli Formation, from which the genus *Orthosphaeridium* has been reported previously in many samples (e.g., Ghavidel-Syooki, 2000a, 2017c). In the frame of a PhD project by the first author more than 160 rock samples were collected for palynological analysis from the type section of the Ghelli Formation (Fig. 1). The Ghelli Formation in this area is about 900 m thick and is subdivided into three members (Fig. 2). The basal part of this rock unit consists mainly of volcanic rocks and subordinate limestones, sandstones, siltstones and shales, but the major part of the formation is composed of highly micaceous shales and sandstones. About 105 samples were treated in the palynology laboratory of Kharazmi University, Tehran, Iran, and in the paleontology research unit of the Evo-Eco-Paleo research department at the University of Lille, France. Palynomorphs were extracted from fine-grained samples such as shales and siltstones following standard palynological techniques, involving cold hydrochloric (HCl), cold hydrofluoric (HF) and hot hydrochloric (HCl) acid maceration to remove carbonates, silicates and fluorosilicates, respectively. The organic residues were then passed through 15 and 20  $\mu\text{m}$  nylon meshes, respectively at Lille and Tehran. No oxidation or alkali treatments have been carried out. All processed samples contain palynomorphs, including acritarchs, chitinozoans, cryptospores and scolecodonts in varying abundance and states of preservation. Figure 2 indicates the stratigraphic column and the position of the investigated samples with the distribution of *Orthosphaeridium* specimens. All rock samples, palynological slides and residues are stored in the paleontology collections of the Faculty of Earth Sciences, Kharazmi University, Tehran, Iran and of the UMR 8198 CNRS department of the University of Lille, respectively.

A few additional samples from the Dawan Formation (Huanghuachang section), Yichang, Hubei, South China, were also used. These latter samples were previously investigated by Li et al. (2010) and Yan et al. (2011, 2017). All relevant information about the Chinese material is provided in these latter publications.

## 3. The genus *Orthosphaeridium*

### 3.1. Historical overview

More than 20 species and one infraspecific taxon have been described so far (Table 1). The description of the individual taxa is presented here in chronological order.

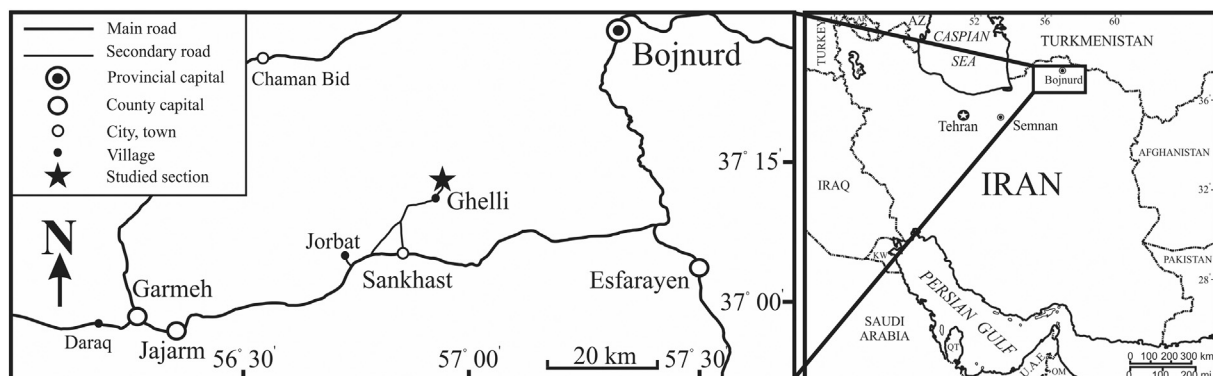


Fig. 1. Geographical map of northeastern Iran showing the location of the study area and the investigated section.

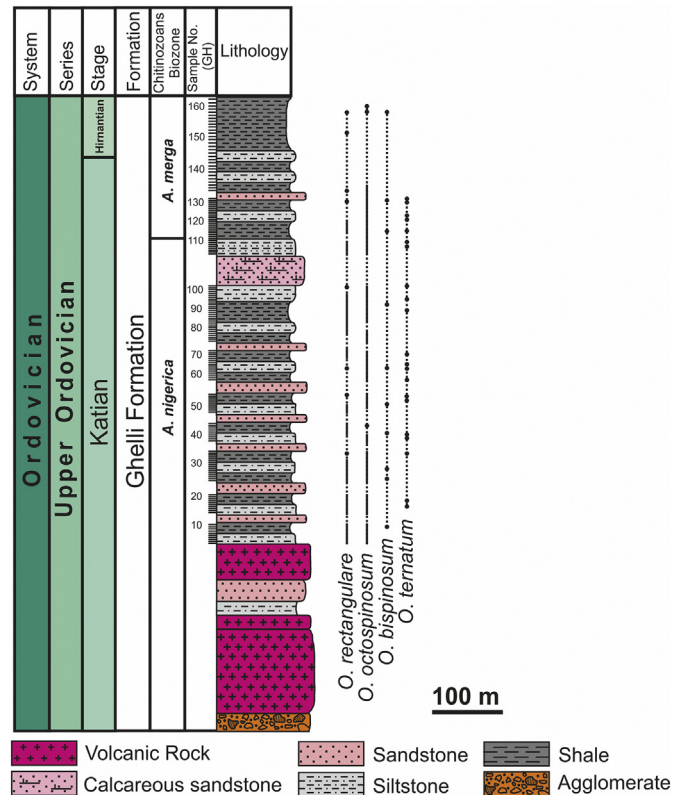


Fig. 2. Synthetic view of the type section of the Ghelli Formation with the position of the investigated samples and the distribution of *Orthosphaeridium* species in the sequence. Chitinozoan biostratigraphy unpublished.

Eisenack (1968) erected the genus *Orthosphaeridium* from erratic boulders derived from the Ordovician of Baltica. He created the new genus based on assemblages containing specimens with a more or less rectangular central body and long, simple, hollow processes that do not communicate with the vesicle cavity due to the existence of a plug at the base of the processes.

The name given by Eisenack (1968) derived from *ortho* (= straight), because of the approximately straight sides and edges of the central body, and *-sphaeridium*, because of the close relationship with the genus *Baltisphaeridium* Eisenack, 1958. The ending *-sphaeridium* indicates on the one hand the spherical outline of the genus, and on the other hand the classical ending *-idium* points out a supposed phytoplanktonic origin. The ending *-idium* is indeed traditionally used for dinoflagellate taxa, and Eisenack (1968) and many other authors considered these acritarch taxa to be the cysts of phytoplanktonic organisms, close to dinoflagellates.

**Table 1**

New classification with four distinctive species of *Orthosphaeridium* with list of all previously described taxa that are now considered as junior synonyms.

Current classification	Original name and junior synonyms	Author
<i>Orthosphaeridium bispinosum</i>	<i>Orthosphaeridium bispinosum</i>	Turner (1984)
<i>Orthosphaeridium ternatum</i>	<i>Baltisphaera ternata</i> <i>Baltisphaera procera</i>	Burmans (1970) Burmans (1970)
<i>Orthosphaeridium rectangulare</i>	<i>Baltisphaeridium rectangulare</i> <i>Orthosphaeridium inflatum</i> <i>Baltisphaera quadrinata</i> <i>Baltisphaera transitoria</i> <i>Baltisphaera quadricornis</i> <i>Baltisphaera abbreviata</i> <i>? Baltisphaera occulata</i> <i>Orthosphaeridium chondrododora</i> <i>Orthosphaeridium vibrissiferum</i> <i>? Orthosphaeridium latispinosum</i>	Eisenack (1958) Loeblich (1970) Burmans (1970) Burmans (1970) Burmans (1970) Burmans (1970) Burmans (1970) Loeblich and Tappan (1971) Loeblich and Tappan (1971) Uutela and Tynni (1991)
<i>Orthosphaeridium octospinosum</i>	<i>Orthosphaeridium octospinosum</i> <i>Orthosphaeridium insculptum</i> <i>Orthosphaeridium densigranosum</i> <i>Orthosphaeridium densiverrucosum</i> <i>? Orthosphaeridium gaspesianum</i> <i>Orthosphaeridium insculptum forma erectum</i> <i>? Orthosphaeridium orthogonium</i>	Eisenack (1968) Loeblich (1970) Kjellström (1971b) Kjellström (1971b) Martin (1980) Uutela and Tynni (1991) Le Hérisse et al. (2015)
Unknown genus <i>Lusatia dendroidea</i>	<i>Orthosphaeridium trabeculatum</i> <i>Orthosphaeridium? extensum</i> <i>Orthosphaeridium? triangulare</i>	Kjellström (1971a) Parsons and Anderson (2000) Parsons and Anderson (2000)

At the time of the original description of the genus, *Baltisphaeridium rectangulare* Eisenack, 1963 was selected as the type species with a “rectangular vesicle and four hollow processes.” In addition, the new species *Orthosphaeridium octospinosum* Eisenack, 1968 was erected with a rectangular vesicle and 7 or 8 hollow processes.

Two years after the erection of *Orthosphaeridium*, Loeblich (1970) also recovered the genus from North America and described the two species *Orthosphaeridium inflatum* and *Orthosphaeridium insculptum* from the Upper Ordovician Sylvan Shale, Oklahoma, USA. These two species subsequently became some of the most commonly recorded species of *Orthosphaeridium*. The species *Orthosphaeridium inflatum* is very similar to *Orthosphaeridium rectangulare* but Loeblich (1970) pointed out that the former has a less rectangular vesicle and that the sides of the body are more inflated. However, the central body shapes of both *O. rectangulare* and *O. inflatum* are very variable and it is impossible to distinguish different taxa in larger populations, which indicates that *Orthosphaeridium inflatum* can be considered as a junior synonym of *Orthosphaeridium rectangulare*. Similarly, the North American species *Orthosphaeridium insculptum* strongly resembles *Orthosphaeridium octospinosum* from Baltica, although the species of Loeblich (1970) was described with a more varying number (4–12) of processes than that of Eisenack (1968) that only bears 7 or 8 processes. *Orthosphaeridium insculptum* was also described to differ by having a greater central body and a less rectangular outline with a strongly granulate wall. All these morphological characteristics are highly variable and make it difficult to separate the two species, that are herein considered to belong to the same entity.

Not being aware of the description of Eisenack's (1968) new genus, Burmann (1970) created the new genus *Baltisphaera* with seven new species from Germany. However, *Baltisphaera* perfectly fits the diagnosis of Eisenack, and most authors follow Eisenack et al. (1976) and Turner (1984) who considered *Baltisphaera* as a junior synonym of

*Orthosphaeridium*. Burmann (1970) described her seven new species on the basis of a very limited number of specimens observed in thin sections (not palynological slides). Only the species *Baltisphaera ternata* Burmann, 1970, illustrated by two specimens, can be considered as new. This species has a circular vesicle with a characteristic tri-radial arrangement of long processes, that has been identified subsequently in many palynological assemblages by different authors. The other taxa, *Baltisphaera quadrinata*, *B. transitoria*, *B. procera*, *B. quadricornis*, *B. abbreviata*, and *B. occulata*, have all been described on the basis of single specimens, and have rarely been reported after their original description. They are all poorly preserved (for most of them only line drawings were provided by Burmann, 1970) and they display either three (*B. procera*, considered to be a junior synonym of *B. ternata*), or four (or possibly five) processes (all of them are considered herein to be junior synonyms of *Orthosphaeridium rectangulare*).

Kjellström (1971a) emended the genus *Orthosphaeridium* based on new material from the Grötlingbo Borehole No. 1, Gotland, Sweden, and erected the new species *Orthosphaeridium trabeculatum*. This species has a psilate rectangular vesicle and was described with nine processes that have a “trabeculate interior structure.” However, the distal endings of the processes are trifurcate, which does not correspond to the genus *Orthosphaeridium*, although Kjellström (1971a) emended the genus diagnosis to include his new species. Such trifurcate terminations have never been reported from other specimens so far and it appears clear that the specimens do not belong to *Orthosphaeridium*, of which the emended diagnosis of Kjellström (1971a) cannot be retained. In the same year, Kjellström (1971b) described two further new species, *Orthosphaeridium densigranosum* and *O. densiverrucosum*, from the same borehole. While the first species is described with a sub-square granulate vesicle and eight processes, the second species differs in having a verrucate ornamentation on both the vesicle and process wall. Both species fall in the range of morphological variation of *O. octospinosum*.

Subsequently, Loeblich and Tappan (1971) described two new species, *Orthosphaeridium chondrododora* and *O. vibrissiferum*, from the Upper Ordovician Eden Formation in Indiana, USA. Both species have four long processes and ornamented vesicle and process walls, and they both fall within the morphological range of *O. rectangulare*. Most interestingly, Loeblich and Tappan (1971) indicated an “apparent phylogenetic trend” of the different *Orthosphaeridium* species.

Eisenack et al. (1976) was the first to consider *Baltisphaera* Burmann, 1970 to be a junior synonym of *Orthosphaeridium*. He therefore placed all of Burmann's species of *Baltisphaera* in the genus *Orthosphaeridium*.

Martin (1980) introduced the new species *Orthosphaeridium gaspesianum* from the Upper Ordovician White Head Formation in the Gaspésie section, Québec, Canada. This species displays a sub-spherical vesicle with a reticulated surface and 6–8 processes and it appears to be clearly related to *O. octospinosum*.

Turner (1984) emended the diagnosis of *Orthosphaeridium* because he found another new species with only two processes, *Orthosphaeridium bispinosum*, in the assemblages of the upper Caradoc (Upper Ordovician) of Shropshire, United Kingdom. He therefore extended the definition of *Orthosphaeridium* to include also those species that display only two “polar” processes.

Uutela and Tynni (1991) introduced the new species *Orthosphaeridium latispinosum* from the Middle Ordovician of the Rapla borehole, Estonia. They considered that *O. latispinosum* has a sub-spherical vesicle with four stout and short processes. It is uncertain if this species belongs to *Orthosphaeridium* due to poor preservation and illustration. If it does, it should be considered a junior synonym of *O. rectangulare*. Uutela and Tynni (1991) also introduced the new forma *Orthosphaeridium insculptum* f. *erectum* from the upper Llanvirnian of Estonia, and they pointed out that this infraspecific taxon differs from *Orthosphaeridium insculptum* in having flagelliform processes. This “forma” displays eight processes of which the length is greater than the vesicle diameter. The processes are straight and have acuminate distal terminations with no clear constrictions at



their proximal contacts. The surface of the vesicle is echinate, and the tubercles on the processes diminish in size from the base towards the distal termination. The vesicle has a median split. **Uutela and Tynni (1991)** described this forma based on three specimens and they only illustrated one microphotograph (plate XXVI, fig. 276). These specimens clearly fall within the range of *Orthosphaeridium insculptum*, i.e., *O. octospinosum*.

**Parsons and Anderson (2000)** described the two new species *Orthosphaeridium? extensum* and *Orthosphaeridium? triangulare* from the Upper Cambrian of Random Island, Newfoundland. However, these two species do not belong to the genus *Orthosphaeridium*, but are junior synonyms of *Lusatia dendroidea* **Burmman, 1970** emend. **Albani et al., 2007** that is a typical acritarch taxon of the Upper Cambrian (**Albani et al., 2006, 2007**).

Finally, **Le Hérisse et al. (2015)** erected the new species *Orthosphaeridium orthogonium* from the Quwarah Member of the Qasim Formation, upper Katian–lower Hirnantian, Qusaiba, central Saudi Arabia. This species has a subrectangular vesicle with 10–12 processes. It has clearly a higher number of processes than all other species of *Orthosphaeridium*, and it possibly does not belong to the genus. Surprisingly, **Le Hérisse et al. (2015, pl. IX, fig. 7)** did not include *O. ternatum* in the genus *Orthosphaeridium*, but attributed it to *Baltisphaeridium*, following the classification by **Rauscher (1974)** that has usually not been followed.

### 3.2. Systematic paleontology

#### Group **Acritarcha** **Evitt, 1963**

Genus: **Orthosphaeridium** **Eisenack, 1968** emend. **Turner, 1984** nov. emend.

Type species: *Orthosphaeridium rectangulare* (**Eisenack, 1963**) **Eisenack, 1968**, by original designation.

*Original diagnosis* (**Eisenack, 1968, p. 91**): “Central body when seen from the top more or less rectangular, in cross section oval to nearly rectangular, with long, hollow and tapering, unbranched processes, that lie preferably at the corners [of the vesicle] and of which the hollow cavity is closed from the central vesicle. The opening of the vesicle occurs through a median transverse tear which is vertical to the long rectangle side.” (new translation).

*Emended diagnosis* (**Turner, 1984**): “Vesicle hollow, rectangular to circular in outline, bearing few (2–8) long, hollow, simple processes that taper to a sharp point; rarely a process may divide. Process interior is always separated from the vesicle cavity by a solid proximal plug. Excystment structure is an apparently straight split in a median or equatorial position.”

*New emended diagnosis*: Vesicle rectangular to circular in outline, with a single-layered and thick wall. Vesicle surface smooth to psilate to granulate, spinous or verrucate. Processes are hollow, long, simple with unbranched end and tapering to a sharp point. The processes do not communicate with the vesicle cavity and display a solid, basal plug. The number of processes varies from two to eight, or more (up to 12), and their surface can be smooth or ornamented like the vesicle surface. The processes may be arranged in polar (if two), tri-radial (if three) position, or concentrated on each corner of the vesicle in quadrate forms, but may also be placed irregularly on the vesicle. A median split is commonly present.

*Remarks*: **Eisenack's (1968)** original diagnosis was rather broad and included a wide variation of morphologies. **Kjellström's (1971a)** emended diagnosis is more restrictive and differs from the original diagnosis by adding trabeculate and trifurcate processes. These features were described on the basis of a few (seven) specimens only, of which one was illustrated (**Kjellström, 1971a, plate 3, fig. 11**). Such specimens with furcated processes were never recorded again and do not belong to *Orthosphaeridium*. For these reasons **Kjellström's (1971a)** emendation cannot be retained. **Turner (1984)** enhanced the diagnosis of the genus because of his record of the species *Orthosphaeridium bispinosum* that displays two polar processes. **Turner's (1984)** emended diagnosis

was necessary at the time, and included that processes are 2–8 in number. However, in some of the Iranian specimens, the number of the processes is clearly more than eight. **Eisenack (1968)** and **Turner (1984)** did not mention the ornamentation on the vesicle and process wall, that has been described in several species diagnoses. However, as many of the *Orthosphaeridium* species have a sculptured vesicle and process wall, the diagnosis is emended herein to take into account the great variety of number in processes (between 2 and 12) and of the surface wall ornamentation (smooth to psilate or verrucate).

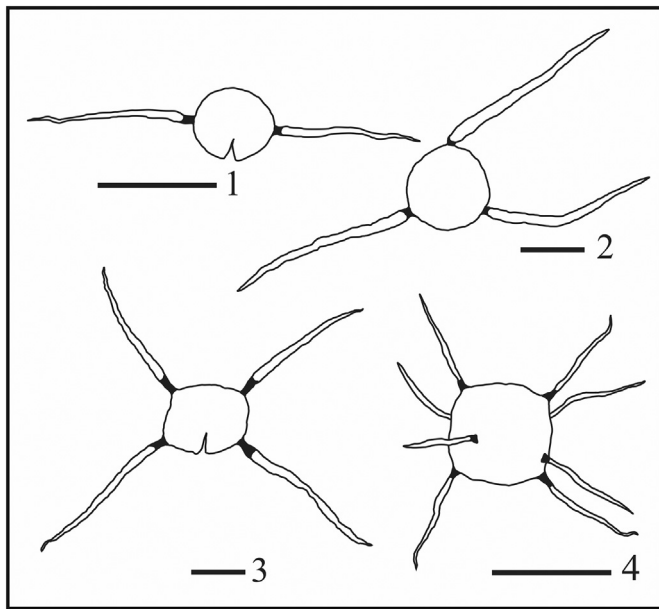
*Comparison*: The variability between “baltisphaerid” acritarchs (related to the genus *Baltisphaeridium*) is very high, and overlapping characteristics between different taxa may be observed. “Baltisphaerid” acritarchs usually display more or less rounded vesicles and have unbranched processes, whereas “multiplicisphaerid” acritarchs (related to the genus *Multiplicisphaeridium*) have branched processes. Several hundreds of species have been described within the “baltisphaerid” “multiplicisphaerid” groups. From these, *Orthosphaeridium* is rather easy to recognize, because it is clearly distinguished from *Baltisphaeridium* due to its large, hollow processes that are closed at their base by a plug. **Turner (1984)** introduced the new genus *Baltisphaerosum*, and pointed out that this genus has a spherical to sub-spherical vesicle with hollow, simple or rarely branching processes, of which the bases are always plugged so that the processes do not communicate with the vesicle cavity. *Baltisphaerosum*, like *Orthosphaeridium*, displays a median split, interpreted as an excystment opening by many authors, whereas *Baltisphaeridium* usually displays a circular opening (pylome). **Turner** mentioned that “*Orthosphaeridium* is distinguished from *Baltisphaerosum* by its few, uniformly distributed processes.” This diagnosis is thus close to that of *Orthosphaeridium*, and **Turner (1984)** already indicated that “*Baltisphaerosum* gen. nov. and *Orthosphaeridium* clearly have close affinities and future research may show them to be congeneric.” **Turner (1984)** assigned the forms with a pylome or without excystment structure to *Baltisphaeridium* and the other forms with a median split to *Baltisphaerosum*. However, **Eiserhardt (1989)** had a different view, when he emended *Baltisphaeridium* and considered the genus *Baltisphaerosum* as a junior synonym. The “baltisphaerid” acritarchs, including several hundreds of species described, clearly need a detailed revision, including morphometrical studies to clarify the taxonomy.

*Proposal of specific and infraspecific classification*: The observation of a limited number of specimens resulted in the fact that some authors erected species with a very narrow description (e.g., **Burmman, 1970**). The analysis of larger populations of *Orthosphaeridium* indicates a broad morphological variability, mainly in the number of processes, but also in the presence of sculptural elements on the vesicle and process surface (from entirely smooth, to slightly psilate or coarsely granulate, including tubercle-like elements). Most taxa described fall within the range of a few distinguishable morphologies. Most specimens described in the literature, that are also found in the palynological assemblages investigated here, display either two, three, four, or more (usually around eight) processes.

Therefore, it is proposed here to retain four species that can easily be distinguished on the basis of the number of processes (**Fig. 3**):

- *Orthosphaeridium bispinosum* **Turner, 1984**: two processes.
- *Orthosphaeridium ternatum* (**Burmman, 1970**) **Eisenack et al., 1976**: three processes.
- *Orthosphaeridium rectangulare* (**Eisenack, 1963**) **Eisenack, 1968**: four processes.
- *Orthosphaeridium octospinosum* **Eisenack, 1968**: more or less eight processes or more.

The proposed new classification scheme with four distinctive species is illustrated in **Table 1**, that includes the list of all previously described taxa that are now considered as junior synonyms. Over 20 species and one infraspecific taxon have been described in the literature so far.



**Fig. 3.** Idealized line drawings of the four general morphotypes of *Orthosphaeridium* retained herein as species. 1. *Orthosphaeridium bispinosum*, 2. *Orthosphaeridium ternatum*, 3. *Orthosphaeridium rectangulare*, 4. *Orthosphaeridium octospinosum*. Scale bar = 50  $\mu$ m.

The taxonomical revision allows to retain only the four above-mentioned, easily recognizable species.

In addition, a distinction can be made at an infraspecific level to classify specimens with smooth or ornamented vesicle and process walls:

- *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. (psilate to verrucate vesicle surface);
- *Orthosphaeridium rectangulare* var. *rectangulare* Autonym (smooth vesicle);
- *Orthosphaeridium octospinosum* var. *insculptum* var. nov. (psilate to verrucate vesicle surfaces);
- *Orthosphaeridium octospinosum* var. *octospinosum* Autonym (smooth vesicle).

*Orthosphaeridium rectangulare* var. *quadricornis* var. nov. and *Orthosphaeridium octospinosum* var. *insculptum* var. nov. are two taxa of which the taxonomical status is changed here. *Orthosphaeridium rectangulare* var. *quadricornis* is based on the original description of *Baltisphaera quadricornis* Burmann, 1970, the first taxon with four processes (thus belonging to *O. rectangulare*) described with a clearly distinctive ornamentation of the vesicle and process surface. *Orthosphaeridium octospinosum* var. *insculptum* is based on the original description of *Orthosphaeridium insculptum* Loeblich, 1970, the first taxon with about eight processes (thus belonging to *O. octospinosum*) described with ornamented vesicle and process surfaces.

#### *Orthosphaeridium bispinosum* Turner, 1984

Plate I, figs. 1–4

1984 *Orthosphaeridium bispinosum* Turner, p. 125, pl. 2, figs. 1–3; pl. 4, figs. 3, 5.

**Original diagnosis** (Turner, 1984, p. 126): “Vesicle very large, sub-spherical, hollow, thick walled (1.5–2.5  $\mu$ m); wall bears a dense ornament of short, robust, solid spines with rounded tips. The two extremely long, slender, simple, homomorphic polar processes have acuminate distal terminations; they possess basal plugs of apparently solid wall material but have little or no proximal constriction; process interior separated from vesicle cavity; process walls ornamented with spines identical to those on vesicle wall.”

**Original description** (Turner, 1984, p. 126): “The dense ornamental spines of the vesicle and process surface appear to be echinate in bright field illumination but the scanning electron microscope shows them to be short, thick, solid, conical spines with broadly rounded tips. They cover the entire vesicle surface and extend onto the process wall, typically becoming sparser distally; rarely they may die away altogether, leaving the distal portion of the process wall smooth. The process wall is much thinner (<0.5  $\mu$ m) and more delicate than the vesicle wall and frequently is folded; the distal tips of processes are infilled and solid. Excystment structure is a median split, with the vesicle often dividing completely (pl. 4, fig. 5).”

**Remarks:** This species is easily distinguishable by its prominent two polar, long, slender and simple processes from all other species of *Orthosphaeridium*. Turner's (1984) diagnosis and description are both very precise and can still be used at present.

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): This species has originally been recorded from the Upper Ordovician (type-Caradoc) of England (Turner, 1984), and subsequently from many other localities: Caradoc-early Ashgill, Jordan (Keegan et al., 1990); Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig, northwestern England (Cooper et al., 1995); Caradoc-Ashgill, Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki and Hosseinzadeh Moghadam, 2010; Mahmoudi et al., 2014; Ghavidel-Syooki et al., 2014; Ghavidel-Syooki and Borji, 2018); late Caradoc, Saudi Arabia (Jachowicz, 1995); late Arenig, northwestern England (Molyneux, 1999); early Caradoc-Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Middle Ordovician–Caradoc, Poland (Jachowicz, 2005); late Darriwilian, northwestern England, (Molyneux, 2009); Caradoc–Ashgill, western Iraq (Al-Ameri, 2010); early late Katian, southwest Libya (Abuhamida, 2013); Katian–Hirnantian, northeastern Iran (Ghavidel-Syooki, 2017c).

#### *Orthosphaeridium ternatum* (Burmann, 1970) Eisenack et al., 1976

Plate I, figs. 5–10

1970 *Baltisphaera ternata* Burmann, p. 306, pl. 7, fig. 1; pl. 9, fig. 4.

1970 *Baltisphaera procera* Burmann, p. 307, pl. 8, fig. 1.

1974 *Baltisphaeridium ternatum* Rauscher, pp. 82, 96, pl. 10, figs. 1–4.

1975 *Baltisphaeridium ternata* Tynni, fig. 10.

1976 *Orthosphaeridium ternatum* Eisenack, Cramer and Díez, p. 529.

**Original diagnosis:** “Vesicle circular in outline with a tri-radial arrangement of long unbranched processes that are distinctly differentiated from the central body by a somewhat thinner basal constriction. The processes are hollow and taper more rapidly at the distal than at the proximal end. They are placed regularly, about 120° apart. Processes and central body may be smooth or may be covered by verrucae. No pylome can be seen; the vesicle opens by splitting of the central body into two smooth-rimmed halves (translation from Eisenack et al., 1976).”

**Remarks:** This species is easily recognizable, because it shows a more or less rounded to circular vesicle with three regularly arranged processes. Burmann (1970) described the two new species *Baltisphaera ternata* and *Baltisphaera procera*, that are clearly belonging to the same unit, but that show slightly different shapes of the central body (due to compaction of the sediment), one having a more circular and the other a more oval to subspherical vesicle. Rauscher (1974) placed *B. ternata* in the genus *Baltisphaeridium*, but Eisenack et al. (1976) transferred all of Burmann's *Baltisphaera* species to *Orthosphaeridium*. *Orthosphaeridium ternatum* has priority and *Orthosphaeridium procerum* is considered here as a junior synonym.

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): *Orthosphaeridium ternatum* has been reported from numerous localities around the world. After its original description from the late Llanvirn of

Germany (Burmans, 1970, 1973) it has been recorded in the following localities: Arenig–Llanvirn, France (Martin, 1973); Llanvirn, France (Rauscher, 1974); Caradoc–Ashgill? of the Algerian Sahara (Jardiné et al., 1974); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); early Llanvirn, Czech Republic (Vavrdová, 1976, 1977); early Arenig–late Llanvirn (Díez and Cramer, 1977); early Llanvirn, Shropshire, England (Booth, 1979); late Llanvirn, Lake District, NW England (Booth, 1979); Caradoc, England (Turner, 1984); early Llanvirn–early Ashgill, England (Downie, 1984); late Arenig–Llanvirn, Morocco (Elaouad-Debbaj, 1984); late Arenig, Wales (Molyneux, 1987, 1990); early Llanvirn, Belgium (Servais and Maletz, 1992); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Caradoc–Ashgill, Iran (Ghavidel-Syooki and Khosravi, 1995); Oretanian–Dobrotivian (Llanvirn–early Caradoc), northern Spain (Gutiérrez-Marco et al., 1996); Llanvirn, Algeria (Vecoli, 1999); Caradoc, southern Iran (Ghavidel-Syooki, 1997); early Caradoc, Zagros Basin, southern Iran (Ghavidel-Syooki, 2000b); early? Ordovician, southeastern Turkey (Erkmen, 1979); Llanvirn–Ashgill, northeastern Iran (Ghavidel-Syooki, 2001); Caradoc–Ashgill, northeastern Iran (Ghavidel-Syooki, 2000a); Darriwilian, Saudi Arabia (Le Hérisse et al., 2007); Darriwilian (4a–4b), southern and southeastern Turkey (Paris et al., 2007); Llanvirn–Llandeilo, western Iraq (Al-Ameri, 2010); early late Katian, southwestern Libya (Abuhamida, 2013); Katian, southeastern Iran (Ghavidel-Syooki et al., 2014); Ashgill, southeastern Caspian Sea (Ghavidel-Syooki, 2017b).

*Orthosphaeridium rectangulare* (Eisenack, 1963) Eisenack, 1968 (type species)

1963 *Baltisphaeridium rectangulare* Eisenack, p. 211, pl. 20, figs. 1–3, 10.

1968 *Orthosphaeridium rectangulare* Eisenack, p. 92, pl. 25, Fig. 1. 1970 *Orthosphaeridium inflatum* Loeblich, p. 733–734, figs. 29A–E.

1970 *Baltisphaera quadrinata* Burmann, p. 306, pl. 8, fig. 1.

1970 *Baltisphaera transitoria* Burmann, p. 306–307, pl. 12, fig. 1.

1970 *Baltisphaera quadricornis* Burmann, p. 307–308, pl. 13, fig. 2.

1970 *Baltisphaera abbreviata* Burmann, p. 308, pl. 14, figs. 7a, b.

? 1970 *Baltisphaera occulta* Burmann, p. 308, pl. 16, fig. 1.

1971 *Orthosphaeridium chondrododora* Loeblich and Tappan, p. 184–186, figs. 2–6.

1971 *Orthosphaeridium vibrissiferum* Loeblich and Tappan, p. 186–188, figs. 7–12.

? 1991 *Orthosphaeridium latispinosum* Uutela & Tynni, p. 103, pl. XXVI: 277, fig. 4: 183.

**Original diagnosis:** Central body flattened, when seen from the top almost rectangular with more or less bulged sides, with four long, hollow processes that arise from the corner of the rectangle and that lie in a plane (new translation).

**Remarks:** This species is very easy to differentiate, because it displays a rectangular to sub-quadrate vesicle with four major processes that are preferentially located at the corners of the vesicle. Several authors described the species under different new names, that are here considered as junior synonyms of *Orthosphaeridium*. Similar to the vesicle shape, the surface ornamentation is also highly variable. For species with an ornamented surface of the vesicle and the processes (psilate, granulate, verrucate ornamentation), the variety *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. is proposed, based on the original description of the first ornamented specimen by Burmann (1970) as *Baltisphaera quadricornis*. All rectangular *Orthosphaeridium* specimens with four processes and smooth vesicle walls can be attributed to *Orthosphaeridium rectangulare* var. *rectangulare* (Autonym).

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): The species *Orthosphaeridium rectangulare* has been recorded under this identification from several localities around the world, in chronological

order: from the Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1963, 1968); Middle Ordovician, Llanvirn–Caradoc, Gotland, Sweden (Kjellström, 1971a); latest Ordovician, Oklahoma, USA (Loeblich, 1970); Llanvirn–Llandeilo (Díez and Cramer, 1974); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc–Ashgill, Portugal (Elaouad-Debbaj, 1978); late Ashgill, Morocco (Elaouad-Debbaj, 1988); Middle Ordovician, Sweden (Kjellström, 1971b); Ashgill, Québec, Canada (Martin, 1988); Ashgill, Jordan (Keegan et al., 1990); Ashgill, Estonia (Uutela and Tynni, 1991); middle-late Ashgill, south-eastern Turkey (Steenmans et al., 1996); Ashgill, northeastern Missouri, USA (Wicander et al., 1999); Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Caradoc–Ashgill, southern Oklahoma, USA (Playford and Wicander, 2006); Ashgill, Michigan, USA (Wicander and Playford, 2008); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a); Llandeilo–Caradoc, western Iraq (Al-Ameri, 2010); Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, southeastern Caspian Sea (Ghavidel-Syooki, 2008, 2017b); Hirnantian, Zagros Mountains, Iran (Ghavidel-Syooki et al., 2011b); Katian–Hirnantian, northern Iran (Ghavidel-Syooki et al., 2011a); late Hirnantian, eastern Alborz, Iran (Mahmoudi et al., 2014); Katian, southeastern Iran (Ghavidel-Syooki et al., 2014); Katian–Hirnantian, central Saudi-Arabia (Le Hérisse et al., 2015); Katian–Hirnantian, northeastern Alborz Mountains, Iran (Ghavidel-Syooki and Borji, 2018).

*Orthosphaeridium rectangulare* var. *quadricornis* var. nov. stat. nov. Plate II, figs. 4–5

**Basionym:** *Baltisphaera quadricornis* Burmann, 1970, p. 307–308, pl. 13, fig. 5.

**Diagnosis:** A variety of *Orthosphaeridium rectangulare* with an ornamented surface of the central vesicle and/or the processes. Ornamentation variable, from psilate to granulate or verrucate.

**Remarks:** The name of this new variety is based on the name of the first rectangular specimens of *Orthosphaeridium* with a clearly ornamented surface described by Burmann (1970) as *Baltisphaera quadricornis*. The body shape and process morphology is similar to that of all *Orthosphaeridium rectangulare* morphotypes, but it differs from *O. rectangulare* var. *rectangulare* (Autonym) in having an ornamented central vesicle wall. This ornamentation may also be present on the wall of the processes.

The ornamentation of the wall of acritarch specimens is highly variable. Possibly ecological changes are responsible for these variations, but such assumptions remain speculative. However, it appears logical not to distinguish the different end members of this variation (from smooth to highly ornamented surfaces) as different species. Therefore, a classification into infraspecific entities, as varieties, is proposed. The identification at the species level is mostly straightforward. The identification at the variety level may sometimes be difficult, due to preservation or observation methods (optical microscopy versus scanning electron microscopy, SEM).

**Discussion:** *Baltisphaera quadricornis*, originally described by Burmann (1970), was placed by Eisenack et al. (1976) into *Orthosphaeridium* and retained as a separate species. It is here considered a variety of *Orthosphaeridium rectangulare* because it displays the same vesicle outline and process number and distribution as *Orthosphaeridium rectangulare* but the surfaces of the vesicle and of the processes have been described to be covered by tubercles. Burmann (1970) described another species, *Orthosphaeridium quadrinatum* (Burmann, 1970) Eisenack et al., 1976, with a vesicle wall being smooth or ornamented. Similarly, *Orthosphaeridium transitorium* (Burmann, 1970) Eisenack et al., 1976 was also described with the vesicle and processes walls being covered by tubercles. The two species *Orthosphaeridium chondrododora* and *O. vibrissiferum* described by Loeblich and Tappan (1971) also correspond to ornamented morphotypes of *Orthosphaeridium rectangulare*. While *O. chondrododora*



was described with an ornamentation by grana, *O. vibrissiferum* was described as displaying granulose spines. Loeblich and Tappan (1971, fig. 1) noted that these changes in the ornamentation were related to a phylogenetic trend (see also discussion below).

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): The species *Orthosphaeridium quadricornis* has been reported under this name from the late Llanvirn of Germany (Burmans, 1970, 1976), but also from the Ashgill–early Llandovery? of northern India (Prasad and Asher, 2001), as well as from the Ashgill of western Iraq (Al-Ameri, 2010).

Specimens identified as *Orthosphaeridium quadrinatum* have been reported after their initial description from the late Llanvirn of Germany by Burmann (1970, 1976) from the following localities: Caradoc, England (Turner, 1984); Caradoc, Czech Republic (Vavrdová, 1974); Caradoc, Britain (Downie, 1984); Ashgill, Jordan (Keegan et al., 1990); late Arenig (lower Darriwilian, stage slice Dw1) from the Grifflschiefer in the Schwarzburg Anticline, Germany (Heuse et al., 1994); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, China (Yin, 1995); Caradoc, western Iraq (Al-Ameri, 2010); Katian–Hirnantian, northeastern Iran (Ghavidel-Syooki, 2017c).

*Orthosphaeridium transitorium* was only reported from the late Llanvirnian, Germany (Burmans, 1970, 1976) and not subsequently by other authors.

*Orthosphaeridium chondrododora* has been identified after its original description from the Late Ordovician of Indiana, USA (Loeblich and Tappan, 1971) from a number of localities: Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc, Indiana, USA (Colbath, 1979); Ashgill, Morocco (Elaouad-Debbaj, 1988); Caradoc–Ashgill (Díez and Cramer, 1974); late Caradoc, United Kingdom (Downie, 1984); Caradoc, England (Turner, 1984); Ashgill, northeastern Libya (Hill and Molyneux, 1988); Ashgill, Scotland (Whelan, 1988); Ashgill, Estonia (Uutela and Tynni, 1991); Caradoc–Ashgill, Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 2000a); late Caradoc, Saudi Arabia (Jachowicz, 1995); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); Caradoc, England (Molyneux et al., 1996); late Ordovician, southeastern Turkey (Erkmen, 1979); early Caradoc–late Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Katian, southeastern Turkey (Paris et al., 2007); Katian–Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, central Saudi Arabia (Le Hérisse et al., 2015).

*Orthosphaeridium vibrissiferum* has been identified after its first description from the Middle Ordovician, Indiana, USA (Loeblich and Tappan, 1971) from a few other localities: Caradoc, Poland (Górka, 1979); Middle–Late Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad-Debbaj, 1988); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); early Caradoc, Argentina (Ottone et al., 1999); early Caradoc–late Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Katian, Estonia (Delabroye et al., 2011a).

*Orthosphaeridium rectangulare* var. *rectangulare* Autonym

Plate II, figs. 1–3, 6

**Diagnosis:** Same as that of the species.

**Remarks:** With the description of the new variety *Orthosphaeridium rectangulare* var. *quadricornis* all other specimens belonging to the species with a smooth surface of the vesicle and process wall can be assigned to *Orthosphaeridium rectangulare* var. *rectangulare* Autonym.

**Discussion:** *Orthosphaeridium inflatum* Loeblich, 1970 has been described with no ornamentation, but according to the present revision, no characteristic differences can be found between this species and *O. rectangulare*. Loeblich (1970) only pointed out that “*Orthosphaeridium inflatum* is very similar to *O. rectangulare* (Eisenack, 1963) Eisenack, 1968, but differs in having a less rectangular central body.” Most specimens identified as *Orthosphaeridium inflatum* could thus be attributed to *O. rectangulare* var. *rectangulare*. Similarly, *Baltisphaera abbreviata*

Burmans, 1970 was described without ornamentation, and therefore corresponds to the same taxon.

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): Smooth specimens of *Orthosphaeridium rectangulare* have been recorded from different localities (see above), whereas *O. inflatum* has been identified as such from the Late Ordovician of Oklahoma, USA (Loeblich, 1970) and a few other localities: early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Ashgill, Jordan (Keegan et al., 1990); Caradoc–Ashgill, Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 1997, 2000a, 2001, 2003, 2006, 2017b); Katian, Québec, Canada (Delabroye et al., 2011b); late Katian, southern Sweden (Badawy, 2012).

A single identification corresponding to *Orthosphaeridium abbreviatum* (Burmans, 1970) Eisenack et al., 1976 is available from the Caradoc of western Iraq (Al-Ameri, 2010).

*Orthosphaeridium octospinosum* Eisenack, 1968

1968 *Orthosphaeridium octospinosum* Eisenack, p. 92, pl. 25, figs. 2–3.

1970 *Orthosphaeridium insculptum* Loeblich, p. 734–735, fig. 30 A–E.

1971b *Orthosphaeridium densigranulosum* Kjellström, p. 28–30, fig. 19.

1971b *Orthosphaeridium densiverrucosum* Kjellström, p. 30, fig. 20.

? 1980 *Orthosphaeridium gaspesianum* Martin, p. 112, pl. 4, figs. 1, 2, 7, fig. 2.

1991 *Orthosphaeridium insculptum* f. *erectum* Uutela and Tynni, p. 103, pl. XXVI: 276, fig. 4: 140

? 2015 *Orthosphaeridium orthogonium* Le Hérisse, Molyneux and Miller, p. 51, pl. X, figs. 1–2.

**Original diagnosis** (Eisenack, 1968, p. 92): Central body rectangular to square, generally throughout cuboid, with eight or respectively seven processes, that are similar to *O. rectangulare* originating and diverging from the corners [of the vesicle], so that they lay in the prolongation of a diagonal line of the [central body] surface. They correspond in their location and design type to those of the genus type (new translation).

**Remarks:** This distinctive species has clearly more than four processes, usually eight, or more. Most interestingly, Eisenack (1968) noted in his remarks that *O. octospinosum* could be a variant of *Orthosphaeridium* due to polyploidy, but that as a fossil it should be considered as a separate species. After the original description of this species by Eisenack (1968), several authors described almost the same morphology under different new species names. Loeblich (1970) created *O. insculptum* by noting simply that it was bigger than Eisenack’s specimens and that the American specimens showed an ornamented vesicle wall. Similarly, Kjellström (1971b) described the two almost identical species *O. densigranulosum* and *O. densiverrucosum*, with the former taxon having smooth and the latter ornamented vesicle walls. Few of the authors, as it was usual at this time, mentioned variations between the individual morphotypes. However, Loeblich and Tappan (1971) noted a gradual change in their sections (see below). Here, all these taxa with more or less eight processes are considered to belong to the same species *O. octospinosum*.

Martin (1980) introduced *Orthosphaeridium gaspesianum* from the Late Ordovician of Québec and mentioned that it has a spherical central body with reticulated surface and six or eight processes. Because the preservation of the specimens is poor and even with the SEM microphotographs it is not possible to observe the basal plug, the attribution of this species to *Orthosphaeridium* remains questionable. It could be that this reticulate ornamentation on the central body surface (illustrated in the drawing in Martin, 1980, fig. 2) might be the result of preservation or corrosion during maceration. This species has not been recorded from elsewhere so far.

The infraspecific taxon *Orthosphaeridium insculptum* f. *erectum* Uutela and Tynni, 1991 also falls within the range of variation of the species *O. octospinosum*, but it is not retained here as a separate form.



The new species *O. orthogonium* Le Hérisse et al., 2015 is possibly related to the genus *Orthosphaeridium* and to the species *O. octospinosum*. This latter taxon has a higher number of processes and a clearly rectangular or trapezoidal central body that does not resemble the general morphology of *Orthosphaeridium*.

**Discussion:** *Orthosphaeridium octospinosum* is one of the four general morphotypes retained as separate species in the present study. It includes those specimens bearing clearly more than four processes. Following the original diagnosis by Eisenack (1968) this species has usually eight processes with the main processes located at the corners of the vesicle and others arising from other parts of the central body.

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): Under its original name *O. octospinosum*, this species has been reported after its original description from the Late Ordovician of Baltica by Eisenack (1968) from other localities of the Middle and Late Ordovician: Late Ordovician (Ashgill), USA (Loeblich, 1970); Middle Ordovician, Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad-Debbaj, 1988); Ashgill, Portugal (Elaouad-Debbaj, 1978); Middle Ordovician, Sweden (Kjellström, 1971b); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Ashgill, Turkey (Dean and Martin, 1992); Caradoc–Ashgill, Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 2000a, 2003); Caradoc, eastern Canada (Martin, 1983); Hirnantian, Saudi Arabia (Miller and Al-Ruwaili, 2007); early late Katian, southwestern Libya (Abuhamida, 2013); late Hirnantian, eastern Alborz, Iran (Mahmoudi et al., 2014); Katian–Hirnantian, northeastern Alborz Mountains, Iran (Ghavidel-Syooki, 2017c; Ghavidel-Syooki and Borji, 2018).

*Orthosphaeridium octospinosum* var. *insculptum* var. nov. stat. nov.  
Plate II, figs. 7–9, 12.

**Basionym:** *Orthosphaeridium insculptum* Loeblich 1971, p. 734–735, fig. 30 A–E.

**Diagnosis:** A variety of *Orthosphaeridium octospinosum* with an ornamented surface of the central vesicle and/or the processes. Ornamentation variable, from psilate to granulate or verrucate.

**Remarks:** In analogy with the proposed classification scheme of the species *O. rectangulare*, an infraspecific classification is also proposed for the species *O. octospinosum* to distinguish smooth and ornamented specimens. The name and conception of the new variety *Orthosphaeridium octospinosum* var. *insculptum* is adopted from the name and diagnosis of the first rectangular specimens bearing about eight processes (*O. octospinosum*) that have been described with an ornamented surface by Loeblich (1970) as *O. insculptum*. The body shape and process morphology is similar to that of all *O. octospinosum* morphotypes, but it differs from *O. octospinosum* var. *octospinosum* (Autonym) in having an ornamented central vesicle wall. This ornamentation may also be present on the wall of the processes.

**Biostratigraphical and paleogeographic distribution** (quoting the original attributions, including the former British regional stages): Many authors identified specimens as *Orthosphaeridium insculptum* from numerous localities making this taxon one of the most widely recorded of the genus: Late Ordovician, Oklahoma USA (Loeblich, 1970; Tappan, 1980); Caradoc, Libya (Deunff and Massa, 1975); Ashgill, Portugal (Elaouad-Debbaj, 1978); Late Ordovician, southeastern Turkey (Erkmen, 1979); Ashgill–Caradoc, Québec, Canada (Martin, 1980); Llandeilo–Caradoc, Ontario, Canada (Martin, 1983); early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad-Debbaj, 1988); Ashgill, northeastern Libya (Hill and Molyneux, 1988); latest Ordovician, Czech Republic (Vavrdová, 1988); Ashgill, Québec, Canada (Martin, 1988); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); middle–late Ashgill, southeastern Turkey (Steenmans et al., 1996); late Ashgill (Hirnantian), southern Norway (Smelror et al., 1997); Ashgill, northeastern Missouri, USA (Wicander et al., 1999); early Caradoc–late Ashgill, “northern” Gondwana (Vecoli

and Le Hérisse, 2004); Ashgill, southern Oklahoma, USA (Playford and Wicander, 2006); Katian, southeastern Turkey (Paris et al., 2007); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a); Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, southwestern Libya (Abuhamida, 2013); Caradoc–Ashgill, Iran (Ghavidel-Syooki, 1997, 2000a, 2001, 2003, 2006, 2008, 2016, 2017a, 2017b, 2017c); Hirnantian, Zagros Mountains, Iran (Ghavidel-Syooki et al., 2011b); Katian, northeastern Alborz Mountains, Iran (Ghavidel-Syooki and Borji, 2018).

Under the taxonomic name *Orthosphaeridium densigranulosum* the species has been reported from the Middle Ordovician (Lower Viruan) of Gotland, Sweden (Kjellström, 1971b), and from the Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975), whereas a few reports were made of *Orthosphaeridium densiverrucosum* after its original description from the Middle Ordovician (Lower Viruan) Gotland, Sweden (Kjellström, 1971b); late Llanvirn, Poland (Górka, 1980); Middle Ordovician, southwestern Finland (Uutela, 1989); Llanvirn–Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig–early Llanvirn, Sweden (Ribecai and Tongiorgi, 1995).

*Orthosphaeridium octospinosum* var. *octospinosum* Autonym  
Plate II, figs. 10–11.

**Diagnosis:** As for the species *Orthosphaeridium octospinosum*.

**Remarks:** With the description of the new variety *Orthosphaeridium octospinosum* var. *insculptum* all other specimens belonging to the species with a smooth surface of the vesicle and process wall can be assigned to *Orthosphaeridium octospinosum* var. *octospinosum* Autonym.

**Discussion:** As the specimens described previously under the identification of *O. insculptum*, *O. densigranulosum*, *O. densiverrucosum* all display an ornamented vesicle wall, and because *O. gaspesianum* and *O. orthogonium* are not clearly attributable to *Orthosphaeridium*, the only smooth *Orthosphaeridium* with about eight processes have been identified in previous studies as *O. octospinosum*.

**Biostratigraphical and paleogeographic distribution:** See that for the species *Orthosphaeridium octospinosum*.

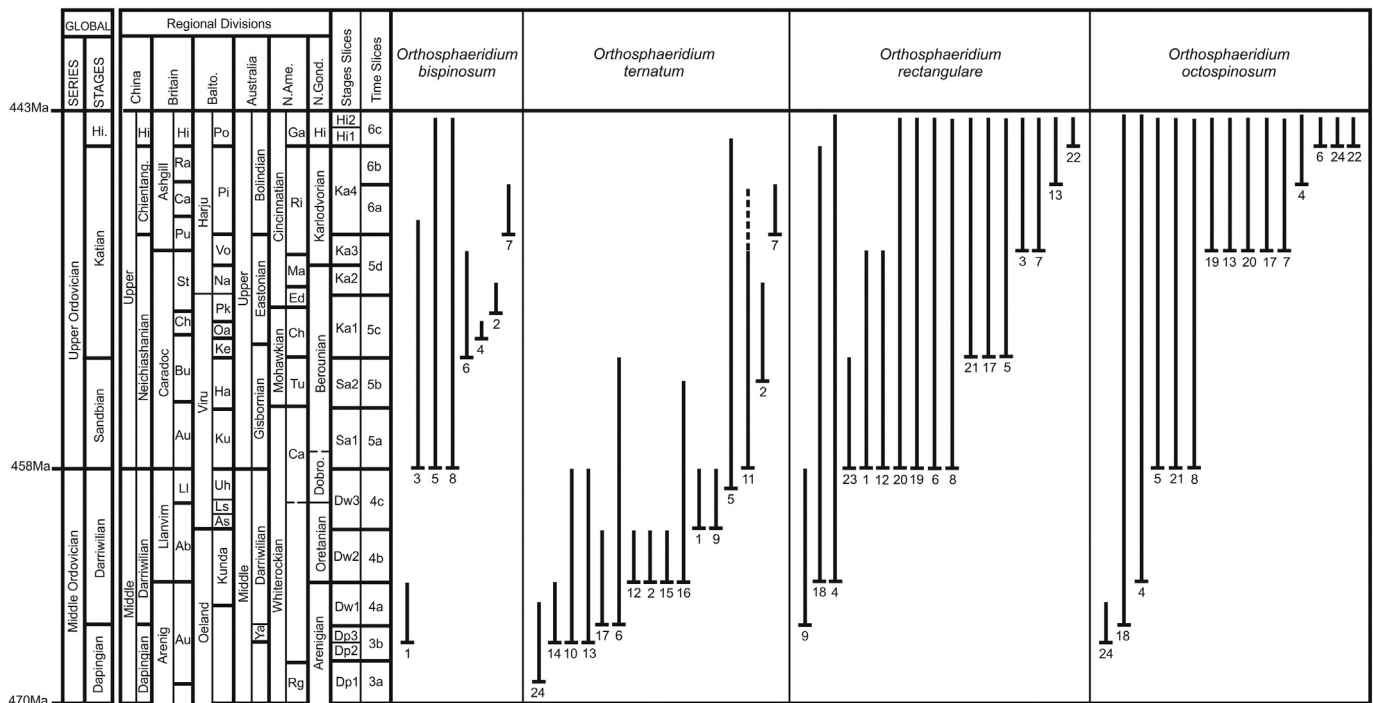
#### 4. Biostratigraphy of *Orthosphaeridium*

From the literature overview and from the taxonomical revision, it becomes clear that *Orthosphaeridium* is largely recorded from the Middle and Late Ordovician strata. The Late Cambrian records (as *O.?* *extensum* and *O.?* *triangulare*) are not corresponding to the genus, and Early Ordovician (Tremadocian and Floian) records have not yet been published. The only report of possible Early Ordovician levels (Erkmen, 1979) is highly questionable.

The interesting question is thus if the genus displays distinctive biostratigraphical distributions depending on the individual taxa (species) or corresponding to different paleocontinents. Therefore, the stratigraphical distribution from different paleocontinents is revised, but also the First (FAD) and Last Appearance Datums (LAD) of the different taxa. Figure 4 illustrates the biostratigraphical distribution of the four different species of *Orthosphaeridium*, based on all published occurrences. In the following paragraphs the stratigraphical range is indicated, as it was described by the authors in the original papers. Very often the traditional British stratigraphical terms were used (Arenig, Llanvirn, Llandeilo, Caradoc, Ashgill) that are now correlated with the current global chronostratigraphy (Fig. 4). The stratigraphical information is summarized below, and presented following different paleobiogeographical areas.

##### 4.1. Stratigraphical distribution in Iran

During the last decades, *Orthosphaeridium* has widely been recorded in a series of studies from several Sandbian–Hirnantian (Caradoc–



**Fig. 4.** Global stratigraphical distribution of the four species of *Orthosphaeridium*. Global Series and Stages, regional divisions, stage slices and time slices of the Ordovician, based on Webby et al. (2004) and Bergström et al. (2009). 1. Northern England (Booth, 1979; Downie, 1984; Turner, 1984; Whelan, 1988; Cooper et al., 1995; Molyneux et al., 1996; Molyneux, 1999, 2009); 2. southwestern England (Booth, 1979; Turner, 1984); 3. Jordan (Keegan et al., 1990); 4. Estonia (Uutela and Tynni, 1991; Delabroye et al., 2011a); 5. Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 1997, 2000a, 2000b, 2001, 2003, 2006, 2008; Ghavidel-Syooki et al., 2011a, 2011b; Mahmoudi et al., 2014; Ghavidel-Syooki and Borji, 2018); 6. Saudi Arabia (Jachowicz, 1995; Miller and Al-Ruwaili, 2007; Le Hérisse et al., 2007, 2015); 7. Libya (Hill and Molyneux, 1988; Abuhamida, 2013); 8. "Northern Gondwana" (Vecoli and Le Hérisse, 2004); 9. Germany (Burmam, 1970, 1973, 1976; Heuse et al., 1994); 10. France (Martin, 1973; Rauscher, 1974); 11. Algerian Sahara (Jardiné et al., 1974); 12. Czechoslovakia (Vavrdová, 1974, 1976, 1977); 13. Morocco (Elaouad-Debbaj, 1984, 1988); 14. Wales (Molyneux, 1987, 1990); 15. Belgium (Servais and Maletz, 1992); 16. Spain (Gutiérrez-Marco et al., 1996); 17. Turkey (Erkmen, 1979; Dean and Martin, 1992; Steemans et al., 1996; Paris et al., 2007); 18. Sweden (Eisenack, 1963, 1968; Kjellström, 1971a, 1971b; Górká, 1987; Badawy, 2012); 19. United States (Loeblich, 1970; Loeblich and Tappan, 1971; Colbath, 1979; Tappan, 1980; Wicander et al., 1999; Playford and Wicander, 2006; Wicander and Playford, 2008); 20. Portugal (Elaouad-Debbaj, 1978); 21. Canada (Martin, 1980, 1983, 1988; Jacobson and Achab, 1985; Delabroye et al., 2011b); 22. Tunisia (Ottone et al., 1999; Vecoli et al., 2009); 23. Norway (Smelror et al., 1997); 24. South China (Yan et al., 2011).

Ashgill in terms of traditional British stratigraphy) sections in Iran (Fig. 4). Due to the general absence of palynological investigations of Middle Ordovician rocks, older occurrences are not yet reported from Iran. All of the four general morphotypes of *Orthosphaeridium* and the new varieties proposed in this study have been reported from previous investigations from Iran. All taxa have also been found in the material investigated in this work (Fig. 2).

*Orthosphaeridium bispinosum* has been found in several localities and the stratigraphical range of the species covers almost the entire Sandbian to Hirnantian interval: Seyahou Formation, Zagros basin, southern Iran (Ghavidel-Syooki and Khosravi, 1995); Abarsaj Formation, Kholin-Darreh, southeastern Caspian Sea (Ghavidel-Syooki and Hosseinzadeh Moghadam, 2010); Ghelli Formation, Khosh-Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Ghelli Formation, Ghelli type section, northeastern Iran (Ghavidel-Syooki, 2017c); Ghelli Formation, Robat-e Gharabil area, northeastern Alborz Mountains (Ghavidel-Syooki and Borji, 2018). Similarly, *Orthosphaeridium ternatum* has been reported from several localities: Seyahou Formation, Zagros basin, southern Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 2000b); Ghelli Formation, northeastern Alborz Mountains (Ghavidel-Syooki, 2000a, 2001); Abarsaj Formation, southeastern Caspian Sea (Ghavidel-Syooki, 2017b). *Orthosphaeridium rectangulare* is recorded from several sections: the so-called Gorgan Schists, southeastern Caspian Sea (Ghavidel-Syooki, 2008); Ghelli Formation, Khoshyeilagh area (Ghavidel-Syooki et al., 2011a); Dargaz Formation, Zagros Mountains (Ghavidel-Syooki et al., 2011b); Ghelli Formation, Khosh-Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Abarsaj Formation, southeastern Caspian Sea, (Ghavidel-Syooki, 2017b); Ghelli Formation, Robat-e Gharabil area, northeastern

Alborz Mountains (Ghavidel-Syooki and Borji, 2018). *Orthosphaeridium octospinosum* has been recorded from the following locations: Seyahou Formation, Zagros basin, southern Iran (Ghavidel-Syooki and Khosravi, 1995); Ghelli Formation, northeastern Alborz Mountains (Ghavidel-Syooki, 2000a, 2003); Ghelli Formation, Khosh-Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Ghelli Formation, Ghelli type section, northeastern Iran (Ghavidel-Syooki, 2017c); Ghelli Formation, Robat-e Gharabil area, northeastern Alborz Mountains (Ghavidel-Syooki and Borji, 2018).

All taxa show thus an almost uniform distribution over the entire Upper Ordovician of Iran, with no preferential distribution of individual species. Similarly, there is no particular trend in the section investigated here, with all species present at almost all intervals (Fig. 2).

#### 4.2. Stratigraphical distribution in Baltica

The different species of *Orthosphaeridium* identified from the margins of the paleocontinent Baltica have so far restricted ranges, which might result from insufficient sampling. Nevertheless, all four major morphotypes have been recorded from this paleocontinent. Similarly to Iran, a preferential distribution of individual morphotypes is not clearly visible so far.

*Orthosphaeridium bispinosum* has so far only been recorded from the Viru Series in the Rapla borehole, Keila to Oandu regional stages, Estonia (Uutela and Tynni, 1991), and from the Middle Ordovician-Caradoc of Poland (Jachowicz, 2005), whereas *Orthosphaeridium ternatum* has only been reported from the Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975). *Orthosphaeridium rectangulare* has been more widely recorded: Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1963,

1968); Middle Ordovician, Llanvirn–Caradoc, Gotland, Sweden (Kjellström, 1971a); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Middle Ordovician, Sweden (Kjellström, 1971b); Ashgill, Estonia (Uutela and Tynni, 1991); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a). Under the name *Orthosphaeridium inflatum* the species was reported from the late Katian, southern Sweden (Badawy, 2012). Records as *Orthosphaeridium chondrododora* and *Orthosphaeridium vibrissiferum* are from the following intervals: Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc, Poland (Górka, 1979); Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Estonia (Uutela and Tynni, 1991); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); Katian, Estonia (Delabroye et al., 2011a). *Orthosphaeridium octospinosum* has also been reported largely: from the Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1968), the Middle Ordovician, Gotland, Sweden (Górka, 1987), and the Middle Ordovician of Sweden (Kjellström, 1971b). *Orthosphaeridium octospinosum* var. *insculptum* var. nov. has been reported from the Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); late Ashgill (Hirnantian), southern Norway (Smelror et al., 1997); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a). The reports under the species names *Orthosphaeridium densigranulosum* and *Orthosphaeridium densiverrucosum* have been reported from a series of localities: the Middle Ordovician (lower Viruan), Gotland, Sweden (Kjellström, 1971a, 1971b); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975), late Llanvirn, Poland (Górka, 1980); Middle Ordovician, southwestern Finland (Uutela, 1989); Llanvirn–Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig–early Llanvirn, Sweden (Ribecai and Tongiorgi, 1995).

#### 4.3. Stratigraphical distribution in Laurentia

Interestingly, *Orthosphaeridium bispinosum* and *O. ternatum* have not yet been recorded from this paleocontinent. Only the species with four (*O. rectangulare*) and about eight processes (*O. octospinosum*) are reported from Laurentia. Similarly to Iran, Middle Ordovician studies are lacking so far, and therefore all occurrences from Laurentia are limited to the Late Ordovician. Although Loeblich and Tappan (1971) mentioned findings from samples of the Middle Ordovician, the investigated Bromide Formation is of early Sandbian (Late Ordovician) age. Thus there are so far no occurrences from the Middle Ordovician, most probably due to the lack of studies. Future palynological investigations of Middle Ordovician sediments will possibly report the presence of the genus and thus an earlier FAD in Laurentia.

*Orthosphaeridium rectangulare* has been found from the following localities: latest Ordovician, Oklahoma, USA (Loeblich, 1970); Ashgill, Québec, Canada (Martin, 1988); Ashgill, northeastern Missouri, USA (Wicander et al., 1999); Caradoc–Ashgill, southern Oklahoma, USA (Playford and Wicander, 2006); Ashgill, Michigan, USA (Wicander and Playford, 2008); Hirnantian, Québec, Canada (Delabroye et al., 2011b). *Orthosphaeridium inflatum* has been reported as such from the Late Ordovician, Oklahoma, USA (Loeblich, 1970), from the early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985) and the Katian, Québec, Canada (Delabroye et al., 2011b). Records with the identification as *Orthosphaeridium chondrododora* and *Orthosphaeridium vibrissiferum* are from the following localities: Middle–Late Ordovician, Indiana, USA (Loeblich and Tappan, 1971; but all corresponding to the Late Ordovician); Caradoc, Indiana, USA (Colbath, 1979); Katian–Hirnantian, Québec, Canada (Delabroye et al., 2011b). *Orthosphaeridium octospinosum* was reported under this identification from the Late Ordovician (Ashgill), USA (Loeblich, 1970) and the Caradoc of eastern Canada (Martin, 1983). *Orthosphaeridium insculptum* has been reported from the Late Ordovician, Oklahoma, USA (Loeblich, 1970; Tappan, 1980); Ashgill–Caradoc, Québec, Canada (Martin, 1980); Llandeilo–Caradoc, Ontario, Canada (Martin, 1983); early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Ashgill, Québec, Canada

(Martin, 1988); Ashgill, northeastern Missouri, USA (Wicander et al., 1999); Ashgill, southern Oklahoma, USA (Playford and Wicander, 2006); Hirnantian, Québec, Canada (Delabroye et al., 2011b).

No obvious discriminative trend for a biostratigraphical distribution of individual taxa is evident. However, it is noteworthy that Loeblich and Tappan (1971) proposed an evolutionary scenario with “a progressive increase in processes” between the Eden Shale Formation and the Sylvain Shale Formation, which might correspond to ecological changes in the succession (see below).

#### 4.4. Stratigraphical distribution in Gondwana

*Orthosphaeridium* specimens have been found from numerous localities from the peri-Gondwanan margin (Fig. 4) covering the entire Middle and Late Ordovician. All four species are recovered from different parts of this wide area, to which the localities in Iran also belong.

*Orthosphaeridium bispinosum* has been recorded from the following localities: Caradoc, England (Turner, 1984); Caradoc–early Ashgill, Jordan (Keegan et al., 1990); late Caradoc, Saudi Arabia (Jachowicz, 1995); early Caradoc–Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); early Katian, southeastern Turkey (Paris et al., 2007); Caradoc–Ashgill, western Iraq (Al-Ameri, 2010); early–late Katian, southwestern Libya (Abuhamida, 2013).

*Orthosphaeridium ternatum* has been recorded as follows: late Llanvirn, Germany (Burmman, 1970, 1973); Arenig–Llanvirn, France (Martin, 1973); Llanvirn, France (Rauscher, 1974); Caradoc–Ashgill?, Algerian Sahara (Jardiné et al., 1974); early Llanvirn, Czech Republic (Vavrdová, 1976, 1977); early Llanvirn, Shropshire, England (Booth, 1979); late Llanvirn, Lake District, northwestern England (Booth, 1979); Caradoc, England (Turner, 1984); early Llanvirn–early Ashgill, England (Downie, 1984); Arenig–Llanvirn, Morocco (Elaouad-Debbaj, 1988); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Oretanian–Dobrotivian (Llanvirn–early Caradoc), northern Spain (Gutiérrez-Marco et al., 1996); Llanvirn, Algeria (Vecoli, 1999); Early? Ordovician, southeastern Turkey, (Erkmen, 1979); Darriwilian (4a–4b), southern and southeastern Turkey (Paris et al., 2007); Llanvirn–Llandeilo, western Iraq (Al-Ameri, 2010); early–late Katian, southwestern Libya (Abuhamida, 2013).

*Orthosphaeridium rectangulare* has been retrieved from: Caradoc–Ashgill, Portugal (Elaouad-Debbaj, 1978); late Ashgill, Morocco (Elaouad-Debbaj, 1988); Ashgill, Jordan (Keegan et al., 1990); middle–late Ashgill, southeastern Turkey (Steevens et al., 1996); Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Hirnantian, southern Tunisia (Vecoli et al., 2009); Llandeilo–Caradoc, western Iraq (Al-Ameri, 2010). Records as *Orthosphaeridium inflatum* have been reported from the Ashgill of Jordan (Keegan et al., 1990), whereas taxa corresponding to *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. have been mentioned from the following localities: late Llanvirn, Germany (Burmman, 1970, 1976); Caradoc, England (Turner, 1984); Caradoc, Czech Republic (Vavrdová, 1974); Late Ordovician, southeastern Turkey (Erkmen, 1979); Caradoc, Britain (Downie, 1984); Caradoc, England (Turner, 1984); Ashgill, northeastern Libya (Hill and Molyneux, 1988); Ashgill, Morocco (Elaouad-Debbaj, 1988); Ashgill, Jordan (Keegan et al., 1990); late Arenig, Germany (Heuse et al., 1994); late Caradoc, Saudi Arabia (Jachowicz, 1995); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, China (Yin, 1995); middle–late Ashgill, southeastern Turkey (Steevens et al., 1996); Caradoc, England (Molyneux et al., 1996); early Caradoc, Argentina (Ottone et al., 1999); Ashgill–early Llandovery, northern India (Prasad and Asher, 2001); early Caradoc–late Ashgill, “northern” Gondwana (Vecoli and Le Hérisse, 2004); Katian, southeastern Turkey (Paris et al., 2007); Caradoc, western Iraq (Al-Ameri, 2010); Katian–Hirnantian, Saudi Arabia (Le Hérisse et al., 2015).

Finally, smooth specimens that are herein attributed to *Orthosphaeridium octospinosum* var. *octospinosum* have been found from the following localities: Ashgill, Morocco (Elaouad-Debbaj,



1988); Ashgill, Portugal (Elaouad-Debbaj, 1978); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Ashgill, Turkey (Dean and Martin, 1992); Hirnantian, Saudi Arabia (Miller and Al-Ruwaili, 2007); early-late Katian, southwestern Libya (Abuhamida, 2013). The ornamented specimens attributable to *Orthosphaeridium octospinosum* var. *insculptum* have been reported from the following locations: Caradoc, Libya (Deunff and Massa, 1975); Ashgill, Portugal (Elaouad-Debbaj, 1978); Late Ordovician, southeastern Turkey (Erkmen, 1979); Ashgill, Morocco (Elaouad-Debbaj, 1988); Ashgill, northeastern Libya (Hill and Molyneux, 1988); latest Ordovician, Czech Republic (Vavrdová, 1988); middle-late Ashgill, southeastern Turkey (Steenmans et al., 1996); early Caradoc-late Ashgill, “northern” Gondwana (Vecoli and Le Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian-Hirnantian, southwestern Libya (Abuhamida, 2013).

Although the biostratigraphical control of many of these localities is not always precise, it clearly appears that some of the oldest occurrences are from the margin of the Gondwanan continent, where the genus was present until its last occurrence in the latest Ordovician.

#### 4.5. The stratigraphical distribution in China

Although the Yangtze Platform (South China) is considered in most paleogeographic reconstructions as being part of the Gondwanan margin, it is treated here separately, because some authors placed this area in the northern hemisphere, and the Chinese acritarch assemblages are usually considered as mixed, with peri-Gondwanan taxa, but also other elements (Li and Servais, 2002; Molyneux et al., 2013). Most Chinese data are from the Early-Middle Ordovician, with few studies in the Late Ordovician (Li et al., 2007; Yan et al., 2011). There are very few reports of *Orthosphaeridium* from China, but they are particularly important, because the oldest *Orthosphaeridium* specimens so far recorded are from the early Dapingian, stage slice Dp1 and time slice 3a (Yan et al., 2011), i.e., from the earliest part of the Middle Ordovician. Two species are present in China (*O. ternatum* and *O. octospinosum*), but recordings remain sparse to date.

#### 4.6. The stratigraphical distribution in Avalonia

During the Middle and Late Ordovician, Avalonia was an isolated microcontinent, first in the periphery of Gondwana, but docking with Baltica during the latest Ordovician. Therefore this microcontinent is here treated separately. Some of the oldest occurrences of *Orthosphaeridium* are from Avalonia, with occurrences in the stage slice Dp2: *Orthosphaeridium bispinosum* has been recorded from the late Arenig of northwestern England (Cooper et al., 1995; Molyneux, 1999), but also from the late Dapingian-early Darriwilian of northwestern England (Molyneux, 2009), whereas *Orthosphaeridium ternatum* has been recorded from the late Arenig of Wales (Molyneux, 1987, 1990) and the early Llanvirn of Belgium (Servais and Maletz, 1992).

#### 4.7. FAD of *Orthosphaeridium*

Many acritarch occurrences are not accurately dated. This is partly due to the fact that acritarchs are often the only fossil group present in poorly preserved sedimentary successions and that they are used themselves to provide first biostratigraphical data. This is, for example, the case in the British Isles, where acritarchs were used to date the rocks when graptolites (or other fossils) were absent (e.g., Molyneux, 1990, 1999). Many occurrences in Fig. 4 are therefore to be considered with some care. Very often, the age provided by the authors is also no longer valid. For example, the “Middle Ordovician” in Loeblich and Tappan (1971) appears to be actually early Late Ordovician in age. Nevertheless, the stratigraphical overview (Fig. 4) indicates that all four major

morphotypes have similar distributions, spanning the Middle and Late Ordovician.

Of particular interest are the first appearances. These have been analyzed herein with care, in particular by searching for independent biostratigraphical control. As a result, it appears that the FAD of *Orthosphaeridium* is located in the early Dapingian of South China, i.e., at the base of the Middle Ordovician. Yan et al. (2011) reported this first occurrence of *Orthosphaeridium ternatum* (*Orthosphaeridium* sp. 1 in Yan et al., 2011) in the *Expansograptus hirundo* graptolite biozone, that can be correlated with the lower part of Dapingian stage slice Dp1, and with the upper part of timeslice 3a. From Avalonia, the first occurrence of *Orthosphaeridium bispinosum* has been reported by Molyneux (2009) from the Skiddaw Group of the English Lake District in northern England, from the *giberulus-cucullus* graptolite biozone that corresponds to the later part of the Dapingian and the early part of the Darriwilian (timeslices 3b–4a). Cooper et al. (1995) recorded *Orthosphaeridium bispinosum* in the upper part of the *Frankea hamata*-*Striatotheca rarirrugulata* acritarch assemblage in northwestern England that corresponds to the late Arenig in terms of British regional stratigraphy, or the late Dapingian-early Darriwilian stages (stage slices Dp2–Dw1).

Although the precise location and origin of Burmann's (1970) samples in eastern Germany is not known and attributed to the Llanvirn, Heuse et al. (1994) recorded *Baltisphaera quadrinata* (now *Orthosphaeridium rectangulare* var. *quadricornis*) from the Griffelschiefer in the Schwarzbürg Anticline, Germany, which they correlated with the late Arenig *D. hirundo* graptolite Biozone (*A. cucullus* biozone). This graptolite biozone can be correlated with the lower Darriwilian stage slice Dw1, and therefore the FAD on the peri-Gondwanan margin neighboring Avalonia can be placed at the base of Dw1, which represents so far also the oldest occurrence of the *Orthosphaeridium rectangulare* morphotype.

The oldest occurrence of the *Orthosphaeridium octospinosum* morphotype is also reported from South China by Yan et al. (2011) who stated that the FAD of *Orthosphaeridium* sp. 2 (now *O. octospinosum* var. *insculptum*) is located in the *clavus-austrodentatus* graptolite biozone which correlates with the base of stage slice Dp3 to Dw1 (late Dapingian-early Darriwilian).

In conclusion, *Orthosphaeridium* clearly appears in the early part of the Middle Ordovician, with the currently oldest occurrence being recorded from South China (early Dapingian, time slice 3a). All other morphotypes are present in the Middle Ordovician and none of them appeared for the first time after the late Dapingian.

#### 4.8. LAD of *Orthosphaeridium*

*Orthosphaeridium* specimens have never passed the Ordovician-Silurian boundary and it seems that they disappeared at the end of the Ordovician. *Orthosphaeridium ternatum* has not been recorded in the latest parts of the Ordovician, but it is too early to assume that it disappeared earlier than other morphotypes. *Orthosphaeridium bispinosum*, *O. rectangulare* and *O. octospinosum* all extended to the end of the Ordovician. Delabroye et al. (2011a) investigated acritarchs from the Ordovician-Silurian boundary in southern Estonia and compared their assemblages with carbon isotope data. They indicated that some of the *Orthosphaeridium* specimens, recorded as *O. insculptum* and *O. rectangulare*, disappeared just before the Ordovician-Silurian boundary (stage slice Hi2 and time slice 6c).

### 5. Paleocology and paleogeography

#### 5.1. Paleocology

While during many years acritarch research was mostly focused on biostratigraphy, investigations on paleoecological aspects became more important recently. It is now well established that acritarch assemblages change according to inshore-offshore conditions (e.g., Li

et al., 2004; Lei et al., 2012). In addition, individual taxa also display morphological changes, in particular regarding process length, that seem to follow inshore–offshore trends, with morphotypes bearing shorter processes being more abundant in nearshore environments (e.g., Stricanne et al., 2004), although this observation can surely not be generalized. These distribution patterns are possibly related to paleosalinity and paleotemperature (e.g., Servais et al., 2004; Van Soelen and Kürschner, 2018). Several authors noted that acritarchs with large processes are typical of open marine environments. There have been no studies integrating *Orthosphaeridium* so far. The genus is absent in the sections investigated by Li et al. (2004). Jacobson (1979) recognized three classes of acritarchs on the basis of morphologic similarity corresponding to three marine paleoenvironments in the Middle and Late Ordovician from the United States. The three classes were defined as the leiosphaerid class, the peteinospaerid–*Dicommopalla* class and the baltisphaerid–veryhachid–*Polygonium* class, corresponding to a near-shore shallow-water environment, a shoal environment, and an open-sea environment, respectively. Although Jacobson (1979) did not include *Orthosphaeridium* in his assemblages, the presence of “baltisphaerid” acritarchs indicate an open-sea environment for this genus. The taxa of this acritarch class, including *Baltisphaeridium*, *Multiplicisphaeridium* and *Ordoviciidium*, are usually found with *Orthosphaeridium*, which suggests that the genus *Orthosphaeridium* is probably characteristic of open marine environments.

*Orthosphaeridium* is an acritarch genus with prominent processes, that appear to have been hollow, and the basic plug was possibly important for gas exchange between the central vesicle and the process chambers, that possibly were used as floating devices. These assumptions remain speculative, as would be the interpretation of a changing ornamentation by granules or tubercles of the wall surface of *Orthosphaeridium*. There are so far no studies about the number of processes in acritarch taxa related to paleoecological parameters. Nevertheless, the process length and the ornamentation of the vesicle and process walls were most probably related to paleoenvironmental conditions. Possibly the changing morphologies were an ecophenotypic response to changing paleoenvironments, although it is difficult, if not impossible to control this on the fossil material.

Loeblich and Tappan (1971) presented a different interpretation for the morphological trends of the genus *Orthosphaeridium*. These authors

brought together their observations from the Late Ordovician of the United States (Bromide Formation, Eden Shale Formation, Sylvain Shale Formation) in relation to the morphologies published by Eisenack (1968) from the Baltic Ordovician (“Borkholmer Stufe,” “Lyckholmer Stufe”). Loeblich and Tappan (1971) mentioned “evolutionary trends” in the Ordovician with specimens of *Orthosphaeridium* having “decreased vesicle ornamentation, increased number of major processes, and decrease in vesicle inflation.” Unfortunately, it is not possible to understand on how many samples these observations and interpretations were based. Loeblich and Tappan (1971, fig. 1) consider that these morphological changes show “apparent phylogenetic trends.” However, it seems that such changes could very well be ecophenotypic rather than genotypic. The analyses of all data at a global level (Fig. 4) does not confirm an increased number of processes over time. All four species of *Orthosphaeridium* with two, three, four or more processes appear to be simultaneously present over the entire Middle and Late Ordovician. Similarly, a global trend is not evident regarding an increase or decrease of vesicle ornamentation over time. These morphological characteristics are possibly related to local paleoenvironmental changes rather than to a phylogenetic trend that would be visible in successive time intervals. Future detailed studies on perfectly well preserved, larger assemblages could clarify these questions.

According to the paleogeographic distribution of *Orthosphaeridium* (see below), the genus occurs widely in marine environments and is present in almost all climatic zones (divided by Boucot et al., 2009) during the Middle and Late Ordovician. This distribution pattern implies that *Orthosphaeridium* would derive from an eurythermic marine organism.

## 5.2. Paleogeography

Fig. 5 shows the paleogeographic distribution of *Orthosphaeridium* on a global reconstruction. The genus and the four species show no preferential distribution pattern. The paleobiogeography of Paleozoic acritarchs has been reviewed in several papers. Li and Servais (2002) listed a selection of Ordovician acritarch taxa that display different latitudinal distribution patterns that might be related to temperature. The genus *Orthosphaeridium* was not included in the study of Li and Servais (2002), but the genus would show the same distribution pattern as *Micrhystridium*, *Baltisphaeridium*, *Peteinosphaeridium* or *Polygonium*,

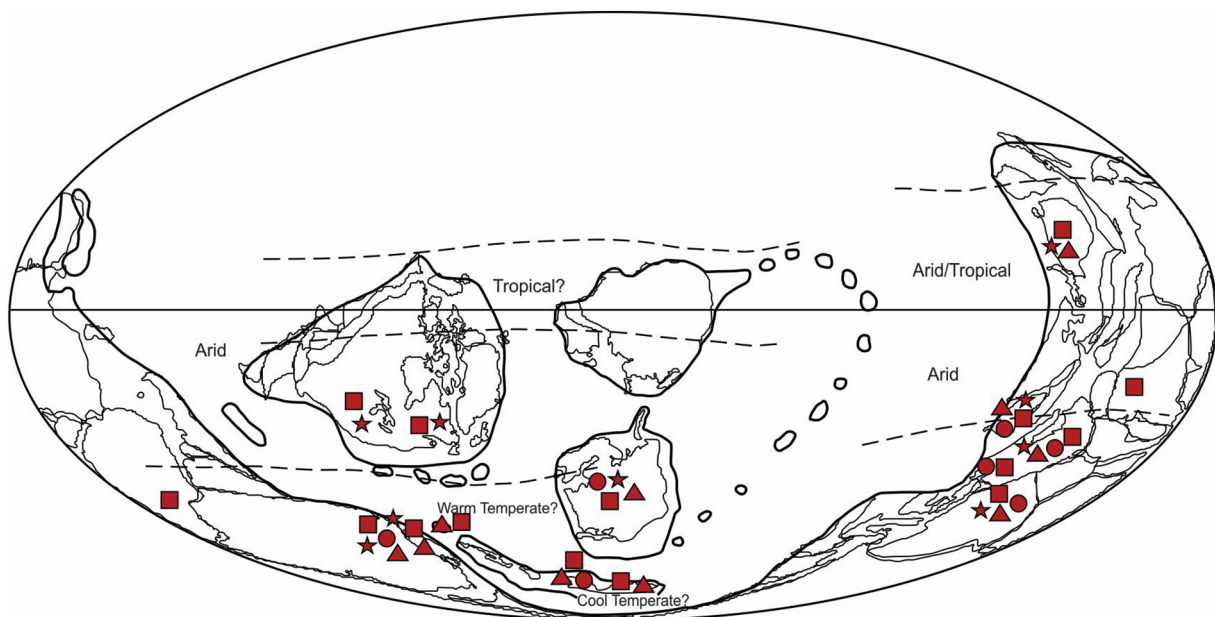


Fig. 5. Paleogeographic distribution of *Orthosphaeridium* in the Middle–Late Ordovician. Paleogeographic reconstruction modified from Boucot et al. (2009). *Orthosphaeridium bispinosum* ●; *Orthosphaeridium ternatum* ▲; *Orthosphaeridium rectangulare* ■; *Orthosphaeridium octospinosum* ★.

that are all present at all paleolatitudes (Li and Servais, 2002, fig. 2). Molyneux et al. (2013) discussed the distribution of Middle Ordovician acritarchs and mapped the “peri-Gondwana,” “Baltica” and mixed provinces on a paleogeographic reconstruction. *Orthosphaeridium* is clearly present in all these provinces, with no preferential distribution. During the Late Ordovician, *Orthosphaeridium rectangulare* was considered to be a cosmopolitan species by Molyneux et al. (2013).

The present review confirms this interpretation. *Orthosphaeridium* possibly has the highest diversity in peri-Gondwana and Baltica, with all of the species and varieties being described from these paleocontinents. *Orthosphaeridium bispinosum* and *Orthosphaeridium ternatum* have not yet been reported from Laurentia and *Orthosphaeridium octospinosum* is not yet recorded from Avalonia. In South China, *Orthosphaeridium bispinosum* still needs to be discovered. The apparent absence of one species from a specific paleocontinent does not seem to be a real evidence of the absence rather than a lack of investigations. Apparently, all taxa are cosmopolitan during the entire period of the Middle and Late Ordovician.

## 6. Conclusions

*Orthosphaeridium* is one of the most frequently recorded acritarch genera in the Middle and Late Ordovician with significance for biostratigraphy and paleobiogeography.

The taxonomic revision based on a detailed literature review and on large assemblages from new material investigated from northeastern Iran and South China, revealed that most of the previously described species are based on limited numbers of specimens, and that many of them are synonyms. Four species belong to the genus: *Orthosphaeridium bispinosum*, *O. ternatum*, *O. rectangulare* (type species), and *O. octospinosum*. Two new subspecific taxa are erected at the *varietas* level. These are based on two previously described species of which the status has been modified: *Orthosphaeridium rectangulare* var. *quadricornis* and *O. octospinosum* var. *insculptum*.

The FAD of *Orthosphaeridium* is in the early Dapingian (stage slice Dp1 and time slice 3a), whereas the LAD of the genus is in the latest Ordovician (stage slice Hi2 and time slice 6c), as *Orthosphaeridium* has never been recorded beyond the Ordovician–Silurian boundary.

*Orthosphaeridium* has been described from many localities of the Gondwanan margin, Baltica, Laurentia and Avalonia. The genus and all species appear to be cosmopolitan with a global distribution. The easily recognizable genus is therefore a good palynological index fossil for the Middle and Late Ordovician at the global scale.

*Orthosphaeridium* seems to be derived from an eurythermic organism, because it has been found in several different climatic zones and paleoenvironments.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2019.104127>.

## Acknowledgments

Navid Navidi-Izad acknowledges the paleontological team of the Evo-Eco-Paleo unit (Lille University – CNRS) for making his research stay possible. The first author also appreciates financial support received from the Iranian Ministry of Science, Research, and Technology (MSRT). The help of two anonymous referees is acknowledged. Stephen Stukins, Natural History Museum, London, UK is acknowledged for his help with the John Williams Card Index, allowing us to complete the literature review. The first author thanks Hamed Bouzari Nezhad for assistance during field work in Iran. This is a contribution to IGCP no 653 “The onset of the Great Ordovician Biodiversification Event.”

## References

Abuhamida, F., 2013. Palynological analysis of the Ordovician to Lower Silurian sediments from the Murzuq Basin, southwest Libya. Ph.D. Thesis. University of Sheffield, United Kingdom.

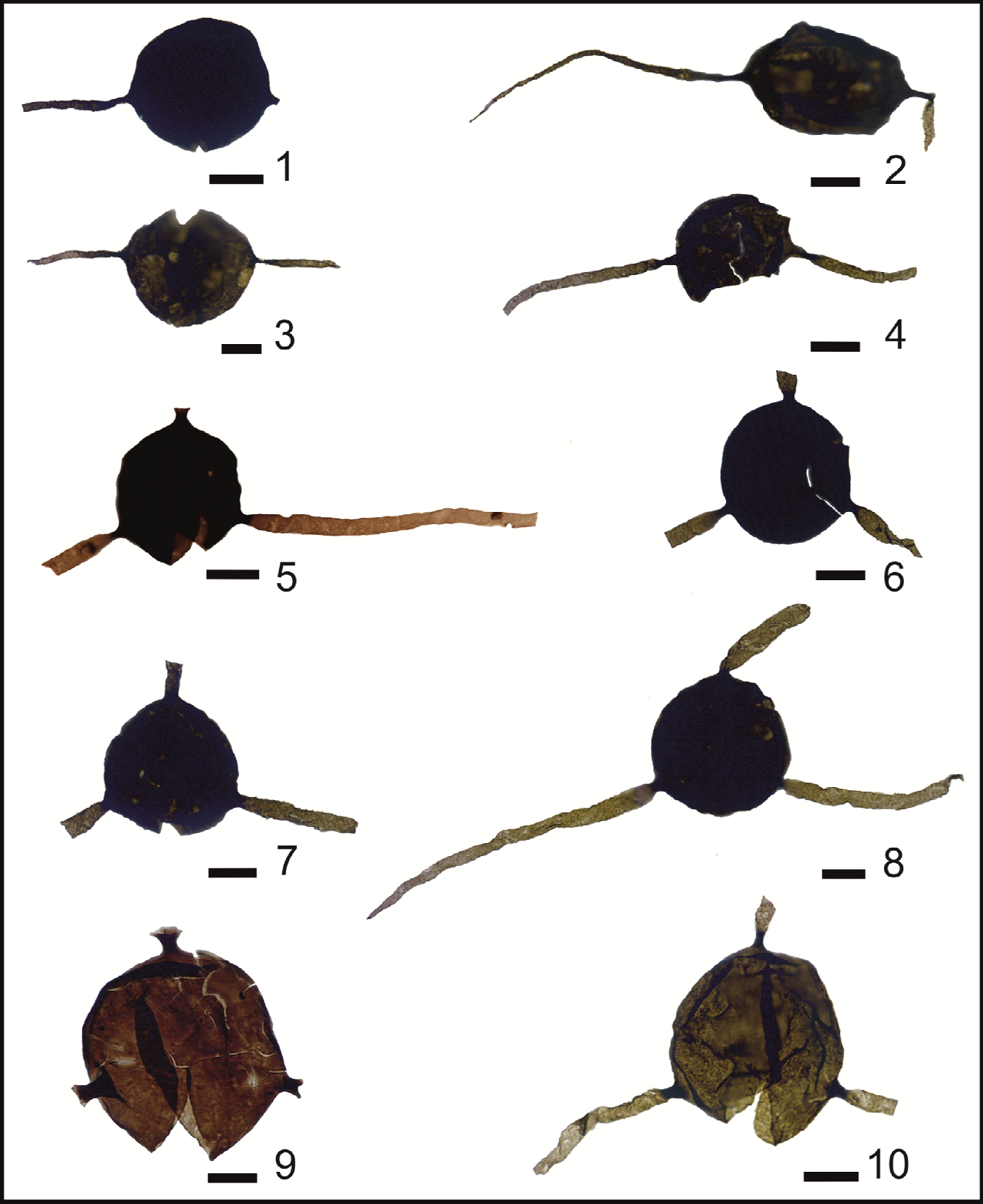
- Al-Ameri, T.K., 2010. Palynostratigraphy and the assessment of gas and oil generation and accumulations in the Lower Paleozoic, Western Iraq. Arab. J. Geosci. 3, 155–179.
- Albani, R., Bagnoli, G., Bernárdez, E., Gutiérrez-Marco, J.C., Ribecai, C., 2006. Late Cambrian acritarchs from the “Tunel Ordovícico del Fabar”, Cantabrian Zone, N Spain. Rev. Paleobot. Palynol. 139, 41–52.
- Albani, R., Bagnoli, G., Ribecai, C., Raevskaya, E., 2007. Late Cambrian acritarch *Lusatia*: Taxonomy, palaeogeography, and biostratigraphic implications. Acta Paleontol. Polon. 52, 809–818.
- Badawy, A.S., 2012. Sequence stratigraphy, palynology and biostratigraphy across the Ordovician–Silurian boundary in the Röstänga–1 core, southern Sweden. MSc Thesis. Lund University, Sweden.
- Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2009. The new chronostratigraphical classification of the Ordovician System and its relations to major series and stages and to  $\delta^{13}\text{C}$  chemostratigraphy. Lethaia 42, 97–107.
- Booth, G.A., 1979. Lower Ordovician acritarchs from successions in England and North Wales. Ph.D. Thesis. University of Sheffield, United Kingdom.
- Boucot, A.J., Chen, W., Scotese, C.R., Fan, J., 2009. A Reconstruction of Palaeozoic Global Palaeoclimate. Science Press, Beijing (in Chinese).
- Brocke, R., Fatka, O., Servais, T., 1997. A review of the Ordovician acritarchs *Aureotesta* and *Marrocanium*. Ann. Soc. Geol. Belg. 120, 1–22.
- Burmam, G., 1970. Weitere organische Mikrofossilien aus dem unteren Ordovizium. Paläontol. Abhandlungen, Abteilung B 3, 289–332.
- Burmam, G., 1973. Das Ordovizium der nördlichen Phyllitzone: Teil II: Wippraer Zone. Zeitschrift für geologische Wissenschaften, Themenhefte 1, 9–43.
- Burmam, G., 1976. Übersicht über das ordovizische Mikroplankton im Südteil der DDR (Vogtland, Wildenfesler Zwischengebirge). Geol. Jahrb. 7 (8), 47–62.
- Colbath, G.K., 1979. Organic-walled microphytoplankton from the Eden Shale (Upper Ordovician), Indiana, U.S.A. Palaeontogr. Abteilungs B 171, 1–38.
- Cooper, A.H., Rushton, A.W.A., Molyneux, S.G., Hughes, R.A., Moore, R.M., Webb, B.C., 1995. The stratigraphy, correlation, provenance and palaeogeography of the Skiddaw Group (Ordovician) in the English Lake District. Geol. Mag. 132, 185–211.
- Dean, W.T., Martin, F., 1992. Ordovician biostratigraphic correlation in southern Turkey. In: Webby, B.D., Laurie, J.R. (Eds.), Global Perspectives on Ordovician Geology. Balkema, Rotterdam, pp. 195–203.
- Delabroye, A., Vecoli, M., Hints, O., Servais, T., 2011a. Acritarchs from the Ordovician–Silurian boundary beds of the Valga–10 drill core, southern Estonia (Baltica) and their stratigraphical and palaeobiogeographical implications. Palynology 35, 4–45.
- Delabroye, A., Munnecke, A., Vecoli, M., Copper, P., Tribouillard, N., Joachimski, M.M., Desrochers, A., Servais, T., 2011b. Phytoplankton dynamics across the Ordovician/Silurian boundary at low palaeolatitudes: Correlations with carbon isotopic and glacial events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 312, 79–97.
- Deunff, J., Massa, D., 1975. Palynologie et stratigraphie du Cambro–Ordovicien (Libye nord–occidentale). Comp. Rend. l’Acad. Séances de Paris (D) 281, 21–24.
- Diez, M., Cramer, F.H., 1974. Range chart of selected Lower Paleozoic Acritarch taxa. Rev. Paleobot. Palynol. 18, 155–170.
- Diez, M., Cramer, F.H., 1977. Range chart of selected Lower Paleozoic Acritarch taxa. II. Index to parts I and II. Rev. Paleobot. Palynol. 24, 1–48.
- Downie, C., 1984. Acritarchs in British stratigraphy. Geol. Soc. Lond. Spec. Rep. 17, 1–26.
- Eisenack, A., 1958. Mikroplankton aus dem nordeutschen Apt nebst einigen Bemerkungen über fossile Dinoflagellaten. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 106, 383–422.
- Eisenack, A., 1963. Mitteilungen zur Biologie der Hystrichosphären und neue Arten. Palaeontogr. Abhandlungen 118, 207–216.
- Eisenack, A., 1968. Mikrofossilien eines Geschiebes der Borkholmer Stufe, baltisches Ordovizium, F2. Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg 37, 81–94.
- Eisenack, A., Cramer, F.H., Diez, C., 1976. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band IV, Acritarcha 2. Teil. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart, p. 863.
- Eiserhardt, K.H., 1989. Baltisphären aus Gotländer Öjlemyrflint (Acritarcha, Oberordoviz Geschiebe, Schweden). Mitteilungen des Geologisch–Paläontologischen Instituts der Universität Hamburg 68, 79–129.
- Elaouad-Debbaj, Z., 1978. Acritarches de l’Ordovicien Supérieur du Synclinal de Buçaco (Portugal). Bull. Soc. Géol. Minér. Bretagne 10, 1–101.
- Elaouad-Debbaj, Z., 1984. Acritarches et chitinozoaires de l’Arénig–Lanvirn de l’Anti-Atlas (Maroc). Rev. Paleobot. Palynol. 43, 67–88.
- Elaouad-Debbaj, Z., 1988. Acritarches de l’Ordovicien supérieur (Caradocian–Ashgillien) de l’Anti-Atlas, Maroc. Rev. Micropaleontol. 30, 232–248.
- Erkmen, U., 1979. Stratigraphical distribution of the Lower Paleozoic acritarchs from southeast Turkey: comparison with other Mediterranean countries. GEOCOME I, First Geological Congress of the Middle East, September 4–7, 1979, Ankara, pp. 472–495.
- Evitt, W.R., 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs. I. Proc. Natl. Acad. Sci. 49, 158–164.
- Fatka, O., Brocke, R., 1999. Morphologic variability in two populations of *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972. Palynology 23, 153–180.
- Fatka, O., Molyneux, S.G., Servais, T., 1997. The Ordovician acritarch *Frankea*: some critical remarks. Geobios 30, 321–326.
- Ghavidel-Syooki, M., 1997. Acritarch biostratigraphy of the palaeozoic rock units in the Zagros Basin, Southern Iran. In: Fatka, O., Servais, T. (Eds.), Acritarcha in Praha (1996) Proceedings of International Meeting and Workshop. Acta Universitatis Carolinae, Geologica. 40, pp. 385–411.
- Ghavidel-Syooki, M., 2000a. Palynostratigraphy and palaeobiogeography of Lower Paleozoic strata in the Ghelli area, northeastern Alborz Range of Iran (Kopet–Dagh Region). J. Sci. Islam. Repub. Iran 4, 32–46.
- Ghavidel-Syooki, M., 2000b. Biostratigraphy and palaeogeography of Late Ordovician and Early Silurian Chitinozoans from the Zagros basin, southern Iran. Hist. Biol. 15, 29–39.

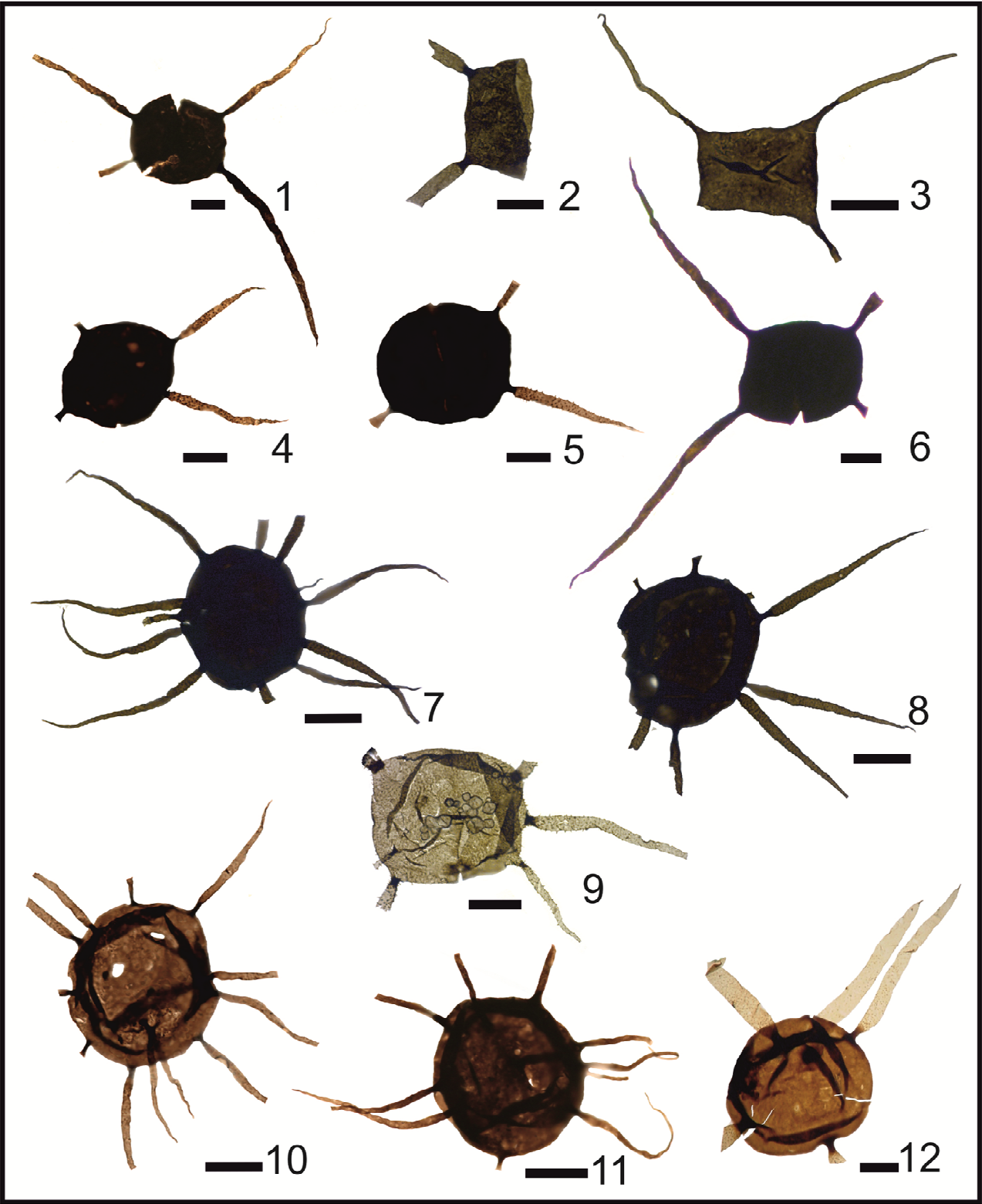


- Ghavidel-Syooki, M., 2001. Palynostratigraphy and paleobiogeography of the Lower Paleozoic sequence in the northern Alborz Range (Kopet–Dagh Region) of Iran. In: Goodman, D.K., Clarke, R.T. (Eds.), Proceedings of the IX International Palynological Congress Houston, Texas, U.S.A., 1996. American Association of Stratigraphic Palynologists Foundation, pp. 17–35.
- Ghavidel-Syooki, M., 2003. Palynostratigraphy and paleogeography of Lower Paleozoic Strata at Kuh–e–Boghrou, Southwest of Kashmar City, at Eastern Central Iran. Iran. Int. J. Sci. 4, 181–207.
- Ghavidel-Syooki, M., 2006. Palynostratigraphy and palaeogeography of the Cambro–Ordovician strata in southwest of Shahrud City (Kuh–e–Kharbush near Deh–Molla), Central Alborz Range, northern Iran. Rev. Palaeobot. Palynol. 139, 81–95.
- Ghavidel-Syooki, M., 2008. Palynostratigraphy and palaeogeography of the Upper Ordovician Gorgan Schists (Southeastern Caspian Sea), Eastern Alborz Mountain Ranges, Northern Iran. Comun. Geol. 95, 123–155.
- Ghavidel-Syooki, M., 2016. Miospore assemblages from Late Ordovician (Katian–Hirnantian), Ghelli Formation, Alborz Mountain Range North–eastern Iran: Palaeophytogeographic and palaeoclimatic implications. J. Sci. Islam. Repub. Iran 27, 135–159.
- Ghavidel-Syooki, M., 2017a. Cryptospore and trilete spore assemblages from the Late Ordovician (Katian–Hirnantian) Ghelli Formation, Alborz Mountain Range, Northeastern Iran: Palaeophytogeographic and palaeoclimatic implications. Rev. Palaeobot. Palynol. 244, 217–240.
- Ghavidel-Syooki, M., 2017b. Biostratigraphy of acritarchs and chitinozoans in Ordovician Strata from the Fazel Abad Area, Southeastern Caspian Sea, Alborz Mountains, Northern Iran: Stratigraphic implications. J. Sci. Islam. Repub. Iran 28, 37–57.
- Ghavidel-Syooki, M., 2017c. Stratigraphic evidence for Hirnantian glaciation in the Alborz Mountain Ranges, northeastern Iran. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 879–898.
- Ghavidel-Syooki, M., Borji, S., 2018. Chronostratigraphy of acritarchs and chitinozoans from upper Ordovician Strata from the Robat–e–Gharabil Area, NE Alborz Mountains, Northern Khorassan Province: Stratigraphic and paleogeographic implications. J. Sci. Islam. Repub. Iran 29, 35–51.
- Ghavidel-Syooki, M., Hosseinzadeh Moghadam, M., 2010. Palynostratigraphy of early Paleozoic sediments in south of Fazel Abad area, Kholin Darreh (South east of Gorgan). Stratigr. Sedimentol. Res. 38, 1–24 (in Persian).
- Ghavidel-Syooki, M., Khosravi, M.E., 1995. Investigation of Lower Paleozoic Sediments at the Tang–e–Zakeen of Kuh–e–Faraghan and Introduction of Seyahou and Sarchahan Formations in the Zagros basin. Geosciences 4, 2–21 (in Persian).
- Ghavidel-Syooki, M., Álvaro, J.J., Popov, L., Ghobadi Pour, M., Ehsani, M.H., Suyarkova, A., 2011a. Stratigraphic evidence for the Hirnantian (latest Ordovician) glaciation in the Zagros Mountains, Iran. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307, 1–16.
- Ghavidel-Syooki, M., Hassanzadeh, J., Vecoli, M., 2011b. Palynology and isotope geochronology of the Upper Ordovician–Silurian successions (Ghelli and Soltan Maidan Formations) in the Khoshyeilagh area, eastern Alborz Range, northern Iran: stratigraphic and palaeogeographic implications. Rev. Palaeobot. Palynol. 164, 251–271.
- Ghavidel-Syooki, M., Popov, L.E., Álvaro, J.J., Ghobadi Pour, M., Tolmacheva, T.Y., Ehsani, M.H., 2014. Dapingian–lower Darriwilian (Ordovician) stratigraphic gap in the Faraghan Mountains, Zagros Range, south–eastern Iran. Bull. Geosci. 89, 679–706.
- Górka, H., 1979. Les acritarches de l'Ordovicien Moyen d'Olsztyn IG 2 (Pologne). Acta Palaeontol. Pol. 24, 351–382.
- Górka, H., 1980. Le microplancton de l'Ordovicien Moyen de Suabla (Pologne). Acta Palaeontol. Pol. 25, 261–277.
- Górka, H., 1987. Acritarches et Prasinophyceae de l'Ordovicien Moyen (Viruén) du sondage de Smedsby Gard no. 1 (Gotland, Suède). Rev. Palaeobot. Palynol. 52, 257–297.
- Gutiérrez-Marco, J.C., Albani, R., Aramburu, C., Arbizu, M., Babin, C., García-Ramos, J.C., Méndez-Bedia, I., Rábano, I., Truyols, J., Vannier, J., Villas, E., 1996. Biostratigrafía de la Formación Pizarras del Sueve (Ordovícico Medio) en el sector septentrional de la escama de Laviana–Sueve (Zona Cantábrica, Norte de España). Rev. Esp. Paleontol. 11, 48–74 (in Spanish with English summary).
- Heuse, T., Erdtmann, B.–D., Kraft, P., 1994. Early Ordovician microfossils (acritarchs, chitinozoans) and graptolites from the Schwarzburg Anticline, Thuringia (Germany). Veröffentlichungen Naturhistorisches Museum Schleusingen 9, 41–68.
- Hill, P.J., Molyneux, S.G., El-Arnauti, A., 1988. Biostratigraphy, palynofacies and provincialism of Late Ordovician–Early Silurian acritarchs from Northeast Libya. In: Owens, B., Thusu, B. (Eds.), Subsurface Palynostratigraphy of northeast Libya. Garyounis University, Benghazi, Libya, pp. 27–43.
- Jachowicz, M., 1995. Ordovician acritarch assemblages from central and northwestern Saudi Arabia. Rev. Palaeobot. Palynol. 89, 19–25.
- Jachowicz, M., 2005. Ordovician acritarchs from the Upper Silesian Block. Przegląd Geol. 53, 756–762 (in Polish with English summary).
- Jacobson, S.R., 1979. Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio and New York. J. Paleontol. 53, 1197–1212.
- Jacobson, S.R., Achab, A., 1985. Acritarch biostratigraphy of the *Dicellograptus complanatus* graptolite zone from the Vaureal Formation (Ashgillian), Anticosti Island, Québec, Canada. Palynology 9, 165–198.
- Jardiné, S., Combaz, A., Magloire, L., Peniguel, G., Vachey, G., 1974. Distribution stratigraphique des acritarches dans le Paléozoïque du Sahara Algérien. Rev. Palaeobot. Palynol. 18, 99–129.
- Keegan, J.B., Rasul, S.M., Shaheen, Y., 1990. Palynostratigraphy of the Lower Paleozoic, Cambrian to Silurian, sediments of the Hashemite Kingdom of Jordan. Rev. Palaeobot. Palynol. 66, 167–180.
- Kjellström, G., 1971a. Ordovician microplankton (baltisphaerids) from the Grötlingbo Borehole NO. 1 in Gotland, Sweden. Sveriges Geologiska Undersökning, Ser. C 65 (665), 1–75.
- Kjellström, G., 1971b. Middle Ordovician microplankton from the Grötlingbo Borehole No. 1 in Gotland, Sweden. Sveriges Geologiska Undersökning, Avhandlingar och Uppsatser Ser. C 65 (669), 1–35.
- Kroeck, D.M., Pardo-Trujillo, A., Plata, A., Romero, M., Servais, T., 2019. Peri-Gondwanan acritarchs from the Ordovician of the Orientales Basin (Colombia, NW South America). Palynology. <https://doi.org/10.1080/01916122.2019.1624279>.
- Le Hérisse, A., Al-Ruwaili, M., Miller, M., Vecoli, M., 2007. Environmental changes reflected by palynomorphs in the early Middle Ordovician Hanadir Member of the Qasim Formation, Saudi Arabia. Rev. Micropaléontol. 50, 3–16.
- Le Hérisse, A., Molyneux, S.G., Miller, M.A., 2015. Late Ordovician to early Silurian acritarchs from the Qusaiba-1 shallow core hole, central Saudi Arabia. Rev. Palaeobot. Palynol. 212, 22–59.
- Lei, Y., Servais, T., Feng, Q., He, W., 2012. The spatial (nearshore–offshore) distribution of latest Permian phytoplankton from the Yangtze Block, South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 363–364, 151–162.
- Li, J., Servais, T., 2002. Ordovician acritarchs in China and their utility for global palaeobiogeography. Bull. Soc. Géol. France 173, 399–406.
- Li, J., Brocke, R., Servais, T., 2002. The acritarchs of the South Chinese *Azygograptus suecicus* graptolite biozone and their bearing on the definition of the Lower/Middle Ordovician boundary. C.R. Palevol 1, 75–81.
- Li, J., Servais, T., Yan, K., Zhu, H., 2004. A nearshore–offshore trend in the acritarch distribution of the Early–Middle Ordovician in the Yangtze platform, South China. Rev. Palaeobot. Palynol. 130, 141–161.
- Li, J., Servais, T., Yan, K., Su, W., 2007. Microphytoplankton diversity curves of the Chinese Ordovician. Bull. Soc. Géol. France 178, 399–409.
- Li, J., Servais, T., Yan, K., 2010. Acritarch biostratigraphy of the Lower–Middle Ordovician boundary: the Global Stratotype Section and Point (GSSP) of Huanghuachang, South China. Newslett. Stratigr. 43, 235–250.
- Li, J., Servais, T., Yan, K., 2014. The Ordovician acritarch genus *Rhopaliophora*: Biostratigraphy, palaeobiogeography and palaeoecology. Rev. Palaeobot. Palynol. 208, 1–24.
- Loeblich, A.R., 1970. Morphology, ultrastructure and distribution of Paleozoic acritarchs. Proceedings of The North American Paleontological Convention 69 (part G), Chicago, pp. 705–788.
- Loeblich, A.R., Tappan, H., 1971. Two new *Orthosphaeridium* (Acritarcha) from the Middle and Upper Ordovician. Trans. Am. Microsc. Soc. 90, 182–188.
- Mahmoudi, M., Sabouri, J., Alimohammadian, H., Majidifard, M.R., 2014. The first report of cryptospore assemblages of Late Ordovician in Iran, Ghelli Formation, eastern Alborz. Geopersia 4, 125–140.
- Martin, F., 1973. Les acritarches de l'Ordovicien inférieur de la Montagne Noire (Hérault, France). Bull. Inst. Roy. Sci. Nat. Belgiq. 48, 1–61.
- Martin, F., 1980. Quelques chitinozoaires et acritarches ordoviciens supérieurs de la Formation de White Head en Gaspésie Québec. Can. J. Earth Sci. 17, 106–119.
- Martin, F., 1983. Chitinozoaires et acritarches ordoviciens de la plate-forme du Saint-Laurent (Québec et sud-est de l'Ontario). Geol. Surv. Can. Bull. 310, 1–59.
- Martin, F., 1988. Late Ordovician and Early Silurian acritarchs. In: Cocks, L.R.M., Rickards, R.B. (Eds.), A global analysis of the Ordovician–Silurian boundary. Bulletin of the British Museum (Natural History), Geology Series 43, London, pp. 299–309.
- Miller, M.A., Al-Ruwaili, M.H., 2007. Preliminary palynological investigation of Saudi Arabian Upper Ordovician glacial sediments. Rev. Micropaléontol. 50, 17–26.
- Molyneux, S.G., 1987. Acritarchs and chitinozoa from the Arenig Series of south-west Wales. Bull. Br. Mus. Nat. Hist. Geol. 41, 309–364.
- Molyneux, S.G., 1990. Advances and problems in Ordovician palynology of England and Wales. J. Geol. Soc. (Lond.) 147, 615–618.
- Molyneux, S.G., 1999. A reassessment of Manx Group acritarchs, Isle of Man. Geol. Soc. Lond. Spec. Publ. 160, 23–32.
- Molyneux, S.G., 2009. Acritarch (marine microphytoplankton) diversity in an Early Ordovician deep–water setting (the Skiddaw Group, northern England): Implications for the relationship between sea–level change and phytoplankton diversity. Palaeogeogr. Palaeoclimatol. Palaeoecol. 275, 59–76.
- Molyneux, S.G., Le Hérisse, A., Wicander, R., 1996. Palaeozoic phytoplankton. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. vol. 2. American Association of Stratigraphic Palynologists Foundation, Salt Lake City, UT, pp. 493–530.
- Molyneux, S.G., Raevskaya, E.G., Servais, T., 2007. The *messauodensis–trifidum* acritarch assemblage and correlation of the base of Ordovician Stage 2 (Floian). Geol. Mag. 144 (1), 143–156.
- Molyneux, S.G., Delabroye, A., Wicander, R., Servais, T., 2013. Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton. In: Harper, D.A.T., Servais, T. (Eds.), Early Palaeozoic Biogeography and Palaeogeography. Memoir 38. Geological Society of London, London, pp. 365–397.
- Ottone, E.G., Albanesi, G.L., Ortega, G., Holfeltz, G.D., 1999. Palynomorphs, conodonts and associated graptolites from the Ordovician Los Azules formation, Central Precordillera, Argentina. Micropaleontology 45, 225–250.
- Paris, F., Le Hérisse, A., Monod, O., Kozlu, H., Ghienne, J.F., Dean, W.T., Vecoli, M., Günay, Y., 2007. Ordovician chitinozoans and acritarchs from southern and southeastern Turkey. Rev. Micropaleontol. 50, 81–107.
- Parsons, M.G., Anderson, M.M., 2000. Acritarch microfloral succession from the Late Cambrian and Ordovician (early Tremadoc) of Random Island, eastern Newfoundland, and its comparison to coeval microfloras, particularly those of the East European Platform. Am. Assoc. Stratigr. Palynol. Contrib. Ser. 38, 1–129.
- Playford, G., Wicander, R., 2006. Organic-walled microphytoplankton of the Sylvan Shale (Richmondian: Upper Ordovician), Arbuckle Mountains, Southern Oklahoma, U.S.A. Oklahoma Geol. Surv. Bull. 148, 1–116.
- Playford, G., Ribecai, C., Tongiorgi, M., 1995. Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cyclospheeridium*: morphology,



- taxonomy, biostratigraphy, and palaeogeographic significance. *Boll. della Soc. Paleontol. Italiana* 34, 3–54.
- Prasad, B., Asher, R., 2001. Acritarch biostratigraphy and lithostratigraphic classification of Proterozoic and Lower Paleozoic sediments (pre-unconformity sequence) of Ganga Basin, India. *Paleontogr. Indica* 5, 151.
- Rauscher, R., 1974. Recherches micropaléontologiques et stratigraphiques dans l'Ordovicien et le Silurien en France. Étude des acritarches, des chitinozoaires et des spores. *Sciences Géologiques. Mémoire* 38. Université Louis Pasteur (Strasbourg), Institut de géologie, pp. 1–224.
- Reitz, E., Höll, R., 1992. Palynological evidence for Lower Ordovician rocks (Tremadoc and Arenig) in the Northern Greywacke Zone (Eastern Alps). *Terra Nova* 4, 198–207.
- Ribecai, C., Tongiorgi, M., 1995. Arenigian acritarchs from Horns Udd (Öland, Sweden): a preliminary report. *Rev. Palaeobot. Palynol.* 86, 1–11.
- Ribecai, C., Tongiorgi, M., 1999. The Ordovician acritarch genus *Pachysphaeridium* Burmann 1970: new, revised, and reassigned species. *Palaeontogr. Italica* 86, 117–153.
- Ribecai, C., Raevskaya, E., Tongiorgi, M., 2002. *Sacculidium* gen. nov. (Acritarcha), a new representative of the Ordovician *Stelomorpha-Tranvikium* plexus. *Rev. Palaeobot. Palynol.* 121, 163–203.
- Servais, T., 1993. The Ordovician acritarch *Frankea*. *Spec. Pap. Paleontol.* 48, 79–95.
- Servais, T., 1997. The Ordovician *Arkonina-Striatotheca* acritarch plexus. *Rev. Palaeobot. Palynol.* 98, 47–79.
- Servais, T., Maletz, J., 1992. Lower Llanvirn (Ordovician) graptolites and acritarchs from the "Assise de Huy", Bande de Sambre-et-Meuse, Belgium. *Ann. Soc. Geol. Belg.* 115, 265–284.
- Servais, T., Brocke, R., Fatka, O., 1996. Variability in the Ordovician acritarch *Dicrodiacrodium*. *Palaeontology* 39, 389–405.
- Servais, T., Stricanne, L., Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs at the Cambrian–Ordovician transition in the Algerian Sahara. *Palaeontology* 47, 395–414.
- Servais, T., Vecoli, M., Li, J., Molyneux, S.G., Raevskaya, E., Rubinstein, C.V., 2007. The acritarch genus *Veryhachium* Deunff 1954: taxonomic evaluation and first appearance. *Palynology* 31, 191–203.
- Servais, T., Li, J., Molyneux, S.G., Vecoli, M., 2008. The Ordovician acritarch genus *Coryphidium*. *Rev. Micropaleontol.* 51, 97–120.
- Servais, T., Molyneux, S.G., Li, J., Nowak, H., Rubinstein, C.V., Vecoli, M., Wang, W., Yan, K., 2018. First Appearance Datums (FADs) of selected acritarch taxa and correlation between Lower and Middle Ordovician stages. *Lethaia* 51, 1–26.
- Smelror, M., Cocks, L.R.M., Mørk, A., Neuman, B.E.E., Nakrem, H.A., 1997. Upper Ordovician–Lower Silurian strata and biota from offshore South Norway. *Nor. Geol. Tidsskr.* 77, 251–268.
- Steenmans, P., Le Hérisse, A., Bozdogan, N., 1996. Ordovician and Silurian cryptospores and miospores from southeastern Turkey. *Rev. Palaeobot. Palynol.* 93, 35–76.
- Stricanne, L., Munnecke, A., Pross, J., Servais, T., 2004. Acritarch distribution along an inshore–offshore transect in the Gorstian (lower Ludlow) of Gotland, Sweden. *Rev. Palaeobot. Palynol.* 130, 195–216.
- Tappan, H., 1980. *The Paleobiology of Plant Protists*. W.H. Freeman and Co, San Francisco, p. 1028.
- Turner, R.E., 1984. Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England. *Palaeontogr. Abteilung B* 190, 87–157.
- Tynni, R., 1975. Ordovician hystichospheres and chitinozoans in limestone from the Bothnian Sea. *Geol. Surv. Finl. Bull.* 279, 1–59.
- Uutela, A., 1989. Age and provenance of sedimentary erratics on the coast of southwest-ern Finland. *Geol. Surv. Finl. Bull.* 349, 100.
- Uutela, A., Tynni, R., 1991. Ordovician acritarchs from the Rapla borehole, Estonia. *Geol. Surv. Finl. Bull.* 353, 1–153.
- Van Soelen, E.E., Kürschner, W.M., 2018. Late Permian to Early Triassic changes in acritarch assemblages and morphology in the Boreal Arctic: New data from the Finnmark Platform. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 505, 120–127.
- Vavrdová, M., 1974. Geographical differentiation of Ordovician acritarch assemblage in Europe. *Rev. Palaeobot. Palynol.* 18, 171–175.
- Vavrdová, M., 1976. Excystment mechanism of Early Paleozoic acritarchs. *Casopis pro Mineralogii a Geologii* 21, 55–64.
- Vavrdová, M., 1977. Acritarchs from the Šárka Formation (Llanvirnian). *Věstník Ústředního Ústavu Geologického* 52, 109–118.
- Vavrdová, M., 1988. Further acritarchs and terrestrial plant remains from the Late Ordovician at Hlásná Třeban (Czechoslovakia). *Casopis pro Mineralogii a Geologii* 33, 1–10.
- Vecoli, M., 1999. Cambro–Ordovician palynostratigraphy (acritarchs and prasinophytes) of the Hassi–R'Mel area and northern Rhadames Basin, North Africa. *Palaeontogr. Italica* 86, 1–112.
- Vecoli, M., Le Hérisse, A., 2004. Biostratigraphy, taxonomic diversity and patterns of morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton) from the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes. *Earth Sci. Rev.* 67, 267–311.
- Vecoli, M., Riboulleau, M., Versteegh, G.J.M., 2009. Palynology, organic geochemistry and carbon isotope analysis of a latest Ordovician through Silurian clastic succession from borehole Tt1, Ghadamis Basin, southern Tunisia, North Africa: Palaeoenvironmental interpretation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 378–394.
- Wang, W., Servais, T., Yan, K., Vecoli, M., Li, J., 2015. The Ordovician acritarch *Dactylofusa velifera* Cocchio 1982: a biostratigraphical and palaeogeographical index species. *Palynology* 39, 125–141.
- Webby, B.D., Cooper, R.A., Bergström, S.M., Paris, F., 2004. Stratigraphic framework and time slices. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, pp. 41–47.
- Whelan, G.M., 1988. *The palynology of selected Ordovician localities in Scotland*. Ph.D. Thesis. University of Glasgow, Scotland.
- Wicander, R., Playford, G., 2008. Upper Ordovician microphytoplankton of the Bill's Creek Shale and Stonington Formation, Upper Peninsula of Michigan, U.S.A.: Biostratigraphy and paleogeographic significance. *Rev. Micropaleontol.* 51, 39–66.
- Wicander, R., Playford, G., Robertson, E.B., 1999. Stratigraphic and paleogeographic significance of an Upper Ordovician acritarch flora from the Maquoketa Shale, northeastern Missouri, U.S.A. *Paleontol. Soc. Mem.* 51, 1–38.
- Yan, K., Servais, T., Li, J., 2010. Revision of the Ordovician acritarch genus *Ampullula* Righi 1991. *Rev. Palaeobot. Palynol.* 163, 11–25.
- Yan, K., Servais, T., Li, J., Wu, R., Tang, P., 2011. Biodiversity patterns of Early–Middle Ordovician marine microphytoplankton in South China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 318–334.
- Yan, K., Li, J., Molyneux, S.G., Raevskaya, E.G., Servais, T., 2017. A review of the Ordovician acritarch genus *Barakella* Cramer & Diez 1977. *Palynology* 41, 80–94.
- Yin, L., 1995. Early Ordovician acritarchs from Hunjiang region, Jilin, and Yichang region, Hubei, China. *Palaeontol. Sin.* 185, 1–170 (in Chinese with an English summary).







## **Article IV**

### **Morphological variability of peteinoid acritarchs from the Middle Ordovician of Öland, Sweden and implications for acritarch classification**

David M. Kroeck, Mats Eriksson, Anders Lindskog, Axel Munnecke, Michel Dubois, Sylvie Régnier,  
Thomas Servais

in preparation; to be submitted to *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*.



# Morphological variability of peteinoid acritarchs from the Middle Ordovician of Öland, Sweden and implications for acritarch classification

David M. KROECK<sup>1</sup>, Mats ERIKSSON<sup>2</sup>, Anders LINDSKOG<sup>2</sup>, Axel MUNNECKE<sup>3</sup>, Michel DUBOIS<sup>4</sup>, Sylvie RÉGNIER<sup>1</sup>, Thomas SERVAIS<sup>1</sup>

<sup>1</sup> Evo-Eco-Paléo, UMR 8198 CNRS, Université de Lille, Avenue Paul Langevin, Bâtiment SN5, Cité Scientifique, 59655 Villeneuve-d'Ascq, France.

<sup>2</sup> Lithosphere and Biosphere Science, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

<sup>3</sup> Geozentrum Nordbayern, Paläobiologie, Friedrich-Alexander Universität Erlangen-Nürnberg, Löwenichstrasse 28, 91054 Erlangen, Germany

<sup>4</sup> LGCcE, LGCgE, Bâtiment SN5, Avenue Paul Langevin, Villeneuve d'Ascq F-59655, France

\*corresponding author. davidmarius.kroeck.etu@univ-lille.fr

## ABSTRACT

The investigation of large populations of peteinoid acritarchs recovered from the Middle Ordovician of the Hälludden section (Öland, Sweden) allow statistical analyses based on morphometric measurements. The results indicate the presence of assemblages displaying a continuous variability of morphotypes, suggesting that all peteinoid acritarch taxa from the section belong to a single entity. The classification based on a differentiation into the three genera *Peteinosphaeridium*, *Cycloposphaeridium* and *Liliosphaeridium*, and into a multitude of different species, cannot be applied. In analogy with recent investigations on modern dinoflagellate cysts that are known to develop variable cyst morphologies depending on environmental factors, it can be hypothesised that the different morphologies observed in the peteinoid acritarchs from Öland are cysts produced by a single phytoplanktonic organism. The different morphotypes cannot be considered as separate species but possibly represent a response to changing environmental conditions.

## 1. Introduction

Several thousands of acritarch taxa have been described between the 1930's and late 1980's (Fensome et al. 1990), with a peak of descriptions of new species between the late 1960's and the late 1980's (Servais & Paris 2000). A great number of jobs for palynologists became available in academic and industrial departments during these years, increasing the quantity of descriptions of acritarch assemblages that were documented for the first time. This time of rapid scientific progress was also a period when numerous 'new' (micro-) fossil taxa have been described, often based on limited number of samples, leading to the erection of new species based on very few specimens, and even based on single specimens (e.g. Burmann 1968, 1970). Many authors erected new taxonomic entities, following the Linnean classification system, with a very high number of new genera and species published. At that time this method was probably the most appropriate way to describe the wide spectrum of morphological variabilities within large population of acritarchs. But the production of species was probably excessive, and took place in a context when the evaluation of a (micro-)palaeontologist was often related to the number of new taxa that the author had described during the evaluation period.



From the early 1990's onwards, simple, generally bivariate, statistical methods allowed a new view on acritarch taxonomy and classification. It was clearly shown that some previously described acritarch species were actually part of a continuum of morphotypes within larger populations, and that some taxa only represented some extreme morphologies in larger assemblages. Such taxa were found to be end-members within large acritarch populations, that, in general, were initially not fully documented (for summaries, see Servais 1996; Fatka & Brocke 2008). Typical examples of this period are the studies of Servais (1993) who indicated that three previously published species of *Frankea* Burmann 1970 were impossible to distinguish, or the investigation of Brocke et al. (1997) who pointed out that the genera *Aureotesta* Vavrdová 1972 and *Marrocanium* Cramer et al. 1974 were actually belonging to the the same taxonomical entity with the first representing the dominant morphotype in Bohemian assemblages, and the second genus being more abundant in the Moroccan samples. Similarly, it was shown that the different 'species' of *Dicrodiacrodium* Burmann 1968 could not be distinguished (Servais et al. 1996) and that the high number of taxa at specific rank of *Arkonina* Burmann 1970 and *Striatotheca* Burmann 1970 were all morphotypes within populations with continuous variabilities (Servais 1997). Similarly, Fatka & Brocke (1999) documented the large variability of the genus *Arbusculidium* (Vavrdová 1965) Vavrdová 1972 and clarified its taxonomy.

Other detailed studies, including complete literature revisions and new investigations of larger populations of acritarch assemblages from different areas, including mostly the topotype material, confirmed that many acritarch 'species', and sometimes even 'genera', are clearly the result of an excessive production of new taxa in the 1960's and 1970's. In recent years, some taxonomic 'cleaning' was performed for the taxa *Coryphidium* Vavrdová 1972 by Servais et al. (2008), *Ampullula* Righi 1991 by Yan et al. (2010), or *Rhopaliophora* Tappan & Loeblich 1971 by Li et al. (2014), pointing clearly out that numerous taxa are junior synonyms of others, as they cannot be distinguished from each other.

Today, it becomes clear to most acritarch specialists that it is impossible to keep several hundreds of different specific names for some of the genera that are now considered as 'waste-basket' taxa. Such acritarch genera are, for example, *Micrhystridium* Deflandre 1937, *Veryhachium* Deunff 1954, *Baltisphaeridium* Eisenack 1958, or *Multiplicisphaeridium* Staplin 1961 (see Sarjeant & Stancliffe 1994; Sarjeant & Vavrdová 1997). For the genus *Veryhachium*, for example, a simplified model of classification was proposed, by integrating all triangular, rectangular, or polygonal specimens in separate groups (Servais et al. 2007; Lei et al. 2013). Nevertheless, some authors continue describing new species, ignoring the already extremely abundant taxa in literature, adding sometimes more confusion.

More complex statistical analyses, including multivariate studies, were introduced in the early 2000's and allow further new perspectives in acritarch classification. Stricanne & Servais (2002) applied multivariate statistics to the galeate acritarchs (Servais & Eiserhardt 1995), pointing out that the four genera and ca. 90 species of the galeates are all belonging to a wide spectrum of morphotypes making them very often difficult or impossible to distinguish and identify. Servais et al. (2004) clearly pointed out that some morphological criteria of the galeate acritarchs, in particular process length and complexity, show a continuous variation within a stratigraphical section in Algeria, making it difficult to draw a clear line between the different previously described taxa, and even to identify separate species. More recently, such multivariate statistics have been applied to a number of acritarch taxa, including *Dactylofusa velifera* Cocchio 1982 by Wang et al. (2015), *Barakella* Cramer & Díez 1977 by Yan et al. (2017) and *Frankea* Burmann 1970 by Wang et al. (2017).

But how should Palaeozoic acritarchs be classified? Does the classification of a modern equivalent provide some insights? Most Palaeozoic acritarchs are today widely considered as being fossil resting cysts of phytoplanktonic organisms, with possible morphological comparisons to modern phytoplanktonic groups, in particular dinoflagellates (e.g. Colbath & Grenfell 1995; Strother 1996). Several acritarch taxa display complex process structures that are highly variable. In particular the

process length may show large ranges of variations, but also the process shapes are very flexible. The changing shapes and lengths of acritarch taxa can be compared with those of modern dinoflagellate cysts, and related to palaeoecological proxies, such as salinity (e.g. Ellegaard 2000). A particular interesting study is that of Mertens et al. (2009) who documented the extreme variability of the process morphology and length of the dinoflagellate cyst *Lingulodinium machaerophorum* (Deflandre & Cookson 1955) Wall 1967. These authors measured 19,611 processes from 144 globally distributed surface sediment samples and were able to relate the process length to the salinity and temperature of the sea water. A single biological species thus produces a wide spectrum of morphologies, depending on different ecological conditions, but all these cysts are classified under the same name *L. machaerophorum*. It appears evident that specialists of Palaeozoic acritarchs use a completely different classification system. Palaeozoic acritarch workers working at the end of the 20th century would have described a high number of different ‘species’ and even ‘genera’ to describe the full spectrum of morphologies displayed by a single biological species, such as the dinoflagellate *L. machaerophorum*.

Another group of acritarchs with an extremely high variability of process shapes and lengths are the peteinoid acritarchs. Several genera have been attributed to this plexus of forms, including the genera *Peteinosphaeridium* Staplin et al. 1965, *Cycloposphaeridium* Uutela & Tynni 1991 and *Liliosphaeridium* Uutela & Tynni 1991. The peteinoid acritarchs were first described from the palaeocontinent Baltica, but have been reported subsequently from all other palaeocontinents, representing a common component of Ordovician assemblages world-wide. The peteinoid acritarch plexus can be considered as a biostratigraphical marker, as the first appearance (FAD) clearly lies in the upper Tremadocian (Servais et al. 2018). However, the taxonomy of the peteinoids is rather confuse, and needs to be revised.

In the present study, the topotype material from the Middle Ordovician of Öland, Sweden, is revised. Several authors worked on the peteinoid acritarchs from these sections, including the palynologists who erected the genus *Peteinosphaeridium* (Staplin et al. 1965). However, first peteinoid acritarchs were described from the Baltic area already by Eisenack (e.g. 1938). Other authors, including Kjellström (1971a, 1971b), Playford et al. (1995), Ribecai & Tongiorgi (1995), and Bagnoli & Ribecai (2000), also worked on the Öland sections, describing additional species.

It becomes clear that a complete revision of the peteinoid acritarchs is needed, but this is not the scope of the present paper. The main objective of this study is to understand if different morphotypes can be identified within the well preserved assemblages of the sections of Öland, in particular by applying multivariate statistical analyses.

## 2. Peteinoid acritarchs

Acritarchs have been defined as an artificial ‘group’ by Evitt (1963), without any taxonomic rank, to classify palynomorphs that could not be attributed to the dinoflagellate cysts. By definition, all acritarchs are therefore of unknown biological affinity (Evitt 1963). Already at the time of the creation, the acritarch group had been subdivided into additional informal subgroups, that mostly correspond to the general outline of the central body (Downie et al. 1963). Although not accepted in a formal classification scheme, these informal categories are largely used by acritarch workers. ‘Sphaeromorph’ acritarchs, for example, are considered to represent all spherical acritarchs without processes. ‘Polygonomorphs’ represent all acritarchs with a polygonal outline, ‘acanthomorphs’ are the more or less circular acritarchs with processes. Among these ‘acanthomorph’ acritarchs the ‘peteinoid’ acritarchs can easily be distinguished. While ‘baltisphaerid’ acritarchs have simple, undivided processes, and the ‘multiplicisphaerid’ acritarchs have branched processes, the ‘peteinoid’ acritarchs are characterized by their typical ‘peteinoid’ processes, i.e., displaying a trunk that is flanked by three lamina (or blades), providing a ‘tri-laminate’ morphology of the process

stem.

It is beyond the scope of the present paper to revise the peteinoid acritarchs in detail. According to Playford et al. (1995), the peteinoid acritarchs include the genus *Peteinosphaeridium* Staplin et al. 1965 (from which the terminology ‘peteinoid’ derives), but also the genera *Cycloposphaeridium* Uutela & Tynni 1991, and *Liliosphaeridium* Uutela & Tynni 1991. Playford et al. (1995) considered that *Peteinosphaeridium*, *Cycloposphaeridium* and *Liliosphaeridium* ‘constitute a morphologically cohesive group’ and pointed out that other genera may also be regarded as belonging to this same general category, such as *Polyancistrodorus* Loeblich & Tappan 1969 and *Asketopalla* Loeblich & Tappan 1969. However, Playford et al. (1995) did not discuss the morphological similarities in detail, although Tappan & Loeblich (1971) already noted the similarities of the different genera and the overlapping morphologies. As indicated by Li et al. (2014), another genus can be compared to the peteinoid acritarchs: *Rhopaliophora* Tappan & Loeblich (1971) may also show triradiate processes and it is clear that intermediates between *Rhopaliophora* and *Peteinosphaeridium* exist (Li et al. 2014, plate I). Tappan & Loeblich (1971) delimited the two genera by pointing out that none of the *Rhopaliophora* appendices have the characteristic buttressed or angular finned structures of *Peteinosphaeridium*, but the distinction in rich and well-preserved assemblages is sometimes impossible (see discussion in Li et al., 2014).

At an intraspecific level, the distinction of individual taxa is also very difficult. For some specimens it is difficult, if not impossible, to classify the material at a specific, but sometimes also at a generic level. *Cycloposphaeridium* was described by Uutela & Tynni (1991) as being distinguished from *Peteinosphaeridium* because of its typical petal- or leaf-like shape. On the other hand, *Liliosphaeridium* displays a more complex distal structure, that Playford et al. (1995) defined as a ‘calyx.’ Both Uutela & Tynni (1991) and Playford et al. (1995) erected several new species, but in none of both studies the intraspecific variability was discussed in detail, and biometrical studies were not presented. Playford et al. (1995, text-fig. 6) attempted to classify the different process shapes of the peteinoid acritarchs into 12 different categories, including ‘elongate attenuated laminate processes’ corresponding to *Peteinosphaeridium*, ‘near-columnar laminate processes’ attributed to *Cycloposphaeridium*, and ‘distally elaborated processes’ that are classified as *Liliosphaeridium*. In well-preserved assemblages with several hundreds of specimens, it becomes evident that intermediates exist between the 12 different categories of Playford et al. (1995).

### 3. Sections and sampling

#### 3.1. Geological Setting

The island of Öland, southeast of the Swedish mainland in the Baltic Sea, is a classical locality for the study of Ordovician fossils, including microfossils and palynomorphs. Ordovician acritarchs and chitinozoans were investigated in detail in monographic studies (Kjellström 1971a,b; Grahn 1980, 1981, 1982) after the initial investigations by Eisenack in the 1930’s (e.g. Eisenack 1938).

During the Middle Ordovician, the palaeocontinent Baltica was situated in southern mid-latitudes and on a drift northwards (Torsvik & Cocks 2017). Shallow epicontinental seas covered most of the continent and marine sediments formed slowly across the seafloor. Today, remnants of these past subaquatic environments are represented by fossiliferous packages of strata, predominantly consisting of reddish and gray limestone that has been and still is heavily quarried for agricultural as well as ornamental purposes (Fig. 1A; e.g., Lindskog & Eriksson 2017). These strata are broadly referred to as the ‘orthoceratite limestone’, due to the common presence of abundant cephalopod conchs (e.g., Grahn 1986). Other macroscopic fossils conspicuously include trilobites and brachiopods, but cystoid echinoderms also occur *en masse* in some levels (Regnéll 1945).

However, closer inspection at higher magnification (i.e., microfacies and thin-section analyses)

reveals that the fossil fauna is more diverse (e.g., Hadding 1958; Jaanusson 1960; Olgun 1987; Tinn & Meidla 2001; Eriksson et al. 2016; Lindskog & Eriksson 2017). The ‘orthoceratite limestone’ is characterized by a variable mixture of carbonate mud and skeletal grains, typically with only a minor siliciclastic component, and it is generally agreed that these strata represent cool-water to temperate deposits (e.g., Lindskog & Eriksson 2017, and references therein).

The geological succession of the island of Öland is mainly comprised of Cambrian–Ordovician sedimentary strata overlying peneplaned Proterozoic basement rocks (Fig. 1B; Jaanusson & Mutvei 1982; Stouge 2004). Given the many natural outcrops and quarries, the island has been the target of numerous geologic investigations over the years. Most of the near-surface rocks comprise flat-lying Middle Ordovician strata of the ‘orthoceratite limestone’.

In the frame of new palynological investigations that have as a main focus the palaeoecological analysis and interpretation of acritarch distribution, several sections on northwestern Öland have been sampled, including localities that have previously been investigated palynologically (from North to South Hälludden, Hagudden, Byrum, and Horns Udde). The present study is focused on the section from Hälludden (Fig. 1B). The sampled strata belong to the informal formations A+B (‘Gillberga Formation’) and C in the lower–middle Kunda regional Stage (Fig. 2; Stouge & Bagnoli 1990; Stouge 2004). This corresponds to a portion of the lower–middle Darriwilian global Stage of the Middle Ordovician (upper Dw1–basal Dw2 stage slices of Bergström et al. 2009). The biostratigraphic subdivision of the studied interval is based on trilobites and conodonts (e.g., Bohlin 1949; Grahn 1982; Jaanusson & Mutvei 1982; Nordlund 1989; Stouge & Bagnoli 1990; Bagnoli & Stouge 1997).

### 3.2. *Material and Methods*

The present study is focused on the analyses of peteinoid acritarchs from the Hälludden section. The other sections sampled for a general palynological study (Hagudden, Byrum, Horns Udde section, Horns Udde quarry) do not provide peteinoid acritarchs in sufficiently high numbers allowing multivariate statistical analyses. A total of 13 samples from the Hälludden section (Fig. 2) were treated using standard procedures to extract palynologic material, which include the use of HF and HCl and micrometric mesh filter extraction. The investigated palynological slides are stored at the Evo-Eco-Paleo CNRS research unit of the University of Lille.

In order to understand if different morphotypes can be distinguished with biometrical studies, and if different taxa can be identified, several morphological criteria have been defined (Fig. 3). The two obvious parameters that are commonly used for biometrical studies are the length of the processes (PL: process length) and the central body diameter of the vesicle (BD: body diameter). In addition, other parameters of the processes are measured, including the width of the bases of the processes (SW: stem width), and also the morphology of the distal crown-like structure, named ‘calyx’ by Playford et al. (1995): CW (calyx width) and CL (calyx length).

In the present study we provide simple statistical studies, with histograms of the different parameters and for the multivariate statistics a principal component analysis (PCA). PCA is a commonly used method for projecting multidimensional spaces in two dimensions. New variables (‘principal components’) are calculated by a linear equation based on the original variables. These principal components account for the variance in the palaeontological data (e.g., Davis 1986; Harper 1999; Hammer et al. 2009). The coefficients for each original variable in this equation are called eigenvectors and display the importance of the different variables in a certain principal component. The principal component analysis and the histograms in this study were performed using the software PAST (Harper 1999; Hammer et al. 2009).

## 4. Results



All investigated samples (Hälludden 1-13) provide well-preserved and highly diverse acritarchs assemblages, that have been described in previous studies (Playford et al. 1995; Ribecai & Tongiorgi 1995; Bagnoli & Ribecai 2000). A total of 221 peteinoid acritarch specimens have been recovered from the 13 samples from Hälludden, and have been measured to be included in the multivariate analyses, in order to understand if different morphotypes can be distinguished. 221 specimens are used in the PCA.

Histograms with kernel density plots have been produced for the following parameters: central body diameter (BD), total process length (PL), the width of the process basis (SW: stem width), as well as the length (CL) and width (CW) of the distal structure, named calyx (Fig. 4). The histograms show that the data are generally unimodal, and usually normally distributed. The central body diameter varies between 30 and 70  $\mu\text{m}$  (with few specimens showing vesicles up to 90  $\mu\text{m}$ ), but is generally between 40 and 50  $\mu\text{m}$ . The process length is more variable, with short processes (about 7  $\mu\text{m}$ ) and long processes (about 35  $\mu\text{m}$ ) being present in the Hälludden section. Most processes are about 15 to 25  $\mu\text{m}$  long. The slightly bimodal histogram does not allow to distinguish two different populations. The base of the processes, or stem width (SW), shows a very normal distribution, with most values lying around 6 and 8  $\mu\text{m}$ . The calyx continuously varies from being very short or even absent to having lengths of up to 20 or 25  $\mu\text{m}$ , but usually being around 5 to 10  $\mu\text{m}$ . The distal width of the calyx is also unimodally distributed with values between 5 and 35  $\mu\text{m}$ , but mean widths of 10 to 15  $\mu\text{m}$ .

The unimodal distributions provide no basis for separation into different morphotypes ('species') and suggest that all of the specimens can be attributed to a single taxonomical entity. Most interestingly, a clear distinction between specimens with or without a calyx cannot be made. The variation of the length and the width of the calyx is continuous. There is a clear overlap of specimens with a calyx (that are attributed in previous studies to the separate genus *Liliosphaeridium*) and those without this distal structure (classified traditionally as *Peteinosphaeridium*). At least in the Hälludden section, it is thus impossible to differentiate these two genera.

The results of the PCA also show that no distinguished clusters can be identified in the three scatter plots, indicating a continuous spectrum of morphologies in the analysed population (Fig. 5). Two morphological parameters show the greatest variations: process length and calyx width. However, the PCA clearly shows a single population, and no distinction into different groups. The entire population of peteinoid acritarchs appears to belong to a single entity.

## 5. Discussion

The sediments of the Ordovician sequence of the island of Öland are well known for their excellent preservation and the high diversity of acritarch taxa that have been described in several previous studies. The analysis of the palynological slides immediately shows an important dilemma: how can the specimens be attributed to different taxonomical entities? It becomes more and more clear that the authors of the pioneering investigations first described the most distinctive morphologies. *Peteinosphaeridium* was described by Staplin et al. (1965) as a clearly distinguishable group within the assemblage, that was already recognized by Eisenack (1938). Many different species have subsequently been described to illustrate the large morphological variation of this plexus of forms. The specimens with shorter processes, that are broadly leaf-like or petal-shaped (and morphologically approaching the genus *Rhopaliophora*) have been classified as a separate taxon by Uutela and Tynni (1991), who erected the genus *Cycloposphaeridium* to host these morphologies. The same authors also described a further genus (*Liliosphaeridium*) to classify those end-members of the wider population of the peteinoids that show distinctively a distal structure, named 'calyx' by

Playford et al. (1995). These attempts of classification have the merit to allow to put a name to some of the end-members of the large population of peteinoids. However, it becomes impossible to name and classify the intermediate forms, that are clearly present, as indicated by the statistical analyses. These intermediate forms were never mentioned or described in the original descriptive studies, and biometrical investigations were not provided, possibly because they put into question the erection of the numerous taxa (species and genera) described as new.

Of particular interest is the investigation of Bagnoli & Ribecai (2001). These authors investigated the different Öland sections, and their study focused on *Liliosphaeridium*, i.e., one fraction of the peteinoid plexus (with the calyx at the distal end of the processes). Bagnoli & Ribecai (2001) recognized a gradual change in morphology of specimens assigned to *L. brevicealix*, with a reduction of 'vesicles on the central body surface' [sic], a reduction of the process number, and an increase of the ratio calyx/stem from older to younger samples. Bagnoli & Ribecai (2001) argued that there might be a continuous trend from *L. pocillum* (short calyx, long stem) through *L. brevicealix* (calyx and stem of equal length) to *L. tintinnabulum* (very long calyx, short stem). Most interestingly, Bagnoli & Ribecai (2001) noted in the discussion paragraph concerning their new species *Liliosphaeridium brevicealix* that they show a gradual morphological change in the succession, and they wrote furthermore: 'as far as our present knowledge is concerned, we are not yet in position to ascertain whether this trend represents an evolutionary lineage or an ecological adaptation.' Several new species were described by Bagnoli & Ribecai (2001): *Liliosphaeridium brevicealix* (based on 50 specimens), *Liliosphaeridium pocillum* (based on 30 specimens), *Liliosphaeridium tintinnabulum* (based on 30 specimens), *Liliosphaeridium trinatum* (based on 30 specimens), in addition to the two previously described taxa *Liliosphaeridium hypertrophicum* (Eisenack 1976) Playford et al. 1995 (24 specimens found) and *Liliosphaeridium kaljoi* Uutela and Tynni 1991 (15 specimens found). While suggesting that the forementioned gradual trend might be representing either an evolutionary lineage or an ecological adaptation, Bagnoli & Ribecai (2001) do not elaborate on each of the hypotheses.

In the present study processes with different calyx/stem ratios on single specimens were found, thus making an assignment to each of the species difficult. Similarly, *L. kaljoi* and *L. hypertrophicum* are differentiated by Bagnoli & Ribecai (2001), aside from a different number of processes, in the length of the calyx in comparison to the process length. Here, too, we observe single specimens showing processes of both morphologies, the *L. kaljoi*-type and the *L. hypertrophicum*-type (e.g., Plate I: 11, 12).

It is thus possible to compare some of the morphotypes with previously described taxa. However, it also is evident that all specimens are part of a large 'cloud' of extremely variable morphotypes, and that it becomes difficult to separate different 'taxonomical' entities.

If we now put these investigations in the light of recent studies on modern dinoflagellates, and in particular on *Lingulodinium machaerophorum* (Deflandre & Cookson 1955) Wall 1967, the peteinoid acritarchs are possibly representing the resting cysts of a single biological species. The different morphotypes described by the previous authors as separate 'species' and even 'genera' are most probably belonging to a single entity. The fossil 'species' and 'genera' are thus clearly 'morphospecies' and 'morphogenera' that may be useful for the identification of individual specimens, but they are most probably not real 'biological species.'

## Conclusion

The classification of acritarchs remains a major problem concerning the study of this group. Previous investigations show that a large morphological variety can indeed be observed within many acritarchs, making the distinction of individual taxa difficult. Here we present a new study on populations of peteinoid acritarchs from the Hälludden section of the Ordovician of Öland, Sweden,

including statistical analyses based on morphometric measurements. While in previously published literature a high number of species of this group were presented from the Öland sections, our results indicate that many of these taxa represent only morphotypes in a wider range of morphologies and therefore can not be considered as distinct species. The assemblages of peteinoid acritarchs recovered from the 13 samples of the Hälludden section all belong to a single entity, for which subdivisions cannot be made easily, or only arbitrarily. It can be assumed that a large part of the taxa described in literature are not real distinguishable taxonomic entities but rather represent different (eco-) phenotypes. In most of the previously published acritarch studies the morphological changes have usually been interpreted as a result of chronological evolution, whereas in many cases it can be assumed that they may only reflect changing environmental conditions. Several dinoflagellate cysts are known to develop variable cyst morphologies depending on environmental factors, e.g., temperature and salinity. Considering that many acritarchs are probably resting cysts of dinoflagellate-like organisms, it is possible that the different morphologies observed in the peteinoid acritarchs represent a response to changing environmental conditions. In addition, it is possible that all these morphotypes were originally produced by a single biological species of a phytoplanktonic organism. Acritarchs should be classified accordingly, taking into consideration the recent investigations on their probable modern analogue.

### **Acknowledgments**

This paper is a result of the CNRS-INSU research project InterrVie “EcoSal” that allowed the initial field work bringing together the sedimentologists and palaeontologists from the universities of Erlangen, Lille, Lund. This study is a part of the PhD research project of D.K., financed by Lille University. M.E.E. acknowledges funding from the Swedish Research Council. A.L. acknowledges funding from the Birgit och Hellmuth Hertz’ Foundation and the Royal Physiographic Society in Lund. This paper is a contribution to IGCP project 653 – ‘The onset of the Great Ordovician Biodiversification Event’.



## References

- Ahlberg P, Lundberg F, Erlström M, Calner M, Lindskog A, Dahlqvist P, Joachimski MM 2019. Integrated Cambrian biostratigraphy and carbon isotope chemostratigraphy of the Grönhögen-2015 drill core, Öland, Sweden. *Geological Magazine*. 156:935–949.
- Bagnoli G, Stouge S. 1997. Lower Ordovician (Billingenian–Kunda) conodont zonation and provinces based on sections from Horns Udde, north Öland, Sweden. *Bolletino della Società Paleontologica Italiana*. 35: 109–163.
- Bagnoli G, Ribecai C. 2001. On the biostratigraphic significance of the Ordovician acritarch genus *Liliosphaeridium* on Öland, Sweden. *Review of Palaeobotany and Palynology*. 117: 195–215.
- Bergström SM, Chen X, Gutiérrez-Marco JC, Dronov A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to  $\delta^{13}\text{C}$  chemostratigraphy. *Lethaia*. 42:97–107.
- Bohlin B 1949. The Asaphus Limestone in northernmost Öland. *Bulletin of the Geological Institutions of the University of Uppsala*. 33:529–570.
- Brocke R, Fatka O, Servais T. 1997. A review of the Ordovician acritarchs *Aureotesta* and *Marrocanium*. *Annales de la Société Géologique de Belgique*. 120:1–21.
- Burmann G. 1968. Diacrodien aus dem unteren Ordovizium. *Paläontologische Abhandlungen Abteilung B*. 2:635–652.
- Burmann G. 1970. Weitere organische Mikrofossilien aus dem unteren Ordovizium. *Paläontologische Abhandlungen, Abteilung B*. 3:289–332.
- Colbath GK, Grenfell HR. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including “acritarchs”). *Review of Palaeobotany and Palynology*. 86:287–314.
- Davis JC. 1986. *Statistics and Data Analysis in Geology*. John Wiley & Sons, New York. 656 pp.
- Downie C, Evitt WR, Sarjeant WAS. 1963. Dinoflagellates, hystrichospheres, and the classification of the acritarchs. *Stanford University Publication Geological Sciences*. 7(3):1-16.
- Eisenack A. 1938. Hystrichosphaerideen und verwandte Formen in baltischen Silur. *Zeitschrift Gesschiebeforschung Flachlandgeologie*. 14:1–30.
- Ellegaard M. 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology*. 109:65–81.
- Eriksson ME, Lindskog A, Servais T., Hints O, Tonarová P. 2016. Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF*. 138: 502–509.
- Evitt WR. 1963. A discussion and proposals concerning fossil dinoflagellates, Hystrichospheres, and acritarchs. II. *Proceedings of the National Science Academy*. 49 (3):298–302.
- Fatka O, Brocke R. 1999. Morphologic variability in two populations of *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972. *Palynology*. 23:53–180.
- Fatka O, Brocke R. 2008. Morphologic variability in Lower Palaeozoic acritarchs: Importance for acritarch systematics. *Acta Musei Nationalis Pragae – Series B – Historia Naturalis*. 64 (2-4): 97–107.
- Fensome RA, Williams GL, Barss MS, Freeman JM, Hill JM. 1990. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. *American Association of Stratigraphic Palynologists Foundation, Serie 25*, pp. 1–771.
- Grahn Y. 1980. Early Ordovician Chitinozoa from Öland. *Sveriges Geologiska Undersökning. Series C 775*:1-41.
- Grahn Y. 1981. Middle Ordovician Chitinozoa from Öland. *Sveriges Geologiska Undersökning. Series C 784*:1-51.
- Grahn Y. 1982. Chitinozoophoran paleoecology in the Ordovician of Öland. *Sveriges Geologiska Undersökning. C 792*:1–17.
- Grahn Y. 1986. Orthocone nautiloid orientations in Arenig and Llanvirn limestones of Öland,

- Sweden. Geologiska Föreningens i Stockholm Förhandlingar. 108: 321–330.
- Hadding A. 1958. The pre-Quaternary sedimentary rocks of Sweden. VII. Cambrian and Ordovician limestones. Lunds Universitets Årsskrift, Ny Följd Afdelning. 2, 54: 1–261.
- Hammer Ø, Harper DAT, Ryan PD. 2009. PAST - PALaeontological STatistics, ver. 1.89. *Palaeontologia Electronica* 4(1):1–92.
- Harper DAT (ed.). 1999. Numerical Palaeobiology. John Wiley & Sons, Chichester. 468 pp.
- Jaanusson V. 1960: The Viruan (Middle Ordovician) of Öland. Bulletin of the Geological Institutions of the University of Uppsala. 38:207–288.
- Jaanusson V, Mutvei H. 1982. Ordovician of Öland. Guide to excursion 3. IV International Symposium on the Ordovician System, Oslo 1982. Swedish Museum of Natural History, Stockholm. 23 pp.
- Kjellström G. 1971a. Ordovician microplankton (baltisphaerids) from the Grötlingbo Borehole No. 1 in Gotland, Sweden. Sveriges Geologiska Undersökning. Series C 65 (665):1–75.
- Kjellström G. 1971b. Middle Ordovician microplankton from the Grötlingbo Borehole No. 1 in Gotland, Sweden. Sveriges Geologiska Undersökning, Series C 65 (669):1–35.
- Lei Y, Servais T, Feng Q, He W. 2013. Latest Permian acritarchs from South China and the *Micrhystridium/Veryhachium* complex revisited. *Palynology*. 37:325–344.
- Li J, Servais T, Yan K. 2014. The Ordovician acritarch genus *Rhopaliophora*: Biostratigraphy, palaeobiogeography and palaeoecology. *Review of Palaeobotany and Palynology*. 208:1–24.
- Lindskog, A, Eriksson ME. 2017. Megascopic processes reflected in the microscopic realm: sedimentary and biotic dynamics of the Middle Ordovician “orthoceratite limestone” at Kinnekulle, Sweden. *GFF*. 139:163–183.
- Mertens KN, Ribeiro S, Bouimetarhan I, Caner H, Combourieu-Nebout N, Dale B, De Vernal A, Ellegaard M, Filipova M, Godhe A, Goubert E, Grøsfjeld K, Holzwarth U, Kotthoff U, Leroy SAG, Londeix L, Marret F, Matsuoka K, Mudie PJ, Naudts L, Peña-Manjarrez JL, Persson A, Popescu SM, Pospelova V, Sangiorgi F, van der Meer MTJ, Vink A, Zonneveld KAF, Vercauteren D, Vlassenbroeck J, Louwye S. 2009. Process length variations in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: Investigation its potential as salinity proxy. *Marine Micropalaeontology*. 70:54–69.
- Nordlund U. 1989. Lithostratigraphy and sedimentology of a Lower Ordovician limestone sequence at Hälludden, Öland, Sweden. Geologiska Föreningens i Stockholm Förhandlingar. 111, 65–94.
- Olgun O. 1987. Komponenten-Analyse und Conodonten-Stratigraphie der Orthoceratenkalksteine im Gebiet Falbygden, Västergötland, Mittelschweden. Sveriges Geologiska Undersökning. Ca70:1–78.
- Playford G, Ribecai C, Tongiorgi M, 1995. Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium*: morphology, taxonomy, biostratigraphy, and palaeogeographic significance. *Bolletino Societa Paleontologica Italiana*. 34:3–54.
- Regnéll G. 1945. Non-crinoid Pelmatozoa from the Paleozoic of Sweden: Meddelanden från Lunds Geologisk-Mineralogiska Institution. 108:1–255.
- Ribecai C, Tongiorgi M. 1995. Arenigian acritarchs from Horns Udde (Öland, Sweden): a preliminary report. *Review of Palaeobotany and Palynology*. 86:1–11.
- Sarjeant WAS, Stancliffe RPW. 1994. The *Micrhystridium* and *Veryhachium* Complexes (Acritarcha: Acanthomorphae and Polygonomorphae): A Taxonomic Reconsideration. *Micropaleontology*. 40 (1):1–77.
- Sarjeant WAS, Vavrdová M. 1997. Taxonomic reconsideration of *Multiplicisphaeridium* Staplin, 1961 and other acritarch genera with branching processes. *GeoLines*. 5:1–53.
- Servais T. 1993. The Ordovician acritarch *Frankea*. In: Molyneux SG, Dorning KJ (Eds). Contributions to acritarch and chitinozoan research. The Palaeontological Association (Special Papers in Palaeontology 48). 79–95.
- Servais T. 1996. Some general considerations on Acritarch Classification. *Review of Palaeobotany and Palynology*, 93:9-22.
- Servais T. 1997. The Ordovician *Arkonio*–*Striatotheca* acritarch plexus. *Review of Palaeobotany*

- and Palynology. 98:47–79.
- Servais T, Eiserhardt KH. 1995. A discussion and proposals concerning the Lower Palaeozoic 'galeate' acritarch plexus. *Palynology*. 19:191–210.
- Servais T, Paris F. 2000. Ordovician Palynology : balance and future prospects at the beginning of the third millenium. *Review of Palaeobotany and Palynology*. 113:1–14.
- Servais T, Brocke R, Fatka O. 1996. Variability in the Ordovician acritarch *Dicrodiacrodium*. *Palaeontology*. 39 (2):389–405.
- Servais T, Stricanne L, Montenari M, Pross J. 2004. Population dynamics of galeate acritarchs at the Cambrian–Ordovician transition in the Algerian Sahara. *Palaeontology*. 47:395–414.
- Servais T, Vecoli M, Li J, Molyneux SG, Raevskaya EG, Rubinstein CV. 2007. The acritarch genus *Veryhachium* Deunff 1954: Taxonomic evaluation and first appearance. *Palynology*. 31:191–203.
- Servais T, Li J, Molyneux SG, Vecol, M. 2008. The Ordovician acritarch genus *Coryphidium*. *Revue de Micropaléontologie*. 51:97–120.
- Servais T, Molyneux SG, Li J, Nowak H, Rubinstein CV, Vecoli M, Wang WH, Yan K. 2018. First Appearance Datums (FADs) of selected acritarch taxa and correlation between Lower and Middle Ordovician stages. *Lethaia*. 51:228–253.
- Staplin F, Jansonius J, Pocock SAJ. 1965. Evaluation of some Acritarchous Hystrichosphere Genera. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*. 123:167–201.
- Stouge S. 2004. Ordovician siliciclastics and carbonates of Öland, Sweden. *Erlanger Geologische Abhandlungen – Sonderband*. 5:91–111.
- Stouge S, Bagnoli G. 1990. Lower Ordovician (Volkhovian–Kundan) conodonts from Hagudden, northern Öland, Sweden. *Palaeontologica Italica*. 77:1–54.
- Stricanne L, Servais T. 2002. A stratistical approach to classification of the Cambro-Ordovician galeate acritarch plexus. *Review of Palaeobotany and Palynology*. 118:239–259.
- Strother PK. 1996. Acritarchs. In: Jansonius J, McGregor DC (Eds.). *Palynology: principles and applications*, American Association of Stratigraphic Palynologists Foundation. 1:81–106.
- Tinn O, Meidla T. 2001. Middle Ordovician ostracods from the Lanna and Holen Limestones, south-central Sweden. *GFF*. 123:129–136.
- Torsvik TH, Cocks LRM. 2017. *Earth History and Palaeogeography*. Cambridge University Press, Oxford. 317 pp.
- Uutela A, Tynni R. 1991. Ordovician acritarchs from the Rapla borehole, Estonia. *Geological Survey of Finland, Bulletin*. 353:1–135.
- Wang W, Servais T, Yan K, Vecoli M, Li J. 2015. The Ordovician acritarch *Dactylofusa velifera* Cocchio 1982: a biostratigraphical and palaeogeographical index species. *Palynology*. 39:125–141.
- Wang W, Monnet C, Servais T. 2017. Quantitative methods used for understanding the taxonomy of acritarchs: a case study of the Middle Ordovician genus *Frankea* Burmann 1970. *Palynology*. 41 S1:69–79.
- Yan K, Servais T, Li J. 2010. Revision of the Ordovician acritarch genus *Ampullula* Righi 1991. *Review of Palaeobotany and Palynology*. 163:11–25.
- Yan K, Li J, Molyneux SG, Raevskaya EG, Servais T. 2017. A review of the Ordovician acritarch genus *Barakella* Cramer & Díez 1977. *Palynology* 41 S1:80–94.

## Figure and Plate captions

**Figure 1. A.** Map of Sweden and its geographic surroundings, with the current distribution of lower Paleozoic rocks indicated by shading; darker shade indicates areas with significant outcrops. Outline of B indicated by rectangle. **B.** Map of Öland, with large-scale geologic units indicated. Figure elements modified from Ahlberg et al. (2019).

**Figure 2.** Stratigraphy of the sampled portion of the Hälludden section. Biostratigraphy after Bohlin (1949), Jaanusson & Mutvei (1982), Nordlund (1989) and Bagnoli & Stouge (1990). The sample from the Horns Udde quarry comes from the *A. expansus* trilobite Zone (Bagnoli & Stouge 1997).

**Figure 3.** Quantitative (continuous) morphological parameters used for the biometrical studies. PL: process length; BD: (vesicle) body diameter, SW: stem width (width of the process basis); CW: (distal) calyx width; and CL: calyx length.

**Figure 4.** Histograms (frequency diagrams) of **A.** body diameter (BD), **B.** process length (PL), **C.** stem width (SW), **D.** calyx length (CL), **E.** calyx width (CW).

**Figure 5. A, B, C.** Principal component analysis (PCA) of body diameter (BD), process length (PL), stem width (SW), calyx length (CL), calyx width (CW), process length/body diameter (PL/BD) and calyx length/process length (CL/PL).

**Plate I.** Selected specimens of peteinoid acritarchs from Öland, followed by slide reference and England Finder™ coordinates. **1, 2.** *Peteinosphaeridium trifurcatum*-type. 1. slide Häll16-3 >51 µm, EF: K25/2; 2. slide Häll16-3 >51 µm, EF: K15/1. **3.** *P. eximium*-type slide Häll16-13 >51 µm, EF: ..... **4, 7, 8.** *P. velatum*-type. 4. slide Häll16-1 >51 µm, EF: R12/3; 7. slide Häll16-2 >51µm, EF: B6/4; 8. slide Häll16-2 >51 µm, EF: J16/4. **5.** *Liliosphaeridium* sp. slide Häll16-2 >51 µm, EF: K25/2. **6.** *P. dissimilae*-type slide Häll16-2 >51 µm, EF: C15/4. **9.** *L. intermedium*-type. slide Häll16-1; >51 µm, EF: H24. **10, 15, 16.** *L. kaljoi*-type. 10. slide Häll16-13 >51µm, EF: .....; 15. Häll16-3; >51 µm, EF: L19. Scale bars = 20 µm; 16. slide Häll16-3 >51µm, EF: L7. **11, 12.** *L. hypertrophicum*-type. 11. slide Häll16-1 >51µm, EF: C22/4; 12. slide Häll16-1 > 51µm, EF: M24/4. **13–14.** *L. brevicalex*-type. 13. slide Häll16-2 >51µm, EF: H17/2; 14. slide Häll16-2 >51µm, EF: W6/1. Scale bars = 20 µm.



Figure 1

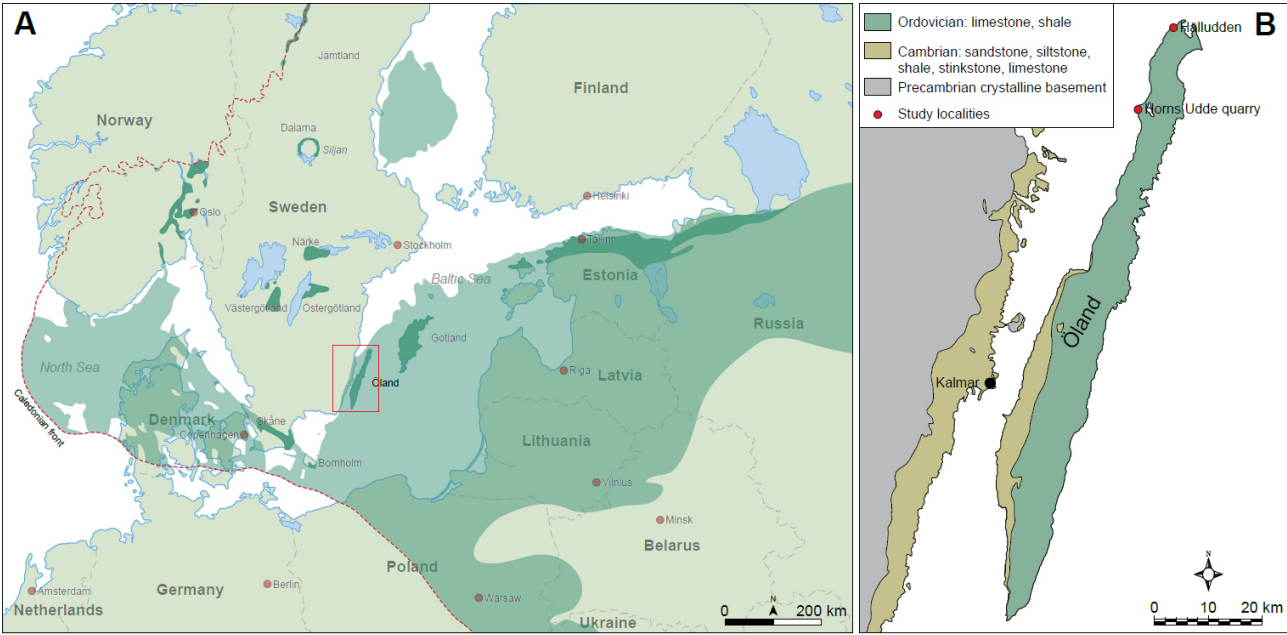


Figure 2

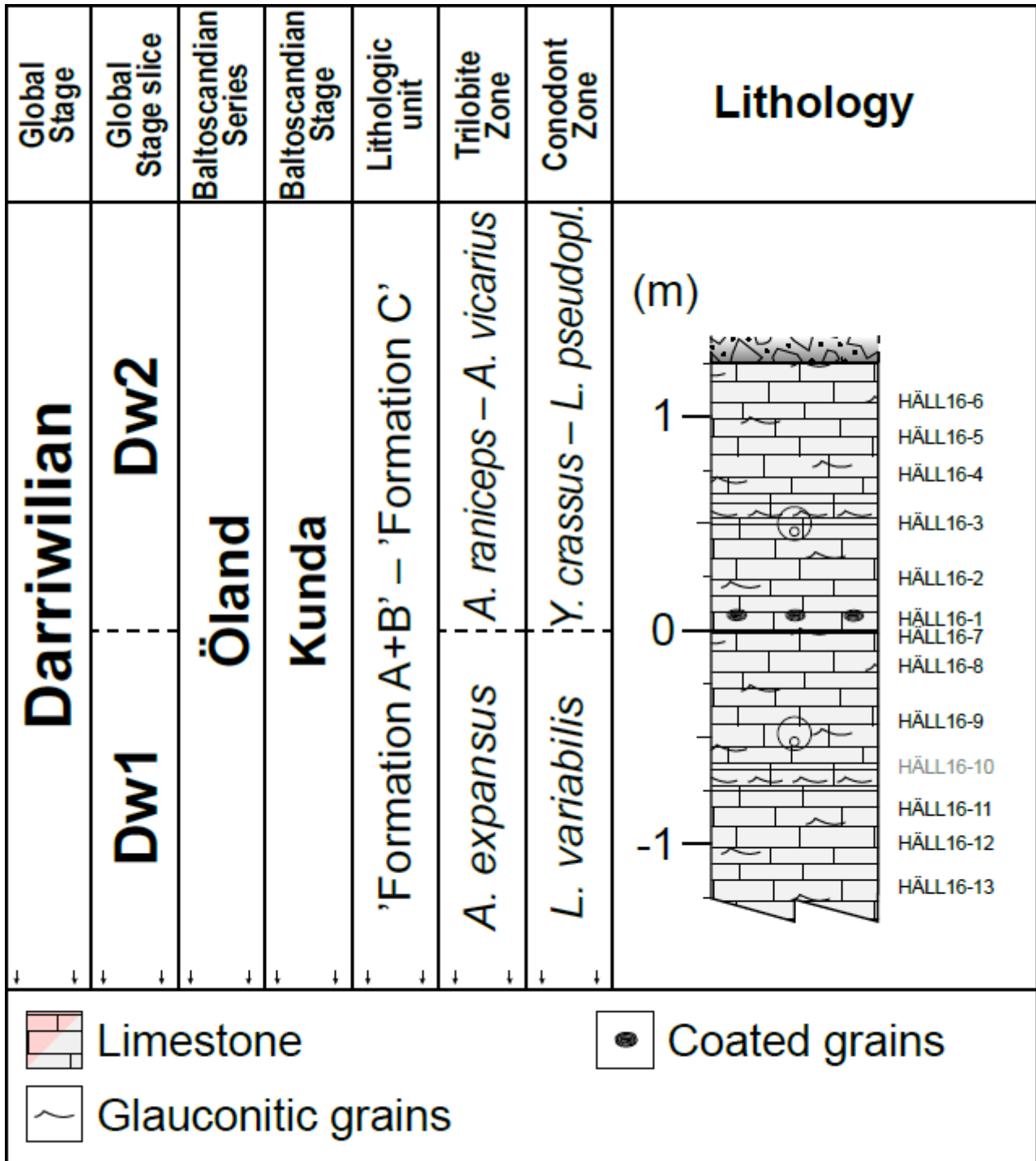




Figure 3

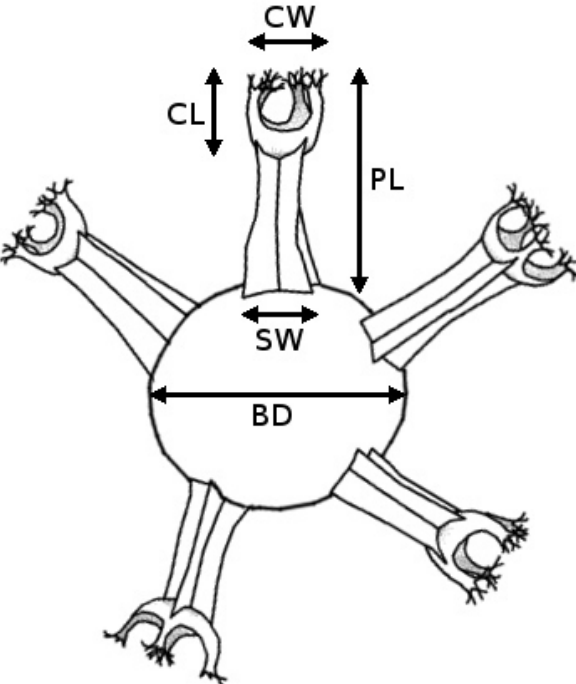


Figure 4

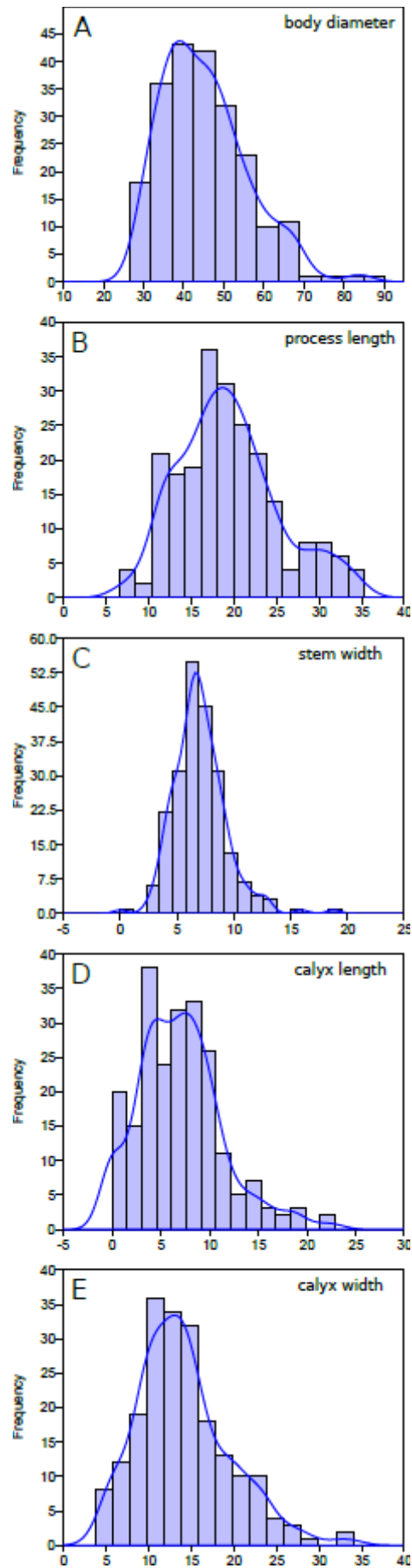


Figure 5

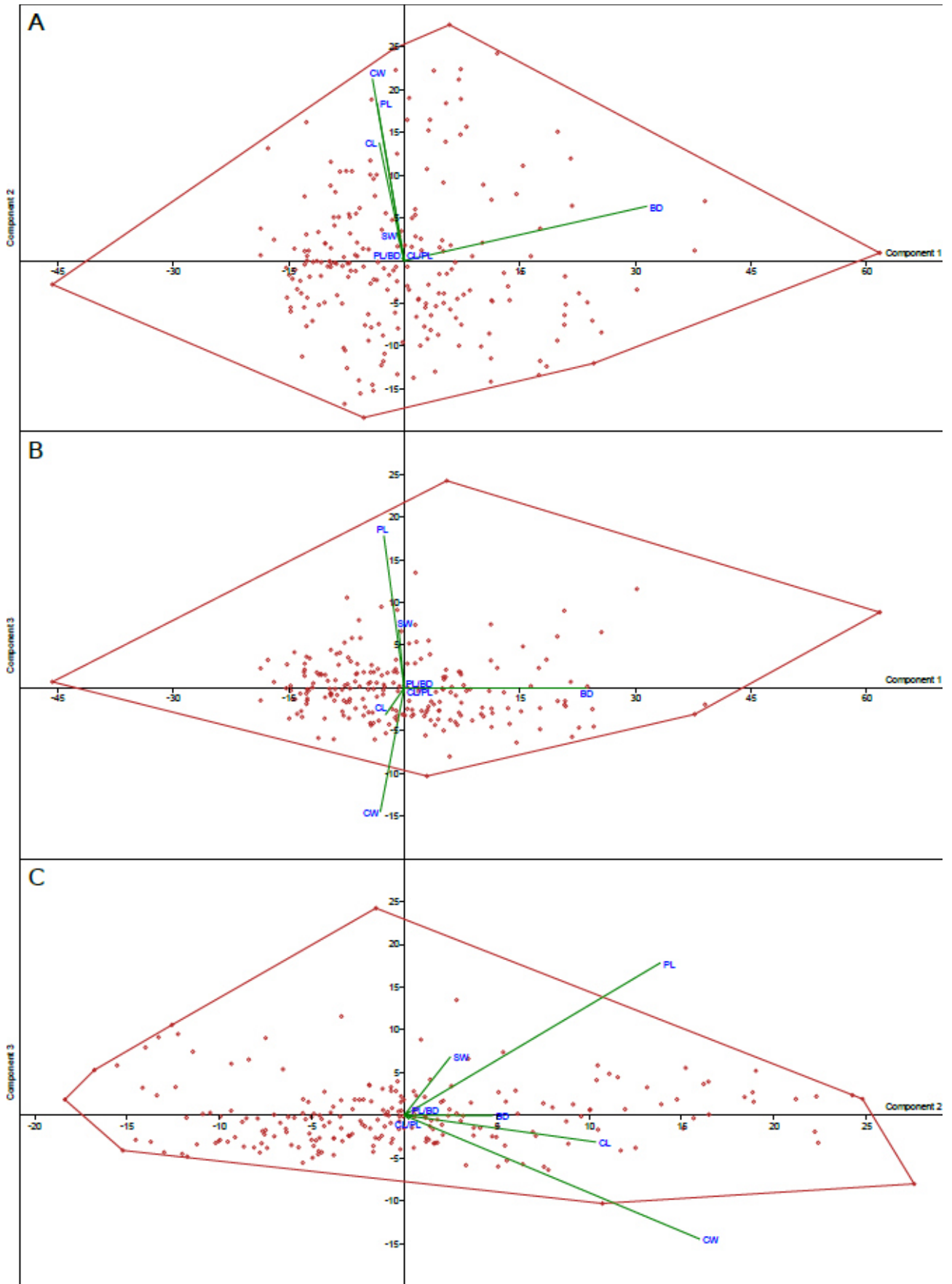
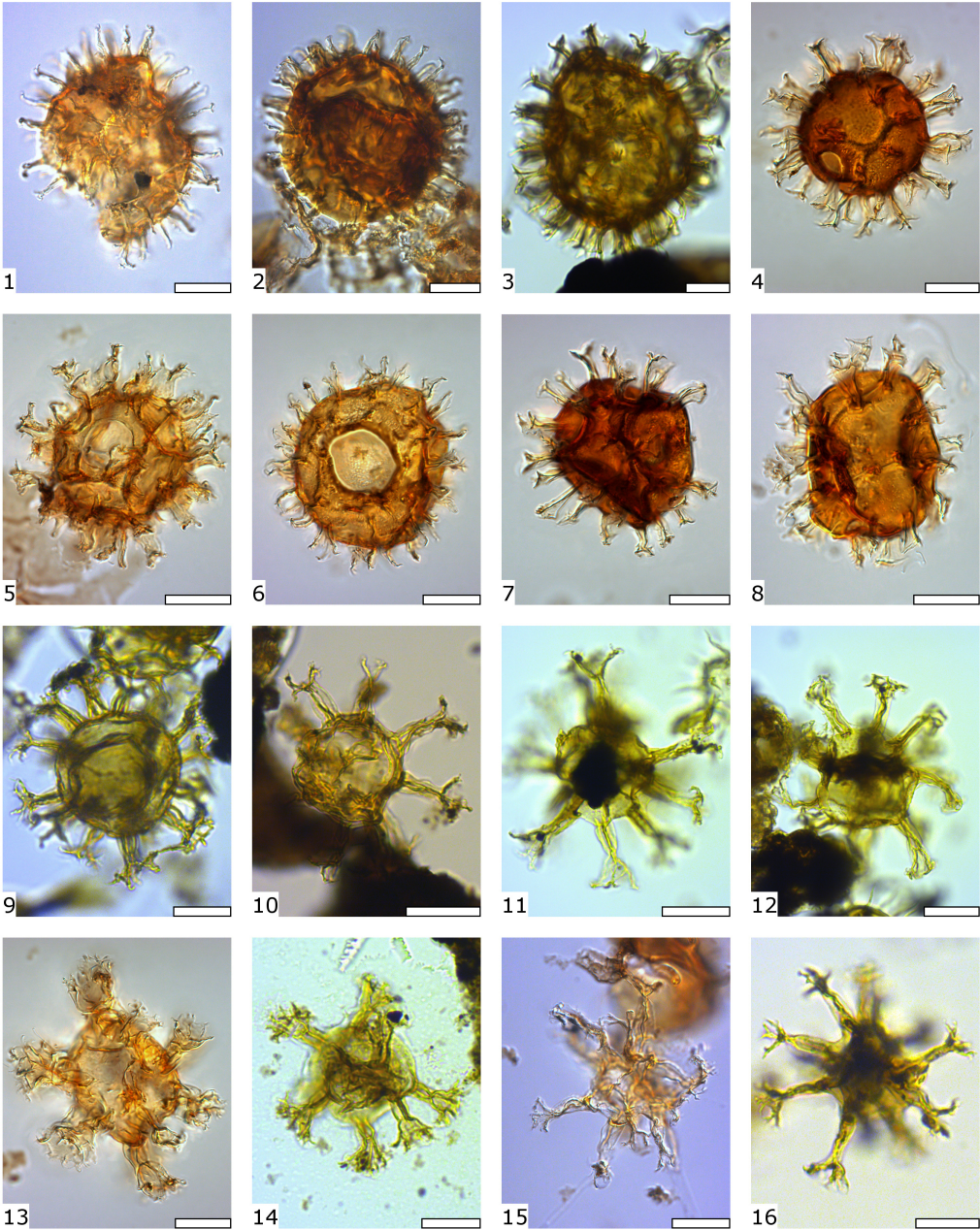


Plate I



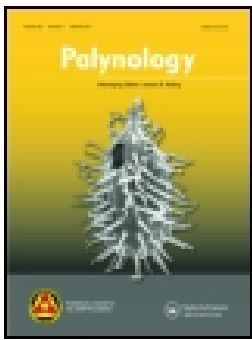


## **Article V**

### **Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia**

David M. Kroeck, Andrés Pardo-Trujillo, Angelo Plata Torres, Millerlandy  
Romero-Baéz & Thomas Servais

published 2019, *Palynology*.



## Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia

David M. Kroeck, Andrés Pardo-Trujillo, Angelo Plata Torres, Millerlandy Romero-Baéz & Thomas Servais

To cite this article: David M. Kroeck, Andrés Pardo-Trujillo, Angelo Plata Torres, Millerlandy Romero-Baéz & Thomas Servais (2019): Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia, *Palynology*, DOI: [10.1080/01916122.2019.1624279](https://doi.org/10.1080/01916122.2019.1624279)

To link to this article: <https://doi.org/10.1080/01916122.2019.1624279>



Accepted author version posted online: 28 May 2019.  
Published online: 03 Jul 2019.



Submit your article to this journal [↗](#)



Article views: 50



View Crossmark data [↗](#)





# Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia

David M. Kroeck<sup>a</sup>, Andrés Pardo-Trujillo<sup>b</sup>, Angelo Plata Torres<sup>b</sup>, Millerlandy Romero-Baéz<sup>b</sup> and Thomas Servais<sup>a</sup>

<sup>a</sup>UMR 8198 Evo-Eco-Paléo, CNRS-Université de Lille, Villeneuve d'Ascq Cedex, France; <sup>b</sup>Departamento de Ciencias Geológicas, IIES – Instituto de Investigaciones en Estratigrafía, Universidad de Caldas, Manizales, Colombia

## ABSTRACT

There are few publications on the precise age and palaeogeography of the Palaeozoic rocks of Colombia. In the present study the Pluspetrol Paisa-1 well, located in the central part of the Colombian Llanos Orientales Basin, is investigated palynologically, in order to determine the age, the palaeoenvironment and the palaeogeography of the sediments. The lowermost stratigraphical interval of the well (4939–5040'; ~1505–1536 m) is composed of alternating sandstone and black shale beds, from which a well-preserved assemblage of Ordovician acritarchs has been identified in five samples (cuttings and sidewall cores). The acritarch assemblage contains some diagnostic taxa, including *Arbusculidium*, *Barakella*, *Coryphidium*, *Dactylofusa*, *Striatotheca*, and *Veryhachium*, among others, indicating an Early to Middle Ordovician age. The presence of a few biostratigraphical index species, such as *Dactylofusa velifera* or *Coryphidium bohemicum*, and the absence of others point to a middle Floian age. As the three diagnostic genera (*Arbusculidium*, *Coryphidium*, *Striatotheca*) are present, the assemblage clearly belongs, in terms of palaeobiogeography, to the peri-Gondwanan acritarch province. Our study thus extends the geographical distribution of this province to the north-western part of South America, extending the palaeobiogeographical distribution map of Early to Middle Ordovician acritarchs. A comparison of the palynoflora with models of acritarch distribution in different palaeoenvironments implies a relatively shallow-water environment.

## KEYWORDS

phytoplankton; South America; peri-Gondwana; biostratigraphy; palaeobiogeography; palaeoenvironment

## 1. Introduction

The Llanos Orientales Basin (LB) is located in eastern Colombia (Figure 1), covering an area of approximately 194,000 km<sup>2</sup> (Campos and Mann 2012). While the Cretaceous and Cenozoic history of northern South America has been studied in detail, the Palaeozoic is still poorly understood, with few palaeontological studies on the early Palaeozoic (e.g. Harrison 1930; Leith 1938; Botero-Arango 1940; Kay in Trumpy 1943; Harrington and Kay 1951; Borrero et al. 2007; Gutiérrez-Marco et al. 2007; Moreno-Sánchez et al. 2008). Data for the sub-Cretaceous in the LB is limited, as only a few wells have penetrated the Palaeozoic successions. Indeed, most palaeontological information from the Lower Palaeozoic of South America comes from the sedimentary successions in the Cordillera Oriental and Sierras Subandinas of southern Peru, Bolivia and north-western Argentina (Benedetto et al. 2009). Despite many stratigraphical intervals with abundant and diverse palynomorph floras, Cuartas et al. (2008) recognised great deficiencies in the palynological knowledge of the sedimentary basins of Colombia. In fact, a stratigraphical subdivision of the Palaeozoic sediments within the LB does not exist, except in the Negritos-1 and Heliera-1 wells, where black mudstones containing Tremadocian trilobites

and graptolites were classified as the Negritos Formation (Ulloa et al. 1982; Baldis 1988; Dueñas and Césari 2006; Sarmiento 2011).

Palynology has been a useful tool for hydrocarbon exploration, and some contributions have been published, especially on the Cenozoic deposits (e.g. Jaramillo et al. 2011). In contrast, the palynology of the Palaeozoic has been poorly studied, and most of the information obtained by oil companies is contained only in internal reports. Unpublished results of Robertson Research (1982; see Cediél 2019) revealed Late Silurian acritarchs, such as *Domasia bispinosa*, *Baltisphaeridium gordonense*, *B. ramusculosum*, *Evittia? molina*, and *Multiplicisphaeridium ramusculosum*, in black shales of the San Juan-1 borehole in the western part of the LB. Théry et al. (1985) described an Ordovician ('Arenigian') assemblage of acritarchs in the Araracuara Formation in the Serranía de Chiribiquete south of the studied area (Figure 1). Grösser and Prössl (1991) showed on the basis of palynomorphs the first evidence of the Silurian in the Cordillera Oriental in Colombia. In an abstract, Dueñas (2002) reported palynological assemblages from Precambrian, Cambrian, Lower Ordovician, Devonian and Early Carboniferous successions in the LB, without providing any details. Dueñas and Césari (2005, 2006) studied palynological assemblages in Early Carboniferous material from boreholes in the LB.



**Figure 1.** Location of the Llanos Orientales Basin in Colombia and the main geotectonic features. AB: Amazonas Basin; BF: Bucaramanga Fault; CC: Cordillera Central; Ch: Serranía de Chiribiquete; CO: Cordillera Oriental; GFS: Guacáramo fault system; GM: Garzón Massif; Mac: Serranía de la Macarena; MMVB: Middle Magdalena Valley Basin; QM: Quetame Massif; SM: Santander Massif; UMBV: Upper Magdalena Valley Basin; VA: Vaupés Arch. Source: Authors, produced using QGIS (QGIS Development Team 2019) and ETOP1 (Amante and Eakins 2009).

Additionally, palynological information from the Precambrian in the LB is provided by Arminio et al. (2013).

In the present study, a detailed palynological investigation of Lower Palaeozoic beds of the Pluspetrol Paisa-1 well, located in the central part of the basin (Figure 1), is reported. The results allow a precise stratigraphical assignment of the studied interval, giving important information about the sedimentary history of the region. Moreover, this study aims to provide new data on the palaeogeographical distribution of certain acritarch taxa and microfloras. Also, this palynological analysis allows an assessment of the depositional environment by evaluating and comparing the acritarch composition with models of acritarch distribution in relation to palaeo-environmental conditions.

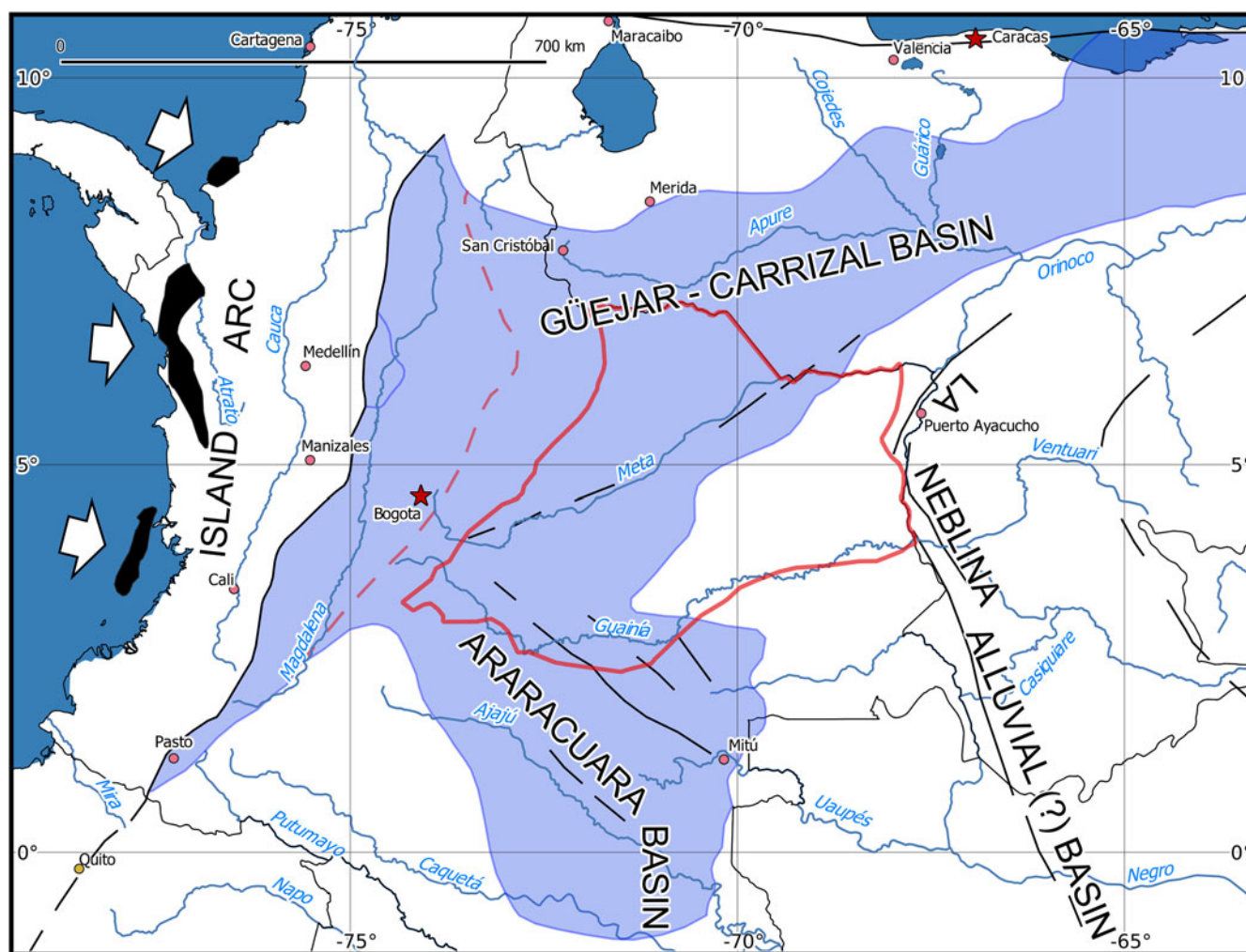
## 2. Geological setting

The LB is today a sub-Andean foreland basin, limited to the west by the Andean Cordillera Oriental (Guacáramo Fault

System), to the East by the Guyana Shield and to the south and south-west by the Serranía de la Macarena and the Vaupés Arch, a basement high separating the Llanos and the Amazonas basins (Barrero et al. 2007). In the north the basin is separated from the Venezuelan Apure Occidental and Barinas basins by the Arauca Arch (Campos and Mann 2012). The LB comprises sedimentary successions from the lower Palaeozoic to the Holocene (Figure 2). As it represents the most important oil basin in Colombia, many stratigraphical and structural studies have been carried out in this area; unfortunately, very few of them are published.

Lower Palaeozoic sedimentary deposits of Colombia are exposed in the Cordillera Oriental (Quetame and Santander massifs) and the Serranía de la Macarena west of the LB, and in the Amazonian region immediately to the south (Vaupés Arch and Serranía de Chiribiquete) (Trumpy 1943; Théry et al. 1985; Sarmiento 2011; Gómez Tapias et al. 2017) (Figure 1). Within the basin, Palaeozoic rocks occur exclusively in the subsurface, and all available information is





**Figure 2.** Depositional basins in north-western South America during the Cambrian–Ordovician. Dashed line: basement boundary between Chicamocha Terrane in the west and the Guyana Shield in the east. Based on Cediél et al. (2011).

derived from seismic data and boreholes that penetrate these successions. Two sedimentary cycles are recognised, which affected the region during the Palaeozoic, forming a Cambrian–Ordovician and an upper Palaeozoic megasequence (Sarmiento 2011). Most of the area of the basin was covered by a relatively shallow epicontinental sea during the early Palaeozoic, which extended from Venezuela to Argentina (Figure 3), as indicated by the close relationship of Colombian fossils (e.g. trilobites, graptolites) with Bolivian, Peruvian and Argentinian assemblages (Harrington and Kay 1951; Baldis et al. 1985; Moreno-Sánchez et al. 2008). Clastic sediments were deposited in extensional grabens developed on the subsiding Precambrian to Cambrian basement (Ecopetrol 1995; Moreno-López and Escalona 2015). Several sedimentary basins have been recognised, i.e. the Güejar Basin in the south-west, the Carrizal Basin in the north-west, and the Chiribiquete or Araracuara Basin in the south to south-east (Figure 2; Cediél et al. 2011; Cediél 2019). The Palaeozoic deposits become thinner towards the east and the south, with an important depocentre located in the Arauca Graben in the northern part of the LB (Figure 3), where Cambrian–Ordovician rocks may show thicknesses of up to 7300 m (24,000 feet; Ecopetrol 1995; also see Sarmiento 2011). The early Palaeozoic sediments are mainly composed

of grey to black marine fossiliferous mudstones with sandstone and siltstone intercalations, and locally red beds, derived from the Guyana Shield (McCollough and Carver 1992; Villegas et al. 1994). In the south-east part of the basin, littoral sediments are known (Ecopetrol 1995; also see Sarmiento 2011). An increase in metamorphism is observable from east to west, with metasedimentary rocks towards the west and undeformed sediments towards the east, likely caused by an early Palaeozoic compressional event (Moreno-López and Escalona 2015). At the end of the Ordovician, compressive deformation, low-grade metamorphism and localised intrusions caused uplift of the area, leading to erosion and peneplanation, and causing an extensive unconformity (Ecopetrol 1995). With most of the LB area emerged throughout the Silurian–Devonian, marine deposits were restricted to the north-west part of the LB, and mainly comprise marine black muds and a few coarse clastics (Dueñas and Césari 2006; Sarmiento 2011). The upper Palaeozoic megasequence was deposited during an extensional regime with associated graben formation and marine transgression (Ecopetrol 1995; Sarmiento 2011; Moreno-López and Escalona 2015). Cediél (2019, fig. 1.23) shows intertidal coastal swamp deposition in the north-western LB area near the foothills in his palaeogeographical interpretation for the

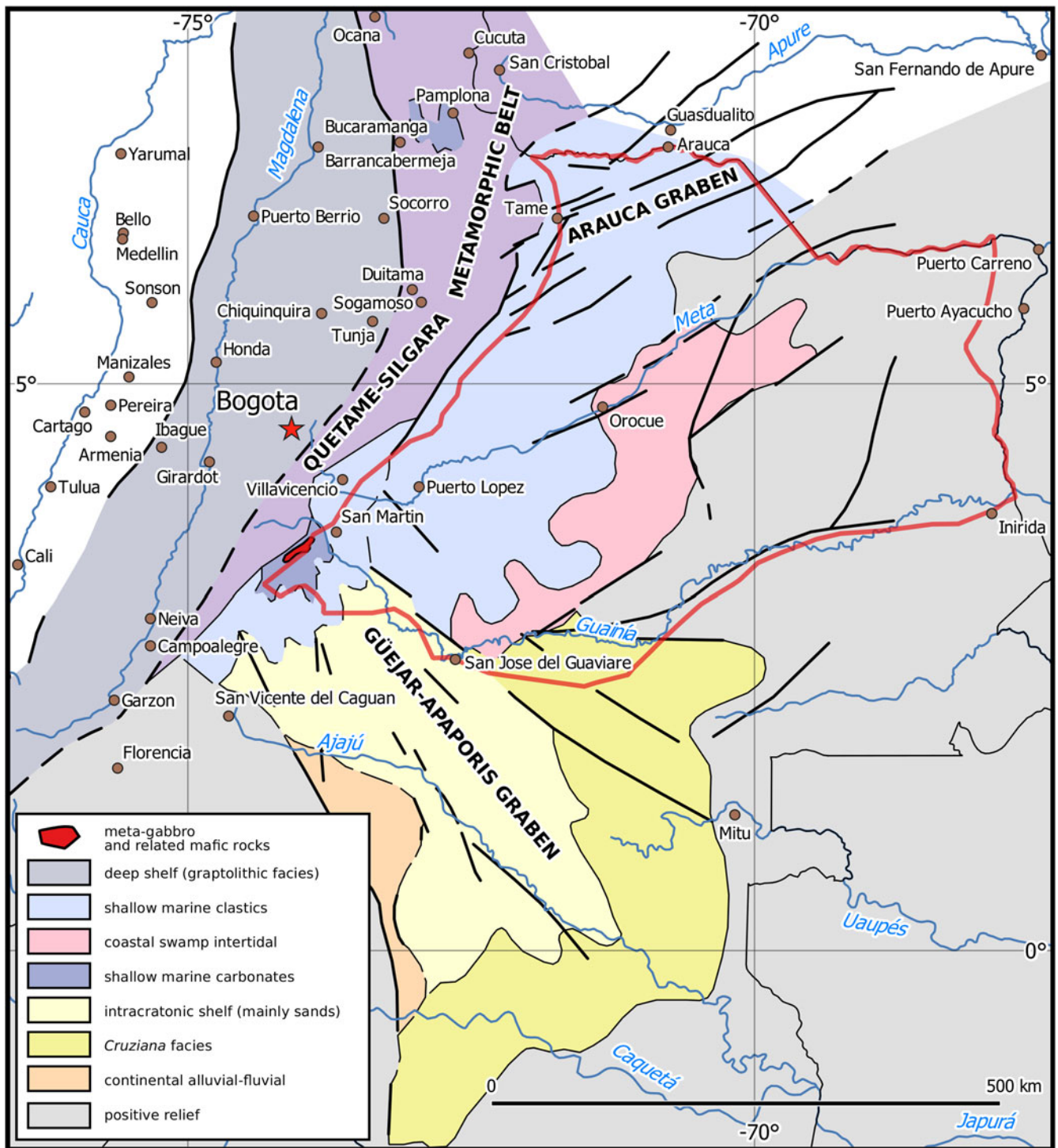


Figure 3. Sedimentary facies distribution in the eastern lower Palaeozoic basins of Colombia. Modified after Cediél (2019).

Devonian (cf. Cediél et al. 2011, fig. 8). In Carboniferous–Permian times, most of the area of the LB was emerged and under an erosional regime, while sedimentation continued in the Cordillera Oriental region. A second major unconformity, caused by a large tectonic event associated with the assembly of Pangaea (Quachita-Marathon orogeny) resulting in regional uplift (Ecopetrol 1995; Ruiz et al. 1999; Malone et al. 2002; Moreno-López and Escalona 2015), separates the upper Palaeozoic rocks from Late Cretaceous and Cenozoic shallow marine successions of the

foreland basin, which formed during the uplift of the Cordillera Oriental (Moreno-López and Escalona 2015). The Cretaceous–Cenozoic deposits are mainly terrigenous (sandstones and shales) (Barrero et al. 2007).

The petroleum potential of the Palaeozoic rocks has been proven in many sub-Andean basins. Possible hydrocarbon generation and accumulation in the Palaeozoic structures of the LB is indicated in data from several wells (Hermoza et al. 2011; Vayssaire et al. 2014). The Thermal Alteration Index of Palaeozoic palynomorphs of the LB indicates that they are in

the hydrocarbon generation window. While the basin is of great interest for hydrocarbon exploration, published palynological studies on the Palaeozoic succession are sparse and limited to the Carboniferous (Dueñas and Cesari 2005, 2006). Heliera and Negritos are classical Ordovician localities that have been published in short communications (Baldis et al. 1985).

### 3. Materials and methods

The studied material was derived from the Paisa-1 well, which was drilled by the hydrocarbon company Pluspetrol for exploration. The Ordovician deposits are located at the basal part of the Paisa-1 well, below 4900'. They are mainly composed of sandstones with thin beds of shale. Five samples from the Palaeozoic interval, including cuttings and sidewall cores (swc), were examined for this study, which are derived from the following depths [in feet ('), from base to top]: 5030–5040', 5021' (swc), 4980–4990', 4939' (swc), 4930–4940'. The material was processed by standard palynological techniques, involving treatment with hydrochloric and hydrofluoric acids in order to eliminate the carbonate and silicate contents, respectively. The organic residuals were filtered at 10 µm. Oxidised slides were produced using nitric acid (60%). The slides were fixed using Canada balsam. Each palynological slide was observed in detail with a Zeiss Axio Imager A2 optical microscope. Images were taken using a Zeiss AxioCam ERc5s. The samples are stored at the Evo-Eco-Paléo unit at the University of Lille, France.

### 4. Results

The palynological association recognised in the studied interval is dominated by acritarchs with few chitinozoans, graptolite fragments and very rare scolecodonts. One sample, 4939' swc, is barren of acritarchs. The most important acritarch taxa recorded are listed in Figure 4. Representative specimens are shown in Plate 1. The authorship of all genera and species mentioned in the text, in Figure 4 and in Plate 1 is given in Appendix 1. While differences in composition between the studied samples are apparent, with several taxa not present in every sample, the data, especially with respect to sample size, is insufficient for the establishment of different assemblages. Therefore, it is convenient to include all recognised taxa in a single composite assemblage in order to stratigraphically assign the whole sample interval.

The palynological assemblage contained a diverse flora (Figure 4), with predominantly occurring polygonomorph (e.g. *Polygonium*, *Tectitheca*) and diacromorph taxa (e.g. *Arbusculidium*, *Acanthodiacrodium*, *Barakella*). The richest assemblage is present in sample 5030–5040', with, among others, *Acanthodiacrodium* spp., *Adorfia* cf. *hoffmanensis*, *Arbusculidium filamentosum*, *Barakella felix*, *Coryphidium bohemicum*, *Cymatiogalea cuvillieri*, *C. granulata*, *C. messaoudensis*, *Dactylofusa velifera*, *Eisenackidium orientalis*, *Leiosphaeridia* sp., *Polygonium* spp., *Striatotheca* sp., *Tectitheca* sp. and a single specimen of *Vogtlandia multiradialis*. A slight successive change of taxonomic composition is evident (Figure 4), with

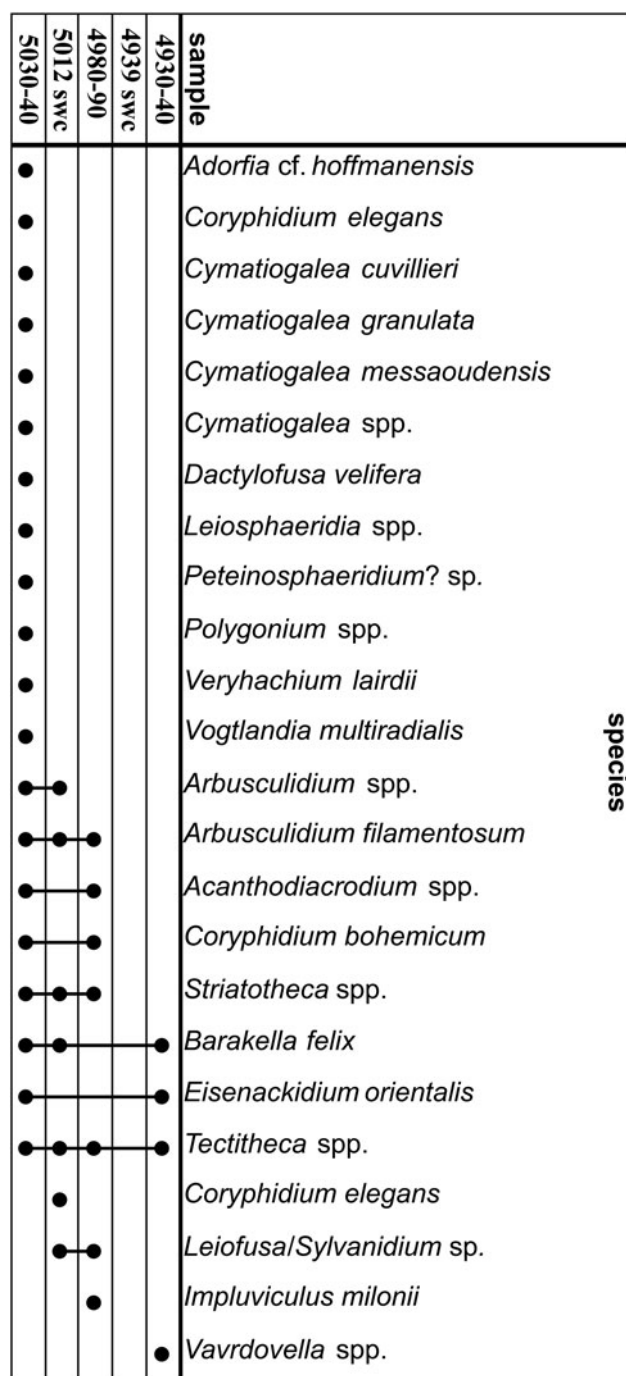


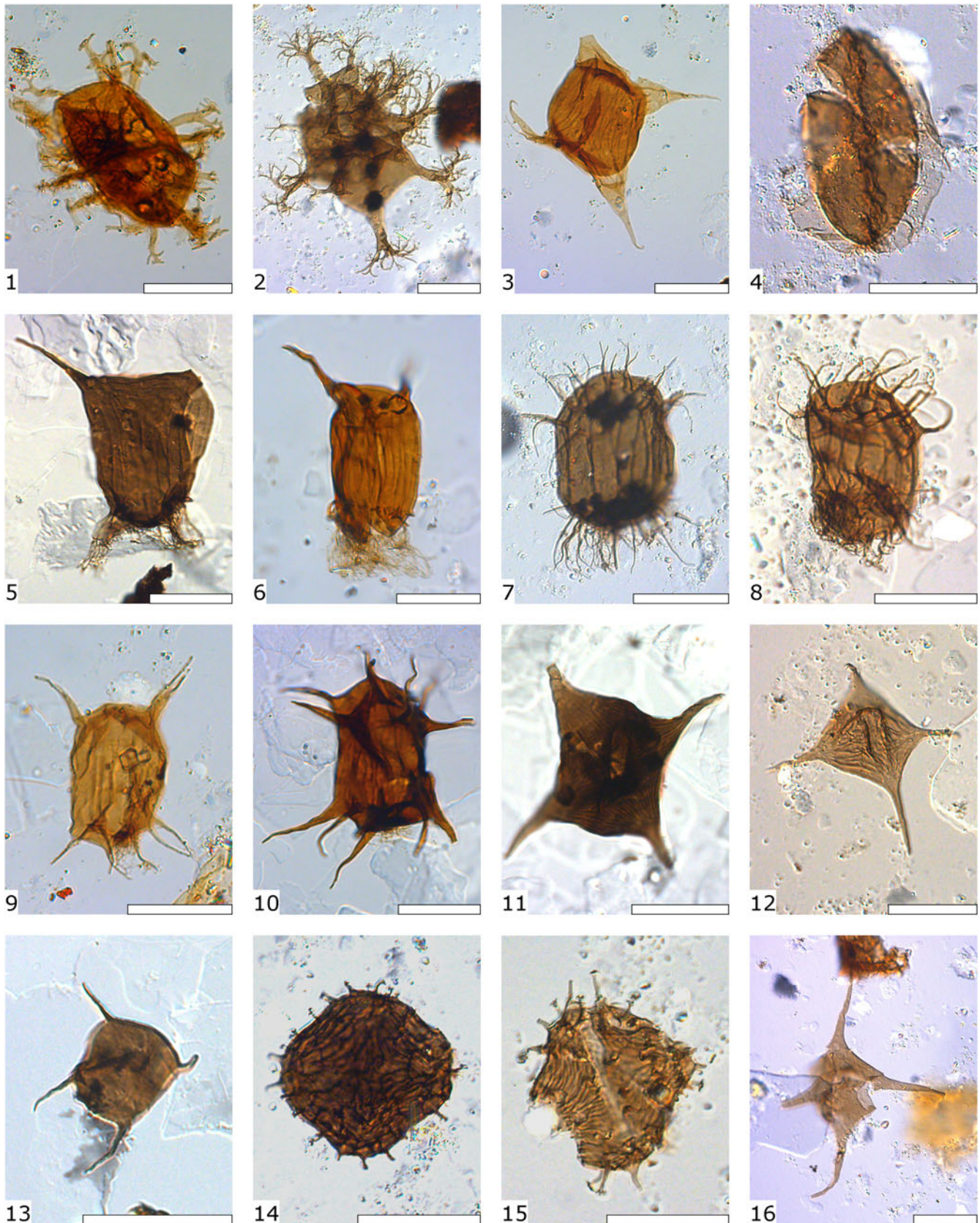
Figure 4. Distribution by sample of acritarch taxa from the Paisa-1 well in the Llanos Orientales Basin in Colombia.

many taxa that are present in the lowest sample not being found in higher samples, i.e. the genera *Cymatiogalea*, *Dactylofusa*, *Leiosphaeridia*, *Polygonium*, and *Vogtlandia*. Conversely, several taxa in the higher samples are not found in the lowest, i.e. *Leiofusa/Sylvanidium*, *C. elegans*, *Impluviculus milonii*, and *Vavrdovella*.

#### 4.1. Stratigraphy

The results of the palynological study reveal valuable information regarding age and palaeobiogeography. The presence of certain diagnostic taxa allows a precise stratigraphical assignment of the studied interval of the Paisa-1 well. The





**Plate 1.** Specimens of selected taxa from the Ordovician of the Paisa-1 well, Llanos Orientales Basin, Colombia. 1. *Adorfia* cf. *hoffmanensis*, Paisa-1 5030–5040' IIES-PAL-0679, England Finder (EF): D10/2. 2. *Vogtlandia multiradialis*, Paisa-1 5030–5040' IIES-PAL-0679; EF: U49. 3. *Eisenackidium orientalis*, Paisa-1 5030–5040' IIES-PAL-0679; EF: C15. 4. *Dactylofusa velifera*, Paisa-1 5030–5040' IIES-PAL-0679; EF: D40. 5, 6. *Arbusculidium filamentosum*, 5: Paisa-1 5030–5040' IIES-PAL-0679; EF: O15/1; 6: Paisa-1 5030–5040' IIES-PAL-0679; EF: M22-1. 7, 8. *Arbusculidium* sp., 7: Paisa-1 5030–5040' IIES-PAL-0679; EF: N49; 8: Paisa-1 5030–5040' IIES-PAL-0679; EF: L34/4. 9, 10. *Barakella felix*, 9: Paisa-1 5030–5040' IIES-PAL-0679; EF: M20; 10: Paisa-1 4980–4990' IIES-PAL-0681; EF: O47/3. 11, 12. *Striatotheca* sp., 11: EF: M20; 10: Paisa-1 4980–4990' IIES-PAL-0681; EF: N37/1; 12: Paisa-1 5030–5040' IIES-PAL-0679; E49/4. 13. *Impluviculus milonii*, EF: M16/4. 14, 15. *Coryphidium bohemicum*, Paisa-1 5030–5040' IIES-PAL-0679; EF: V31/4; 15: Paisa-1 5030–5040' IIES-PAL-0679; EF: V12/3. 16. *Veryhachium lairdii*, Paisa-1 5030–5040' IIES-PAL-0679; EF: O10. Scale bars = 20  $\mu$ m.



assemblage includes several forms whose first appearance datum (FAD) is in the Tremadocian. Additionally, taxa characteristic of the Floian to Dapingian appear. *Arbusculidium*, *Barakella*, *Coryphidium*, *Dactylofusa*, *Striatotheca*, and *Veryhachium* indicate an Early to Middle Ordovician age. *Dactylofusa velifera* appears in the latest Tremadocian in high southern palaeolatitudes and on or adjacent to the western margin of Gondwana, and in the lower Floian F1 on the eastern margin (de la Puente and Rubinstein 2013; Wang et al. 2015; Servais et al. 2018). Similarly, *Striatotheca* has a FAD in the late Tremadocian in southern Gondwana, but is not recorded from lower palaeolatitudes in strata earlier than the early Floian, with a FAD at the base of the Floian in South China (Yan et al. 2011, 2013). On the eastern Gondwana margin *Striatotheca* is known to occur in the middle Floian (F12) (Ottone et al. 1992; Rubinstein and Toro 1999, 2001; Rubinstein et al. 1999; de la Puente and Rubinstein 2013). *Coryphidium bohemicum* and *Arbusculidium filamentosum* have FADs in the lower to middle Floian throughout their biogeographical range (Servais et al. 2018). *Eisenackidium orientalis* is widely distributed in the Floian of the Central Andean Basin and is considered diagnostic of this age in north-western Argentina by de la Puente et al. (2009), with the oldest record in the late Tremadocian of the Pascha-Incamayo region. The FAD of *Barakella felix* is in the early Floian in South China, but outside China it is not described from strata older than the middle Floian (Yan et al. 2017). In north-west Argentina it is known from the 'B. deflexus' graptolite biozone (de la Puente and Rubinstein 2013), which correlates with the middle Floian Stage Slice F12 (Servais et al. 2018).

The absence of taxa that are characteristic of younger intervals, such as *Frankea*, *Arkonina*, *Dicrodiacrodium* and *Orthosphaeridium*, points to an age older than the late Floian (Servais et al. 2018). Accordingly, the acritarch assemblage of the studied interval is probably of middle Floian (F12) age, but this deduction needs to be regarded with caution, since the stratigraphical distributions of the aforementioned taxa range into the Middle Ordovician, and, given the type of samples used in this study, caution has to be taken into consideration.

#### 4.2. Comparison with other South American phytoplankton palynofloras

Several of the observed taxa were also described in the Araracuara Formation in the Serranía de Chiribiquete of Colombia (Théry et al. 1985). *Cymatiogalea cuvillieri*, *Impluviculus milonii* (as *Veryhachium valiente*, Théry et al. 1985, pl. 1, fig. 4), *Acanthodiacrodium* spp., *Polygonium* spp., *Leiosphaeridia* spp., and veryhachiid acritarchs occur in the material from the Araracuara Formation. Several biostratigraphically important taxa, such as *Arbusculidium filamentosum*, *Barakella*, *Coryphidium*, *Dactylofusa velifera*, and *Eisenackidium orientalis*, recovered from the Paisa-1 assemblage were not found, but a different species of *Dactylofusa* (*D. striata*) was recorded in the material from the Serranía de Chiribiquete (Théry et al. 1985). In addition to age differences,

the different depositional environment of the Araracuara Basin (intracratonic shelf, *Cruziana* facies, continental alluvial-fluvial facies), as implied by the facies distribution map (Figure 3), might account for these differences in composition.

The results show similarities between the studied samples with coeval assemblages from the Argentinian Cordillera Oriental. While many forms are known from the Acoite Formation (Floian–Dapingian), a correlation to specific assemblages proves to be rather difficult as palaeoenvironmental differences are evidently causing strong discrepancies. Ottone et al. (1992) describe two acritarch associations, with one appearing in the lower and one in the upper Acoite Formation. The latter includes forms such as *Acanthodiacrodium*, *Adorfia*, *Arbusculidium*, *Cymatiogalea*, *Eisenackidium*, *Micrhystridium*, *Polygonium*, *Striatotheca* and *Veryhachium lairdii*, with *Polygonium* being the dominant taxon. Clear differences in comparison to the Colombian assemblage are observable, including the occurrence of several easily recognisable taxa such as *Veryhachium trispinosum* and *Aureotesta clathrata simplex* (as *Marrocanium simplex*), and the absence of *Coryphidium* and *Dactylofusa*. As the assemblage of the lower Acoite Formation is stated to comprise ca. 50% *Leiosphaeridia* sp., and to include relatively commonly occurring taxa which are not found in the present study (among others, *Cristallinium* and *Vulcanisphaera tuberculata*), the palynoflora is rather dissimilar.

Another study on the Acoite Formation (Aráoz 2009) revealed assemblages with different compositions from those of Ottone et al. (1992). Association ASZ 2 of Aráoz (2009) from the lower Acoite Formation (Floian) consists of *Cymatiogalea*, *Dactylofusa velifera*, *Eisenackidium orientalis*, *Acanthodiacrodium* spp., *Micrhystridium* spp., *Polygonium* spp., and *Vavrdovella (areniga?)*, all described also in the present study, but lacks the important peri-Gondwanan taxa *Arbusculidium*, *Striatotheca* and *Coryphidium*. ASZ 3 from the upper part of the formation (Dapingian) includes (along with *Barakella felix* and *Tectitheca*) other taxa that also occur in this study, among several already known from ASZ 2 (*Micrhystridium* spp., *Polygonium* spp., *Vavrdovella areniga*), but *Dactylofusa velifera* and *Eisenackidium orientalis* are not found there. Therefore, the assemblage described in the present study has a composition which is intermediate between ASZ 2 and 3.

Rather close in similarity to the present acritarch flora is Assemblage 5 of Rubinstein et al. (1999), from the upper part of the formation, which includes many common taxa, such as *Veryhachium lairdii*, *Arbusculidium filamentosum*, *Eisenackidium orientalis*, *Dactylofusa velifera*, *Acanthodiacrodium*, *Barakella*, *Coryphidium*, *Cymatiogalea*, *Polygonium*, and *Striatotheca*. *Cymatiogalea*, *Dactylofusa velifera*, *Eisenackidium orientalis* and *Vavrdovella areniga* are also known from the Floian of the Zanjón Formation of the Sierra de Zapla in north-western Argentina (Rubinstein and de la Puente 2008).

Acritarch assemblages from the Suri Formation in the Famatina region in north-west Argentina (Achab et al. 2006) show a similar composition to the Paisa-1 microflora. They are dominated by *Polygonium*, *Micrhystridium* and



*Leiosphaeridia*, with records of *Arbusculidium filamentosum*, *Striatotheca*, *Vavrdovella*, *Dactylofusa velifera*, and *Acanthodiacrodiium* spp. Marked differences are evident in the presence of taxa characteristic of assemblages from South China, Baltica and Australia in the palynofloras from the Famatina region (i.e. *Ampullula*, *Tongzia*, *Rhopaliophora*, *Peteinosphaeridium*, and *Pachysphaeridium*) (Achab et al. 2006).

#### 4.3. Palaeobiogeography

While, on a global scale, the Cambrian and most of the Upper Ordovician are characterised by a high degree of cosmopolitanism, the Lower Ordovician shows a marked provincialism, with two major distinguishable microfloras, the peri-Gondwanan and the Baltic provinces (Molyneux et al. 2013). This provincialism was probably controlled by several palaeoenvironmental factors, such as water temperature and ocean currents (Playford et al. 1995; Tongiorgi et al. 1995; Molyneux et al. 2013; Servais et al. 2014). Further putative provinces have been recognised in North America and Australia (Playford et al. 1995). Furthermore, a peri-Gondwanan subprovince, in which additional taxa appear that have Baltic and Australian affinities, is known from South China (Tongiorgi et al. 1995, 2003; Molyneux et al. 2013), which was located in northern Gondwana at equatorial palaeolatitudes. Similarly, microfloras of north-west Argentina are known to contain forms which are more characteristic of Baltica and South China than of peri-Gondwana, such as *Ampullula?* sp. and *Liliosphaeridium intermedium* in material of probably Darriwilian age from the Sierras Subandinas (Rubinstein et al. 2011), or *Ampullula*, *Ammonidium* sp. cf. *A. [Sacculidium] anduncum* in the Dapingian of the Famatina region (Achab et al. 2006). While the data coverage of peri-Gondwana is in many parts very good, with most studies based on material from Europe, North Africa and the Avalonian part of North America, many other regions have not yet been sufficiently investigated. Therefore, the complete extent of the distribution of the different acritarch provinces is yet unknown, particularly in the case of the eastern margin of Gondwana, where data are restricted to north-west Argentina (Rubinstein 1997; Rubinstein et al. 1999, 2003, 2011; Achab et al. 2006; de la Puente and Rubinstein 2009). One purpose of this study is to determine the palaeobiogeographical affinities of the Colombian Lower Ordovician microfloras. Thus, it aims to contribute to the knowledge of the composition and distribution of peri-Gondwanan palynofloras, helping to complete information on the palaeogeographical spread of certain acritarch taxa, and provinces, which in turn will allow us to reassess the palaeogeographical information about this region (e.g. palaeolatitudes, palaeocurrents, temperature gradients) in the early Palaeozoic. Indeed, the palaeogeographical evolution of the northern part of the Andes (Ecuador, Colombia, and Venezuela) is poorly known, as available information is very limited (Benedetto et al. 2009).

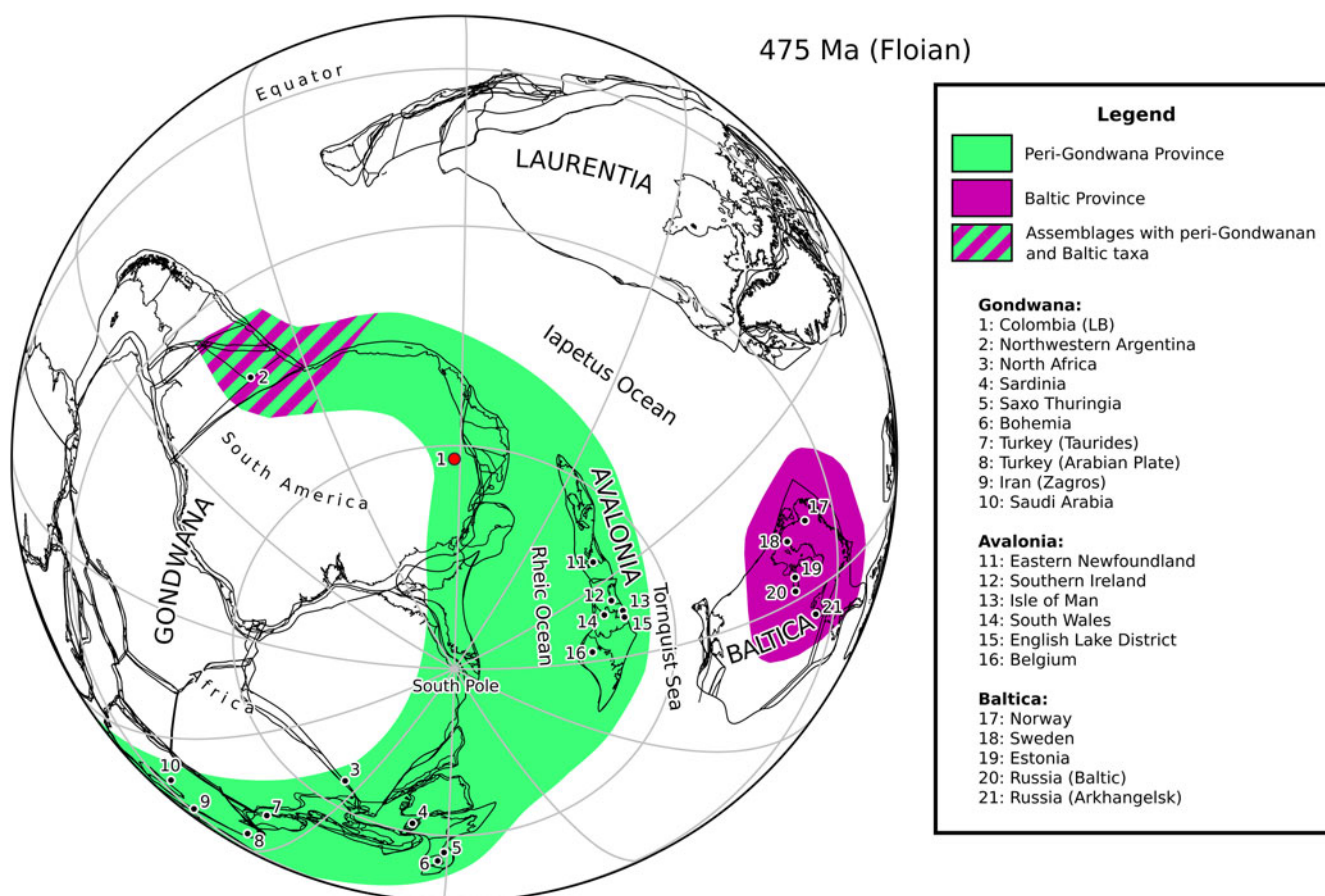
On the basis of the composition of the recognised acritarch assemblage, some palaeobiogeographical inferences can be proposed. According to the definition of Li (1989),

three acritarch taxa appear exclusively in the peri-Gondwanan province, and therefore are considered diagnostic: *Arbusculidium*, *Coryphidium* and *Striatotheca*. With all of these genera present, the Colombian assemblage clearly has a peri-Gondwanan affinity. Likewise, occurrences of the genus *Barakella* are restricted to the peri-Gondwana margin, except for a doubtful record from Öland, Sweden (Ribecai and Tongiorgi 1995; also see Yan et al. 2017). Additional taxa that are considered to be characteristic of this province, such as *Vavrdovella* (Tongiorgi and Di Milia 1999; Li and Servais 2002), also occur. These taxa are found more commonly in higher latitudes, thus possibly indicating a cold-water environment. Furthermore, the high number of diacromorph taxa indicates an affinity with this province. Although diacromorph forms appear in lower latitude areas such as Baltica, they show higher abundances at higher latitudes (Li and Servais 2002). Thus, the results allow the extension of the geographical distribution of the peri-Gondwanan Province to the north-western part of South America, augmenting the palaeobiogeographical distribution map of Early–Middle Ordovician acritarchs by Molyneux et al. (2013) (Figure 5).

As mentioned before, a peri-Gondwanan affinity of the acritarch assemblages from north-west Argentina is evident; however, as several forms occur which are typical of South China, Baltica and Australia, this region is interpreted to have been located in intermediate latitudes during the Early Ordovician (Achab et al. 2006) (see Figure 5). In contrast to the acritarch association recovered from the Colombian material, the microfloras of the Famatina region show a high number of acanthomorphs, such as *Baltisphaeridium* and *Peteinosphaeridium*, and occurrences of *Ampullula*, *Rhopaliophora* and *Tongzia*, which indicate a stronger relationship with temperate-water assemblages (Achab et al. 2006). *Rhopaliophora* can be found at high latitudes, but is more common at low latitudes (Li and Servais 2002). However, palaeoenvironmental changes throughout the succession in the Famatina assemblages must be taken into account. Indeed, the highest numbers of *Baltisphaeridium*, *Peteinosphaeridium* and *Rhopaliophora* are found in one sample (7036) in the lower Molles Formation, and can be related to a deeper-water interval with a greater distance to the shoreline (see Section 4.4: Palaeoenvironmental implications). As stated before, the assemblages found in the Lower Ordovician of the Famatina region resemble the microflora of the Paisa-1 material quite strongly, but include the temperate-water elements *Tongzia* and *Ampullula*. These differences are probably caused by different palaeoenvironmental conditions, such as temperature and salinity, possibly related to different latitudinal positions of the palaeohabitats (Figure 5).

#### 4.4. Palaeoenvironmental implications

Unrestored facies distribution maps for the Lower Palaeozoic of north-western South America are provided by Cediel et al. (2011) and Cediel (2019) (Figure 3). As mentioned before, the recovered assemblage includes many forms, such as *Arbusculidium filamentosum*, *Coryphidium*, *Striatotheca*, *Vavrdovella*,



**Figure 5.** Lower Ordovician (Floian, 475 Ma) palaeogeographical reconstruction (orthographic projection) showing the distribution of the Lower Ordovician phytoplankton palaeobioprovinces in accordance with the plotted study locality (in red) and selected acritarch localities (from Molyneux et al. 2013). Reconstruction based on the PALAEOMAP project (Scotese 2016), using the software GPlates (Boyden et al. 2011). See also Servais et al. (2003, figs 1, 2).

and abundant diacromorph taxa, that are known to be more common at higher latitudes, possibly preferring cold-water environments. Furthermore, a comparison of the composition of the observed microflora with palaeoenvironmental studies on acritarch assemblages provides useful information about the depositional environment of the studied sediments. Several works concern variations of diversity and composition of lower Palaeozoic acritarch associations in different palaeoenvironments and provide models for palaeoenvironmental interpretations (e.g. Staplin 1961; Smith and Saunders 1970; Jacobson 1979; Dorning 1981; Al-Ameri 1983; Wicander and Wood 1997; Vecoli 2000, 2004; Tongiorgi et al. 2003; Li et al. 2004; Stricanne et al. 2004; Molyneux 2009; Lei et al. 2012; Yan et al. 2013). For the Middle and Upper Ordovician of the American Midcontinent, Jacobson (1979) described three different 'classes' of acritarch taxa, each attributed to a distinct palaeoenvironment. The 'leiosphaerid class' represents a nearshore shallow-water habitat, the 'peteinospaerid-*Dicommopalla* class' is characteristic of a shoal environment, and the 'baltisphaerid-veryhachid-*Polygonium*-michrystridid class' represents an open-sea environment. Dorning (1981) and Dorning and Bell (1981) discuss different assemblages from the Wenlock and Ludlow of Wales and the Welsh Borderland. According to their findings, a low-diversity association with genera of the 'leiosphaerid class' reflects a near-shore assemblage,

higher diversities without dominant species are found on an offshore shelf, and lower diversities in a deep-water, open-marine setting. In a study on Cambrian–Ordovician strata from the northern Sahara Platform in Algeria, Vecoli (2000) attributes assemblages of the high-abundance, high-diversity 'diacromorphitae-herkomorphitae-acanthomorphitae class' to an open-marine environment, while the high-abundance, low-diversity 'leiosphaerid-Netromorphitae, *Veryhachium*' and '*Polygonium*-*Michrystridium* classes' represent a nearshore, shallow-marine environment. The assemblage observed in the studied interval of the Paisa-1 well might be an intermediate association with elements of both the 'diacromorphitae-herkomorphitae-acanthomorphitae' class and the '*Polygonium*-*Michrystridium* class', as polygonomorph forms of the latter and diacromorph forms of the former are very abundant, while herkomorphs and acanthomorphs are much less common. Accordingly, the studied material was probably deposited in an environment with relatively shallow water but not nearshore conditions, which is also indicated by the rarity of forms of the 'leiosphaerid-Netromorphitae' class.

Probably the best model to apply to the results of the present study is provided by the works of Li et al. (2004) and Yan et al. (2013), since they are based on the Floian to Dapingian and therefore can be considered contemporaneous. However, it should be taken into consideration that

these studies are concerned with a different palaeogeographical area (lower latitudes of South China) which is known to have acritarch associations with mixed peri-Gondwanan and Baltic affinities (Li and Servais 2002; Li et al. 2004; Molyneux et al. 2013). Li et al. (2004) observed, in a shallow- to deep-water transect of the Yangtze Platform in South China, differences in the composition and distribution of acritarch assemblages. Polygonomorphs dominate the assemblages, except in the outer shelf environment. A high abundance of *Leiofusa* is evident in nearshore environments, while the group appears to be almost absent in other parts of the platform. Micrhystrid forms occur more abundantly closer to the palaeoshoreline. Diacromorphs and leiosphaerids appear in all localities throughout the described transect, but are more common in nearshore areas. Baltisphaerid and peteinoid acritarchs show low abundances in nearshore environments, with the peteinoids not observed close to the palaeoshoreline but occurring very abundantly in the outer shelf area. Based on the data of Li et al. (2004), Yan et al. (2013) recognise four acritarch associations reflecting different palaeoenvironments in the Floian to Dapingian of the Yangtze Platform in South China. The first assemblage shows a low diversity and is dominated by *Polygonium*, *Micrhystridium* and *Coryphidium*; it is attributed to a nearshore environment. Within this assemblage, they interpret a higher relative abundance of *Leiofusa* as reflecting a closer proximity to the shore. The second association is dominated by *Polygonium*, *Leiosphaeridia*, *Coryphidium*, and *Cymatiogalea* and shows a moderate diversity. It is recorded mainly from localities belonging to an inner-shelf environment, but appears also in one location (Ningqiang) attributed to a nearshore environment, and another location assigned to the outer shelf (Jishou). It is noteworthy that a sub-assemblage ('Association B') was recognised in four localities (Tongzi, Guiyang, Ningqiang, Jishou), which is described as dominated by *Polygonium*, *Striatotheca*, *Coryphidium*, and *Cymatiogalea*. The third assemblage represents a typical outer-shelf environment and is dominated by *Baltisphaeridium* and *Peteinosphaeridium* with high diversities. An offshore slope environment is reflected in the fourth association, dominated by *Leiosphaeridia* and *Baltisphaeridium*, with rather low diversity. Given these observations from South China, the results of the present study from Colombia show great similarities to the first and second assemblages, especially when compared with the sub-assemblage 'Association B'. Polygonomorph taxa are dominant, and *Polygonium* and *Micrhystridium* are found abundantly, while *Coryphidium*, *Striatotheca* and *Cymatiogalea* also occur frequently. Likewise, the rarity of baltisphaerid and peteinoid acritarchs is an indicator for this depositional environment. In fact, only one specimen of a peteinoid form with bad preservation was observed. Also, the high number of diacromorph forms indicates a relatively shallow palaeoenvironment. However, as fusiform acritarchs are relatively rare, the location was probably not very close to the shoreline. Therefore, the depositional environment was presumably a shallow-marine inner-shelf area. This is consistent with the facies distribution maps of Cediel et al. (2011) and Cediel (2019), in which the area of the Paisa-1 well is assigned to a

shallow-marine clastic environment (Figure 3), indicating a strong terrestrial input and proximity to the palaeocoastline. Although the location is very close to an intertidal coastal swamp facies, this does not necessarily indicate a close proximity to the palaeoshoreline, as the map does not represent a palaeogeographical reconstruction but shows the unrestored distribution of the different facies.

## 5. Conclusions

1. The palynological analysis of Lower Palaeozoic sediments from the Paisa-1 well in the Llanos Orientales Basin reveals a diverse and abundant acritarch flora that allows a precise dating of the studied interval. Several easily recognisable taxa have been found which are characteristic of the Lower and Middle Ordovician, e.g. *Arbusculidium filamentosum*, *Barakella*, *Coryphidium bohemicum*, *Dactylofusa velifera*, *Striatotheca*, and *Veryhachium*. Considering the FADs of these genera and species, as well as the absence of typical taxa of younger strata, such as *Frankea*, *Arkonina* and *Orthosphaeridium*, the studied material is probably of middle Floian age.
2. The studied palynoflora contains taxa which are characteristic of the peri-Gondwanan acritarch province, including all three diagnostic taxa, *Arbusculidium*, *Coryphidium* and *Striatotheca*. Other typical taxa for this province appear, such as *Vavrdovella* and *Dactylofusa velifera*, as well as a high number of diacromorph forms. Therefore, the results of this study provide new data of the South American margin of Gondwana, permitting to expand the peri-Gondwanan acritarch province into this area.
3. The observed acritarch assemblage shows similarities to coeval associations from north-west Argentina, but differs in the absence of forms characteristic of temperate-water assemblages. This implies a colder-water depositional environment in higher latitudes for the Lower Ordovician sediments of Colombia.
4. The composition of the microflora recovered from the Lower Palaeozoic suggests some palaeoenvironmental implications. Comparisons with acritarch assemblage distributions and compositions in known depositional environments indicate a relatively shallow-marine, probably inner-shelf environment.

## Acknowledgements

We acknowledge the Ecole Doctorale ED 104 (Sciences de la Matière, du Rayonnement et de l'Environnement), Université de Lille, for financial support. This work is a contribution to the CPER research project CLIMBIO (we acknowledge the French Ministry for Higher Education and Research, the Hauts de France Region and the European Funds for Regional Economic Development for their financial support for this project). We thank the Pluspetrol company for kindly allowing the use of the palynological data. The Instituto de Investigaciones en Estratigrafía – IIES (Universidad de Caldas, Colombia) gave important logistic support. This is a contribution to IGCP 653 'The onset of the Great Ordovician Biodiversification Event'.



## Notes on contributors



**DAVID M. KROECK** received his MSc in earth sciences in 2016 from the University of Bonn, Germany. Since 2016 he is a PhD student at the Evo-Eco-Paléo unit of the University of Lille working on the biodiversity, palaeoecology, palaeogeography and biostratigraphy of the phytoplankton, mainly acritarchs, of the Palaeozoic.



**ANDRÉS PARDO-TRUJILLO** is a Geologist of the Department of Geological Sciences of the University of Caldas (Manizales, 1998). Andres obtained his M.Sc. in Vegetal micropalaeontology at 1997 and his PhD in Science at Liège University (Belgium, 2004). He has worked as a professor in the department of Geological Sciences at Universidad de Caldas (Colombia) since 1989. During 2006–2009 he

worked as an advisor to the National Hydrocarbons Agency, where participated in the geological study of several Colombian sedimentary basins. Andres is currently director of the Instituto de Investigaciones en Estratigrafía-IIES and of the Research Group in Stratigraphy and Vulcanology-GIEV Cumanday at the Universidad de Caldas.



**ANGELO PLATA TORRES** obtained his bachelor's degree in biology from the Universidad Industrial del Santander, Colombia in 2007. Angelo worked at the Colombian oil company ECOPEPETROL for 5 years as a junior biostratigrapher before going to the Spain in 2012 to obtain his Master of Earth Science degree from the Department of Geology, Salamanca University. At coming back of Salamanca University,

he works as palynologist in chief of the Palynology Lab for Instituto de Investigaciones en Estratigrafía (IIES), Universidad de Caldas, where research about terrestrial palynomorphs and marine diatoms. Currently, Angelo is candidate to PhD in Salamanca University.



**MILLERLANDY ROMERO-BAÉZ** is a biologist with a Master of Science from Rice University in Houston. With 10+ years of experience in oil & gas and environmental research, her primary focus has been palaeoecology/ecology, environmental science, and sustainable development and design. Her career started as a junior biostratigrapher in Ecopetrol, the Colombia national oil company, followed by a more

senior career as a palynologist and palaeoecologist intern at Smithsonian Tropical Research Institute. She also consulted for energy production companies, government petroleum agencies, and research groups around the world. Currently, she is applying her prior experience as an environmental researcher to provide advice on sustainability topics related to the use of natural resources in a highly competitive business environment. She is an avid advocate of low carbon and circular economy in a society with a growing demand for energy, water, food, and human well-being.



**THOMAS SERVAIS** is a research director at the French Centre of Scientific Research (CNRS). He was trained as a geologist at the universities of Namur and Liège in Belgium, and received a PhD on Ordovician acritarchs in 1993. After postdoctoral studies in Belgium, Germany and the United Kingdom, Thomas was recruited as a CNRS research associate at the University of Lille in 1997. His

research is focused on Lower Palaeozoic microphytoplankton. Thomas is currently vice-chairman of the International Subcommittee of Ordovician Stratigraphy (ISOS) and co-leader of the International Geoscience Programme (IGCP) 653 'The onset of the Great Ordovician Biodiversification Event' (2016–2020).

## References

- Achab A, Rubinstein CV, Astini RA. 2006. Chitinozoans and acritarchs from the Ordovician peri-Gondwana volcanic arc of the Famatina System, northwestern Argentina. *Review of Palaeobotany and Palynology*. 139(1–4):129–149.
- Al-Ameri TK. 1983. Acid-resistant microfossils used in the determination of Palaeozoic palaeoenvironments in Libya. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 44:103–116.
- Amante C., Eakins BW. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. doi:10.7289/V5C8276M
- Aráoz L. 2009. Microfloras ordovícicas en Sierra de Zenta, Cordillera Oriental Argentina [Ordovician microfloras of the Sierra de Zenta, Cordillera Oriental Argentina]. *Serie Correlación Geológica*. 25:37–94. Spanish with English abstract.
- Aminio JF, Yoris F, Quijada C, Lugo JM, Shaw D, Keegan JB, Marshall JEA. 2013. Evidence for Precambrian stratigraphy in graben basins below the Eastern Llanos Foreland, Colombia. *AAPG Search and Discovery*. 50874:1–35.
- Baldís BA. 1988. Posibilidades de correlación del Ordovícico de los llanos colombianos y la alta Amazonia brasileño-ecuatoriana [Possibilities of correlation of the Ordovician of the Colombian plains and the Brazilian-Ecuadorian highland]. *Proceedings of the 7th Congreso Latino-Americano de Geología*; nov 6–13; Belém, Brasil. São Paulo: Sociedade Brasileira de Geologia – SBG; Brasília: Departamento Nacional da Produção Mineral – DNPM; p. 500–506. Spanish.
- Baldís BA, González SB, Pérez VE. 1985. Trilobites tremadocianos de la Formación Negritos (Perforación “La Heliera”), Llanos de Colombia [Tremadocian trilobites of the Negritos Formation (well “La Heliera”), Llanos of Colombia]. In: Perrilliat C, editor. *Proceedings of the 3rd Congreso Latinoamericano de Paleontología Mexico*; Oct 16 1984; Oaxtepec, Mexico. Mexico City: Universidad Nacional Autónoma de México - Instituto Nacional de Geología; p. 28–41. Spanish.
- Barrera D, Pardo A, Vargas CA, Martínez JF. 2007. Colombian Sedimentary Basins: Nomenclature, boundaries and petroleum geology, a new proposal. Bogotá: Agencia Nacional de Hidrocarburos (ANH).
- Benedetto JL, Vaccari NE, Waisfeld BG, Sánchez TM, Foglia RD. 2009. Cambrian and Ordovician biogeography of the South American margin of Gondwana and accreted terranes. *Geological Society, London, Special Publications*. 325(1):201–232.
- Borrero C, Sarmiento GN, Gómez-González C, Gutiérrez-Marco JC. 2007. Los conodontos de la Formación el Hídalo y su contribución al conocimiento del metamorfismo y la paleogeografía del Ordovícico en la Cordillera Central Colombiana [The Conodonts from the El Hídalo Formation and its contribution to the knowledge of metamorphism and Ordovician paleogeography in the Central Cordillera of Colombia]. *Boletín de Geología*. 29(2):39–46. Spanish with English abstract.
- Botero-Arango G. 1940. Geología sobre el Ordoviciano de Antioquia. *Revista de Minería (Oragnio de la Asociación Colombiana de Mineros)*. 17(99):8249–8256.
- Boyden JA, Müller RD, Gurnis M, Torsvik TH, Clark JA, Turner M, Ivey-Law H, Watson RJ, Cannon JS. 2011. Next-generation plate-tectonic reconstructions using Gplates. In: Keller GR, Baru C, editors. *Geoinformatics: Cyberinfrastructure for the Solid Earth*. Cambridge: Cambridge University Press; p. 95–114.
- Campos H, Mann P. 2012. Tectonic and subsidence history of the Llanos foreland basin of Colombia. *Proceedings of the 11th Simposio Bolivariano - Exploracion Petrolera en las Cuencas Subandinas*; Jul 29–Aug 1; Cartagena, Colombia. Bogotá: ACGGP.
- Cediel F. 2019. Phanerozoic Orogens of Northwestern South America: Cordilleran-Type Orogens. *Taphrogenic Tectonics. The Maracaibo Orogenic Float. The Chocó-Panamá Indenter*. In: Cediel F, Shaw RP, editors. *Geology and Tectonics of Northwestern South America: The Pacific-Caribbean-Andean Junction*. Cham: Springer Nature Switzerland AG (Frontiers in Earth Sciences); p. 3–96.

- Cediel F, Leal-Mejía H, Shaw RP, Melgarejo JC, Restrepo-Pace PA. 2011. Regional Geology of Colombia. In: Cediel F, Ojeda GY, Colmenares F, editors. *Petroleum Geology of Colombia - Geology and Hydrocarbon Potential*. Vol. 1. Medellín: Fondo Editorial, University Eafit; p. 1–223.
- Cuartas C, Jaramillo C, Arjona A, da Silva S. 2008. Informe Final del Inventario y Evaluación de la Información Micropaleontológica en las Cuencas Sedimentarias de Colombia (caso palinología) [Final Report of the inventory and evaluation of micropalaeontological information in the sedimentary basins of Colombia (case palynology)]. Panama City: Smithsonian Tropical Research Institute (STRI); p. 140. Spanish.
- de la Puente GS, Rubinstein CV. 2009. Late Tremadocian chitinozoans and acritarchs from northwestern Argentina (Western Gondwana). *Review of Palaeobotany and Palynology*. 154(1–4):65–78.
- de la Puente GS, Rubinstein CV. 2013. Ordovician chitinozoans and marine phytoplankton of the Central Andean Basin, northwestern Argentina: a biostratigraphic and palaeobiogeographic approach. *Review of Palaeobotany and Palynology*. 198:14–26.
- de la Puente GS, Rubinstein CV, Toro BB. 2009. Nuevos registros de quitinozoos, acritarcos y graptolitos del área de Pascha-Incamayo, Cordillera Oriental, Argentina [New records of chitinozoans, acritarchs and graptolites from the Pascha-Incamayo area, Cordillera Oriental, Argentina] [abstract]. XIV Simposio Argentino de Paleobotánica y Palinología; Dec 6–9; Mar del Plata, Argentina. Spanish.
- Dorning KJ. 1981. Silurian acritarch distribution in the Ludlovian Shelf Sea of South Wales and the Welsh Borderland. In: Neale RG, Brasier MD, editors. *Microfossils from Recent and Fossil Shelf Seas*. Chichester: Ellis Horwood; p. 31–36.
- Dorning KJ, Bell DG. 1981. The Silurian carbonate shelf microflora: acritarch distribution in the Much Wenlock Limestone Formation. In: Hart MB, editor. *Micropalaeontology of Carbonate Environments*. Chichester: Ellis Horwood; p. 266–287.
- Dueñas H. 2002. Paleozoic palynological assemblages from the Colombian Llanos Basin [abstract]. *Proceedings of the AASP 34th Annual Meeting 2001*; Oct 21–24; Vol. 26; San Antonio, (TX): Palynology. p. 264.
- Dueñas H, Césari S. 2005. Systematic study of Early Carboniferous palynological assemblages from the Llanos Orientales Basin, Colombia. *Revista Del Museo Argentino de Ciencias Naturales*. 7(2): 139–152.
- Dueñas H, Césari S. 2006. Palynological evidence of Early Carboniferous sedimentation in the Llanos Orientales Basin, Colombia. *Review of Palaeobotany and Palynology*. 138(1):31–42.
- Ecopetrol. 1995. Cuenca de los Llanos Orientales, Estudio geológico regional [Llanos Orientales Basin, geological study]. Santafé de Bogotá, Vol. 1–2. Paris: Beicip-Franlab (special publication for Ecopetrol). Spanish.
- Gómez Tapias J, Montes Ramírez N, Almanza Meléndez M, Alcárcel Gutiérrez F, Madrid Montoya C, Diederix H. 2017. Geological Map of Colombia 2015. *Episodes*. 40(3):201–212.
- Grösser JR, Prössl KF. 1991. First evidence of the Silurian in Colombia: Palynostratigraphic data from the Quetame Massif, Cordillera Oriental. *Journal of South America Earth Sciences*. 4(3):231–238.
- Gutiérrez-Marco JC, Sarmiento GN, Gómez-González C. 2007. First Ordovician conodonts from Colombia. *Acta Paleontologica Sinica*. 6: 170–175.
- Harrington HL, Kay M. 1951. Cambrian and Ordovician faunas of the eastern Colombia. *Journal of Paleontology*. 25(5):655–668.
- Harrison JV. 1930. The Magdalena Valley, Colombia, South America. *Proceedings of the 15th International Geological Congress*; Jul 29–Aug 7, 1929; Pretoria; Vol. 2. p. 399–409.
- Hermoza W, Zamora G, Macellari C, Tocco R. 2011. Paleozoic deformation and its hydrocarbon potential in the northern Andean Foreland Basin. *Proceedings of the 7th International Seminar on Oil and Gas Exploration and Production (INGEPET)*; Nov 7–11; Lima, Peru. Lima: Perúpetro S.A. p. 1–11.
- Jacobson SR. 1979. Acritarchs as palaeoenvironmental indicators in Middle and Upper Ordovician Rocks from Kentucky, Ohio and New York. *Journal of Paleontology*. 53(5):1197–1212.
- Jaramillo C, Rueda M, Torres V. 2011. A palynological zonation for the Cenozoic of the Llanos and Llanos foothills of Colombia. *Palynology*. 35(1):46–84.
- Leith E. 1938. A Middle Ordovician fauna from the Venezuelan Andes. *American Journal of Science*. 36(215):337–334. (5th series)
- Lei Y, Servais T, Feng Q, He W. 2012. The spatial (nearshore-offshore) distribution of latest Permian phytoplankton from the Yangtze Block, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 363–364:151–162.
- Li J. 1989. Early Ordovician Mediterranean province acritarchs from Upper Yangtze Region, China. In: Sun S, editor. *Developments in Geoscience: Contribution to the 28th Geological Congress, 1989*; July 9–19; Washington (DC). Beijing: Science Press. p. 231–234.
- Li J, Servais T. 2002. Ordovician acritarchs of China and their utility for global palaeobiogeography. *Bulletin de la Société Géologique de France*. 173(5):399–406.
- Li J, Servais T, Yan K, Zhu H. 2004. A nearshore-offshore trend in acritarch distribution from the Early-Middle Ordovician of the Yangtze Platform, South China. *Review of Palaeobotany and Palynology*. 130(1–4):141–161.
- Malone JR, Nance RD, Keppie JD, Dostal J. 2002. Deformational history of part of the Acatlán Complex: Late Ordovician–Early Silurian and Early Permian orogenesis in southern Mexico. *Journal of South American Earth Sciences*. 15(5):511–524.
- McCollough CN, Carver JA. 1992. The Giant Caño Limon Field, Llanos Basin, Colombia. In: Halbouty MT, editor. *Giant Oil and Gas Fields of the Decade 1978–1988*. Tulsa (OK): American Association of Petroleum Geologists (AAPG Memoir; Vol. 54); p. 175–195.
- Molyneux SG. 2009. Acritarch (marine microphytoplankton) diversity in an Early Ordovician deep-water setting (the Skiddaw Group, northern England): implications for the relationship between sea-level change and phytoplankton diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 275(1–4):59–76.
- Molyneux SG, Delabroye A, Wicander R, Servais T. 2013. Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton. In: Harper DAT, Servais T, editors. *Early Palaeozoic Biogeography and Palaeogeography*. London: Geological Society of London (Memoirs 38); p. 365–397.
- Moreno-López MC, Escalona A. 2015. Precambrian–Pleistocene tectonostratigraphic evolution of the southern Llanos basin, Colombia. *AAPG Bulletin*. 99(08):1473–1501.
- Moreno-Sánchez M, Gómez A, Castillo H. 2008. Graptolitos del Ordovícico y geología de los afloramientos del río Venado (norte del departamento del Huila) [Early Ordovician graptolite and geology of the outcrops of Venado River (Huila region)]. *Boletín de Geología UIS*. 30(1):9–19. Spanish with English abstract.
- Ottone EG, Toro BA, Waisfeld BG. 1992. Lower Ordovician palynomorphs from the Acoite Formation, northwestern Argentina. *Palynology*. 16(1):93–116.
- Playford G, Ribecai C, Tongiorgi M. 1995. Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cyclospheeridium*: morphology, taxonomy, biostratigraphy, and palaeogeographic significance. *Bollettino Della Società Paleontologica Italiana*. 34:3–54.
- QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Ribecai C, Tongiorgi M. 1995. Arenigian acritarchs from Horns Udde (Öland, Sweden): a preliminary report. *Review of Palaeobotany and Palynology*. 86(1–2):1–11.
- Rubinstein CV. 1997. Tremadocian acritarchs from northwestern Argentina. *Review of Palaeobotany and Palynology*. 98(1–2):41–45.
- Rubinstein CV, de la Puente GS. 2008. Bioestratigrafía del Paleozoico inferior en las Sierras Subandinas, Provincia de Jujuy [Lower Palaeozoic Biostratigraphy of the Subandean Sierras, Jujuy Province]. In: Coira BL, Zappettini, EO, editors. *Geología y Recursos Naturales de la provincia de Jujuy: relatorio: XVII Congreso Geológico: 7 al 10 de octubre de 2008, San Salvador de Jujuy*. Buenos Aires: Asociación Geológica Argentina; p. 128–133.
- Rubinstein CV, Toro BA. 1999. Acritarch and graptolite biostratigraphy in the lower Arenig of the peri-Gondwana relates Eastern Cordillera, Argentina. *Acta Universitatis Carolinae, Geologica*. 43(1/2):255–258.

- Rubinstein CV, Toro BA. 2001. Review of acritarch biostratigraphy in the Arenig of Eastern Cordillera, northwestern Argentina. New data and calibration with the graptolite zonation. In: Weiss RH, editor. Contributions to Geology and Palaeontology of Gondwana – In Honour of Helmut Wopfner. Cologne: Geological Institute, University of Cologne; p. 421–439.
- Rubinstein CV, Toro B, Waisfeld Conicet B. 1999. Acritarch biostratigraphy of the upper Tremadoc-Arenig of the Eastern Cordillera, northwestern Argentina: relationships with graptolite and trilobite faunas. *Bollettino Della Società Paleontologica Italiana*. 38(2–3):267–286.
- Rubinstein CV, Mángano MG, Buatois LA. 2003. Late Cambrian acritarchs from the Santa Rosita Formation: Implications for the Cambrian-Ordovician Boundary in the Eastern Cordillera, northwest Argentina. *Revista Brasileira de Paleontologia*. 6:43–48.
- Rubinstein CV, Vecoli M, Astini RA. 2011. Biostratigraphy and palaeoenvironmental characterization of the Middle Ordovician from the Sierras Subandinas (NW Argentina) based on organic-walled microfossils and sequence stratigraphy. *Journal of South American Earth Sciences*. 31(1):124–138.
- Ruiz J, Tosdal RM, Restrepo PA, Murillo-Muñetón G. 1999. Pb isotope evidence for Colombia-southern Mexico connections in the Proterozoic. In: Ramos VA, Keppie JD, editors. Laurentia-Gondwana connections before Pangea. Boulder (CO): Geological Society of America (Special Papers 336):183–197.
- Sarmiento LF. 2011. Llanos Basin. In: Cediell F, Ojeda GY, Colmenares F, editors. Petroleum Geology of Colombia - Geology and Hydrocarbon Potential. Vol. 9. Medellin: Fondo Editorial, University Eafit; p. 1–174.
- Scotese CR. 2016. PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project [accessed 2019 Jan 25]. <http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/>
- Servais T, Danelian T, Harper DAT, Munnecke A. 2014. Possible ocean circulation patterns, surface water currents and upwelling zones in the Early Palaeozoic. *GFF*. 136(1):229–223.
- Servais T, Molyneux SG, Li J, Nowak H, Rubinstein CV, Vecoli M, Wang WH, Yan K. 2018. First Appearance Datums (FADs) of selected acritarch taxa and correlation between Lower and Middle Ordovician stages. *Lethaia*. 51:1–26.
- Smith ND, Saunders RS. 1970. Palaeoenvironments and their control of acritarch distribution: Silurian of east-central Pennsylvania. *Journal of Sedimentary Petrology*. 40:324–333.
- Staplin FL. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*. 4:392–424.
- Stricanne L, Munnecke A, Pross J, Servais T. 2004. Acritarch distribution along an inshore-offshore transect in the Gorstian (lower Ludlow) of Gotland. *Review of Palaeobotany and Palynology*. 130(1–4):195–216.
- Théry JM, Peniguel T, Haye G. 1985. Descubrimiento de acritarcos del Arenigiano cerca a Araracuara (Caquetá, Colombia). Ensayo de interpretación de esta región de la saliente del Vaupés [Discovery of Arenigian acritarchs near Araracuara (Caquetá, Colombia). Interpretation Attempt for the Saliente Del Vaupés Region]. *Geología Norandina*. 9:3–17.
- Tongiorgi M, Di Milia A. 1999. Differentiation and spread of the Baltic acritarch province (Arenig–Llanvirn). *Bollettino Della Società Paleontologica Italiana*. 38:297–312.
- Tongiorgi M, Yin L-M, Di Milia A. 1995. Arenigian acritarchs from the Daping section (Yangtze Gorges area, Hubei Province, Southern China) and their palaeogeographical significance. *Review of Palaeobotany and Palynology*. 86(1–2):13–48.
- Tongiorgi M, Yin L-M, Di Milia A. 2003. Lower Yushanian to lower Zhejiangian palynology of the Yangtze Gorges area (Daping and Huanghuachang sections), Hubei Province, South China. *Palaeontographica Abteilm. B*. 266:1–160.
- Trumpy D. 1943. Pre-Cretaceous of Colombia. *Geological Society of America Bulletin*. 54:1261–1304.
- Ulloa C, Pérez VE, Baldis B. 1982. Unidades litoestratigráficas del Ordovícico de los Llanos Orientales de Colombia [Lithostratigraphic units of the Ordovician of the Llanos Orientales of Colombia]. Proceedings of the 5th Congreso Latinoamericano de Geología; Oct 17–22; Buenos Aires, Argentina. Buenos Aires, Servicio Geológico Nacional, Subsecretaría de Minería. Spanish.
- Vayssaire A, Abdallah H, Hermoza W, Figari Negri EG. 2014. Regional Study and Petroleum System Modeling of the Eastern Llanos Basin. *AAPG Search and Discovery*. 10564:1–9.
- Vecoli M. 2000. Palaeoenvironmental interpretation of microphytoplankton diversity trends in the Cambrian–Ordovician of the northern Sahara Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 160:329–346.
- Vecoli M. 2004. Stratigraphic and palaeoenvironmental distribution of organic-walled microfossils in Cambrian–Ordovician transitional strata of borehole Bir Ben Tartar-1 (Tt-1; Ghadamis Basin, southern Tunisia). *Memoir of the Association of Australasian Palaeontologists*. 29:13–30.
- Villegas ME, Bachu S, Ramon JC, Underschultz JR. 1994. Flow of formation waters in the Cretaceous–Miocene succession of the Llanos Basin, Colombia. *AAPG Bulletin*. 78(12):1843–1862.
- Wang W, Servais T, Yan K, Vecoli M, Li J. 2015. The Ordovician acritarch *Dactylofusa velifera* Cocchio 1982: a biostratigraphical and palaeogeographical index species. *Palynology*. 39(1):125–141.
- Wicander R, Wood GD. 1997. The use of microphytoplankton and chitinozoans for interpreting transgressive/regressive cycles in the Rapid Member of the Cedar Valley Formation (Middle Devonian), Iowa. *Review of Palaeobotany and Palynology*. 98(1–2):125–152.
- Yan K, Servais T, Li J, Wu R, Tang P. 2011. Biodiversity patterns of Early–Middle Ordovician marine phytoplankton in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 299(1–2):318–334.
- Yan K, Li J, Servais T. 2013. An Early–Middle Ordovician acritarch and prasinophyte assemblage from Houping, Chongqing city, South China: Biostratigraphical and palaeoenvironmental implications. *Review of Palaeobotany and Palynology*. 198:110–133.
- Yan K, Li J, Molyneux SG, Raevskaya EG, Servais T. 2017. A review of the Ordovician acritarch genus *Barakella* Cramer & Díez 1977. *Palynology*. 41(51):80–94.

## Appendix 1

- List of palynomorph taxa mentioned in the text.
- All palynomorphs mentioned in the text and in the plate captions are listed below alphabetically by genus and species.
- Acanthodiacrodium* Timofeev 1958 emend. Deflandre et al. 1962
- Acanthodiacrodium* spp.
- Adorfia* Burmann 1970
- Adorfia* cf. *hoffmanensis* (Cramer et al. 1974) Ottone 1982
- Ammonidium* sp. cf. *A. [Sacculidium] anduncum* Playford & Martin 1984 [Ribecai et al. 2002]
- Ampullula* Righi 1991 emend. Brocke 1997
- Ampullula?* sp.
- Arbusculidium* Deunff 1968
- Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972 emend.
- Fatka & Brocke 1999
- Arkonion* Burmann 1970
- Aureotesta clathrata simplex* (Cramer et al. 1974) Brocke et al. 1997
- Baltisphaeridium* Eisenack 1958 emend. Eisenack 1969
- Baltisphaeridium gordonense* Cramer 1964
- Baltisphaeridium ramusculosum* (Deflandre 1945) Downie 1959
- Barakella* Cramer & Díez 1977
- Barakella felix* Cramer & Díez 1977
- Coryphidium* Vavrdová 1972
- Coryphidium bohemicum* Vavrdová 1972
- Coryphidium elegans* Cramer et al. 1974
- Cristallinium* Vanguetaine 1978
- Cymatiogalea* Deunff 1961 emend. Deunff et al. 1974
- Cymatiogalea cuvillieri* (Deunff 1961) Deunff 1964
- Cymatiogalea granulata* Vavrdová 1966
- Cymatiogalea messaoudensis* Jardiné et al. 1974
- Dactylofusa* Brito & Santos 1965
- Dactylofusa striata* Staplin et al. 1965
- Dactylofusa velifera* Cocchio 1981
- Dicommopalla* Loeblich 1970
- Dicrodiacrodium* Burmann 1970
- Domasia bispinosa* Downie 1960
- Eisenackidium* Cramer & Díez 1968 ex Eisenack et al. 1973

- Eisenackidium orientalis* Rubinstein 1999  
*Evittia? molina* (Cramer 1964) Sarjeant & Vavrdová 1997  
*Frankea* Burmann 1970  
*Impluviculus milonii* (Deunff 1968) Loeblich & Tappan 1969  
*Leiofusa* Eisenack 1938  
*Leiosphaeridia* Eisenack 1958 emend. Bernier & Courtinat 1979  
*Leiosphaeridia* spp.  
*Liliosphaeridium intermedium* (Eisenack 1976) Playford et al. 1995  
*Marrocanium simplex* Cramer et al. 1974  
*Micrhystridium* Deflandre 1937 emend. Sarjeant 1967  
*Micrhystridium* spp.  
*Multiplicisphaeridium ramusculosum* (Deflandre 1945) Lister 1970  
*Orthosphaeridium* Eisenack 1968 emend. Kjellström 1971  
*Pachysphaeridium* Burmann 1970  
*Peteinosphaeridium* Staplin et al. 1965 emend. Eisenack 1969  
*Polygonium* Vavrdová 1966  
*Polygonium* spp.  
*Rhopaliophora* Tappan & Loeblich 1971 emend. Playford & Martin 1984  
*Striatotheca* Burmann 1970  
*Striatotheca* sp.  
*Sylvanidium* Loeblich 1970  
*Tectitheca* Burmann 1968  
*Tectitheca* sp.  
*Tongzia* Li 1987  
*Vavrdovella* Loeblich & Tappan 1976  
*Vavrdovella areniga* (Vavrdova) Loeblich & Tappan 1976  
*Veryhachium* Deunff 1954  
*Veryhachium lairdii* Deflandre 1946 ex Loeblich 1970  
*Veryhachium trispinosum* (Eisenack 1938) Stockmans & Willièrè 1962  
*Veryhachium valiente* Cramer 1964  
*Vogtlandia multiradialis* Burmann 1970  
*Vulcanisphaera tuberrata* (Downie 1958) Eisenack et al. 1973



## **Article VI**

### **Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton**

Axelle Zacaï, Claude Monnet, Alexandre Pohl, Grégory Beaugrand,  
Gary Mullins, David Kroeck, Thomas  
Servais

submitted to *PNAS*.



1

2 **Main Manuscript for**

3 Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton

4

5 Axelle Zacaï<sup>1\*</sup>, Claude Monnet<sup>1</sup>, Alexandre Pohl<sup>2,3</sup>, Grégory Beaugrand<sup>4</sup>, Gary Mullins<sup>5</sup>, David Kröck<sup>1</sup>,  
6 Thomas Servais<sup>1</sup>

7 <sup>1</sup> Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

8 <sup>2</sup> Department of Earth Sciences, University of California, Riverside, CA, USA

9 <sup>3</sup> Biogéosciences, UMR 6282, CNRS, Université Bourgogne Franche-Comté, 6 boulevard Gabriel, F-  
10 21000 Dijon, France

11 <sup>4</sup> Univ. Lille, CNRS, UMR 8187 - Laboratoire d'Océanologie et de Géosciences, F-59000 Lille, France

12 <sup>5</sup> Robertson, a CGG Company, Llandudno, LL30 1SA, UK

13 \* Corresponding author: Axelle Zacaï

14 **Email:** [axelle.zacai@univ-lille.fr](mailto:axelle.zacai@univ-lille.fr)

15

16 **Keywords:** latitudinal diversity gradient, Acritarcha, phytoplankton, early Paleozoic, biogeography

17

18 **Author contributions:** A.Z., C.M. and T.S. designed the research project; A.Z. and C.M. performed

19 research and data analyses; G.M. constructed the original dataset; A.Z. and D.K. cleaned and completed

20 the dataset; A.P. conducted paleoclimate simulations; G.B. performed species distribution simulations;  
21 A.Z, C.M., T.S., A.P. and G.B. wrote the paper.

22

23 **This PDF file includes:**

24 Main Text

25 Figures 1 and 2

26 Tables 1 and 2

27

28 **Abstract**

29 The decline in species richness from the equator to the poles, known as the latitudinal diversity gradient  
30 (LDG), is probably the most commonly observed macroecological pattern nowadays, but the timing of its  
31 establishment, its ubiquity in the geological past and controlling factors remain uncertain. Here we  
32 analyze the latitudinal distribution of diversity of the earliest representatives of marine phytoplankton in  
33 the fossil record, i.e. the acritarchs, for the early Paleozoic (Cambrian—Ordovician interval, ca. 541 to 444  
34 Ma) at the global scale. We show that acritarchs exhibited a LDG since the early Cambrian, and that this  
35 unimodal gradient was centered on the mid-latitudes of the Southern Hemisphere instead of the equator, as  
36 classically observed for most modern taxa. This atypical pattern stems from the fact that this LDG actually  
37 corresponds to a truncated bimodal gradient (i.e. having its northern peak of diversity missing) that  
38 probably results from an uneven preservation of sediment/acritarchs, a smaller sampling effort, and/or a  
39 lower initial diversity in the Northern Hemisphere due to the limited amount of suitable ecospace. Our  
40 findings suggest that variation in the shape of the acritarch LDG through time resulted primarily from the  
41 long-term climate cooling that characterized the early Paleozoic, as shown by both empirical and modeled  
42 data; and that the latitudinal distribution of acritarch diversity was influenced by both mean annual and  
43 seasonal fluctuations in sea-surface temperature, and to a lesser extent salinity and the extent of  
44 continental shelves.

45

## 46 **Significance statement**

47 The latitudinal diversity gradient (LDG) – the decrease in species number from the equator to the poles –  
48 is considered as the most pervasive large-scale biological pattern on Earth, but the timing of its  
49 establishment, its ubiquity in the geological past and explanatory mechanisms remain uncertain. Here, we  
50 show that acritarchs – the first representatives of marine phytoplankton in the fossil record – exhibited a  
51 LDG as early as the beginning of the Cambrian, when most major marine phyla appeared. However, this  
52 LDG was atypical, showing a single peak of diversity in the Southern and not in the Northern Hemisphere.  
53 Our findings suggest that variation of this LDG through time resulted from both annual sea-surface  
54 temperature and long-term climate fluctuations.

55 \body

56

## 57 **Main Text**

### 58 **Introduction**

59

60 The latitudinal diversity gradient (LDG), i.e. the increase in taxonomic diversity from the poles to the  
61 equator, is probably the most striking and pervasive biogeographical pattern on Earth (1–3). Despite being  
62 a ubiquitous phenomenon documented for a large variety of functional and taxonomic groups, its origin,  
63 frequency among fossil groups, as well as its explanatory mechanisms remain widely debated. Proposed  
64 explanations for this pattern can be grouped into six categories: geographic area (4), geometric constraints  
65 (5), energy availability (6), habitat heterogeneity (7), evolutionary mechanisms (8), and niche theory (9,  
66 10). While some of these explanations can be tested through neontological approaches, the effect of long-  
67 term phenomena such as climate changes and biological evolutionary events are inextricable using only  
68 extant taxa (11–13). The fossil record thus offers a unique and complementary perspective for studying  
69 the LDG as it can provide insights on its appearance, stability through time and long-term control  
70 mechanisms. Studies of the LDG on fossil data have shown that it extends back to the Paleozoic (ca.  
71 541–252.9 Ma; 13–16), but that the strength of the gradient has varied through time (17), and the pattern

72 even disappeared during intervals of mass extinctions (8). For the early Paleozoic (i.e.  
73 Cambrian–Ordovician, ca. 541–444 Ma), the presence of a LDG has been documented for three marine  
74 groups – brachiopods (13, 18), bryozoans (18) and chitinozoans (19) – as well as for the whole marine  
75 diversity of the Paleobiology Database (20; <https://paleobiodb.org>). Their LDGs consist of unimodal  
76 gradients (i.e. one diversity peak) centered on low to mid-latitudes of the Southern Hemisphere (i.e.  
77 between 0 and 45°S), whereas for most extant organisms, the LDG is either unimodal with a peak of  
78 diversity centered at the equator, or bimodal with two peaks of diversity centered on the mid-latitudes of  
79 each hemisphere (21–25). In the present study, we expand our perspective on the LDG to the main  
80 representatives of phytoplankton in the early Paleozoic, i.e. the acritarchs. Defined as organic-walled  
81 microfossils of uncertain biological affinity (26), most of them are now considered to be cysts of marine,  
82 generally phytoplanktonic unicellular algae (27), and some may have a close biological affinity with  
83 dinoflagellates, as suggested by biomarkers and morphological similarities (28). So far, acritarchs have  
84 been mainly used as tools for biostratigraphical, paleogeographical and paleoenvironmental  
85 reconstructions (29–31), but only few researchers considered them for what they are, i.e. the main source  
86 of information on phytoplankton in the early Paleozoic, and studied them as such through  
87 macroevolutionary and macroecological approaches (32, 33). Yet, acritarchs have the most densely and  
88 continuously sampled fossil record of any phytoplanktonic group at the global scale over the early  
89 Paleozoic (34), and therefore constitute a unique material to study macroecological dynamics during this  
90 crucial period of the history of Life. Our approach was to (i) determine the potential timing of  
91 establishment of a LDG for early Paleozoic acritarchs and its evolution through time according to long-  
92 term climate changes, (ii) analyze the relationship between the latitudinal distribution of acritarch  
93 diversity and abiotic factors whose values were reconstructed using paleoclimate simulations, and (iii)  
94 compare the shape of acritarch LDGs to modeled LDGs based on the same paleoclimatic and  
95 paleogeographic context.

96 We conducted our analyses over 11 time bins covering the Cambrian–Ordovician interval with a new  
97 database of more than 9k occurrences of acritarch genera from localities with known paleogeographic



98 coordinates (*SI Appendix*, Table S1). Latitudinal paleobiodiversity curves were reconstructed by means of  
99 range-through indices (see Material & Methods). The relationships between acritarch diversity and abiotic  
100 factors (i.e. continental shelf area, sea-surface temperature and salinity) were tested for three key stages,  
101 i.e. the Cambrian stage 4, the Darriwilian and the Hirnantian, by means of (i) the non-parametric  
102 Kendall's rank correlation coefficient applied between the LDG and each abiotic factor separately, and (ii)  
103 a generalized linear model (GLM, see *SI Appendix*) with a response variable (i.e. diversity) following a  
104 Poisson distribution. Finally, we modeled species diversity for the Cambrian stage 4, the Darriwilian and  
105 the Hirnantian using a model based on the MacroEcological Theory on the Arrangement of Life (METAL;  
106 see *SI Appendix* and 10, 35, 36) forced with the sea surface temperature (SST) values simulated using the  
107 climate model (see *SI Appendix*) on available paleogeographical reconstructions (37).

108

109

## 110 **Results and Discussion**

111

112 We find a unimodal latitudinal gradient of acritarch genus diversity for each time bin (i.e. four  
113 Cambrian series and seven Ordovician stages; Fig. 1 & *SI Appendix*, Fig. S1). The small amplitude  
114 gradient observed at the beginning of the Cambrian (i.e. Terreneuvian, ca. 531 Ma) may be explained by a  
115 poor sampling effort or preservation bias (*SI Appendix*, Fig. S2). Contrary to the classical unimodal LDG  
116 observed for many modern taxa (e.g. neritic and terrestrial taxa, 25, 38), the acritarch LDG does not  
117 exhibit a diversity maximum at the equator or near the tropics, but rather over mid-latitudes of the  
118 Southern Hemisphere (i.e. 35–40°S) during the Cambrian series 2 (ca. 515 Ma; Fig. 1, *SI Appendix*, Fig.  
119 S1). The diversity peak then slowly drifts southwards, reaching 45°S during the Furongian (ca. 491.2 Ma)  
120 and its highest latitudinal position (i.e. 50–60°S) during the Tremadocian–Dapingian interval (ca.  
121 485.4–467.3 Ma), before splitting in two peaks corresponding to the drift of areas of high diversity (i.e.  
122 Baltica and the Armorican Terrane Assemblage; *SI Appendix*, Fig. S4) during the Middle Ordovician (Fig.  
123 1, *SI Appendix*, Fig. S1). Only the peak located at the lowest latitude and corresponding to Baltica persists

124 until the end of the Ordovician (Fig. 1, *SI Appendix*, Fig. S1). Additionally to the position of peak  
125 diversity, the steepness of the LDG also changes through time. It drastically increases during the Floian in  
126 the Southern Hemisphere (ca. 473.85 Ma), paralleling an augmentation in diversity in the equatorial and  
127 low latitudes of the Northern Hemisphere (Fig. 1, *SI Appendix*, Fig. S1). A similar tropical diversification  
128 is apparent for marine organisms considered as a whole, and it does not reflect changes in the relative  
129 abundance of depositional environments, in environmental and lithological heterogeneity, or in  
130 paleogeography (20). This transition from a poor Cambrian to a highly diversified Ordovician intertropical  
131 zone is probably related to a global climate change (19, 39, 40). While the Cambrian corresponded to a  
132 greenhouse climate with equatorial SST probably too high to sustain highly diverse communities (*SI*  
133 *Appendix*, Fig. S3; 41), a steady cooling trend occurred through the Early Ordovician to reach the range of  
134 modern equatorial SST by the Middle Ordovician (*SI Appendix*, Fig. S3; 39), allowing all major marine  
135 groups to colonize low latitudes (42), before ending in a glaciation associated to a massive extinction  
136 during the Hirnantian (43). Temporal variations in the position of the LDG diversity peak of early  
137 Paleozoic acritarchs and the general shape of this LDG thus appear to have been related to the climatic  
138 regimes of the Cambrian–Ordovician interval, and to a lesser extent to the position of continental masses.  
139 Brayard et al. (23) have shown through a modeling approach that the position of peak diversity and  
140 steepness of LDGs in marine environments depend on the shape and magnitude of the latitudinal SST  
141 gradient: sigmoid-like SST gradients generate a bimodal LDG with peaks of diversity located at mid-  
142 latitudes, while a reduced steepness of the SST gradient leads to a weakened unimodal LDG with a  
143 plateau of equal diversity between the tropics. This implies that bimodal LDGs with diversity peaks at  
144 intermediate latitudes are a characteristic feature of icehouse periods, whereas unimodal LDGs with an  
145 equatorial peak or a plateau of equal diversity are characteristic of greenhouse periods (see 12 and  
146 references therein). Alternatively, Beaugrand et al. (36, fig. 4) have shown that in case of a global cooling,  
147 the LDG steepness increases because of the movement of species towards the equator, leading to a  
148 unimodal gradient centered at the equator, whereas in case of global warming, it is attenuated because of  
149 the poleward shift of species, leading to a bimodal gradient with peaks of diversity at intermediate

150 latitudes. The LDG of early Paleozoic acritarchs is steeper and its peak of diversity closer to the equator  
151 during the colder Middle-Late Ordovician than during the Cambrian, and no equatorial peak or plateau of  
152 equal diversity is observed under the Cambrian greenhouse climatic conditions (*SI Appendix*, Fig. S1).  
153 This more corresponds to the model of Beaugrand et al. (36) and its deviation from Brayard et al.'s (23)  
154 model might be explained by a threshold temperature effect: peak diversity could not occur at the equator  
155 during the Cambrian because equatorial temperatures were too high to allow most organisms to survive;  
156 and this peak slowly shifted towards more equatorial latitudes during the Ordovician cooling, with a rapid  
157 first step of diversification at equatorial latitudes during the Early Ordovician (i.e. Floian, *SI Appendix*,  
158 Fig. S1). As such, it seems that – as for the majority of marine groups of organisms – long-term climate  
159 trends had an important influence on the distribution of diversity of early Paleozoic phytoplankton.

160 The results of our analyses of correlation between SST and acritarch diversity support this  
161 hypothesis. For the Cambrian stage 4, seasonal variation in SST ( $SST_{diff}$ , i.e. the difference between  
162 summer and winter SST) appears as a positive predictor of acritarch diversity in the three best GLMs  
163 ( $169.95 < AICc < 171.28$ ,  $R^2=0.58$ ; Table 1). For the Darriwilian, which corresponds to the major  
164 diversity peak of the GOBE and during which global climate was cooler than during the Cambrian (*SI*  
165 *Appendix*, Fig. S3; 42),  $SST_{diff}$  is also significantly correlated to diversity as revealed by Kendall's test ( $\tau =$   
166  $0.53$ ,  $p < 0.01$ ; Table 2), and mean annual SST ( $SST_{an}$ ) is a negative predictor of diversity ( $AICc=186.59$ ,  
167  $R^2=0.61$ ; Table 1). Eventually, during the colder Hirnantian stage (*SI Appendix*, Fig. S3), the best GLM  
168 shows that  $SST_{an}$  and  $SST_{diff}$  negatively and positively predict the latitudinal distribution of acritarch  
169 diversity, respectively ( $AICc = 133.83$ ,  $R^2=0.88$ ; Table 1); and Kendall's test shows significant  
170 correlations with both  $SST^2$  ( $\tau = -0.36$ ,  $p < 0.05$ ; Table 2) and  $SST_{diff}$  ( $\tau = 0.40$ ,  $p < 0.05$ ; Table 2). Taken  
171 together, these results – which are complementary as the Kendall's coefficient and GLMs do not test the  
172 same relationship between the variable of interest and its potential predictors – clearly show the existence  
173 of a relationship between SST, and especially its seasonal variations, and the spatial distribution of  
174 acritarch diversity throughout the early Paleozoic. Temperature has often been cited as one of the main  
175 explanatory factors for large-scale distribution patterns of organisms (10, 24, 44). Many studies, in both

176 marine and terrestrial environments, have shown that present-day temperature, along with some other  
177 environmental factors such as precipitation on land and productivity in the sea, are powerful first-order  
178 predictors of LDG patterns (44 and references therein). In the marine realm, Tittensor et al. (45) have  
179 shown that SST was the only environmental predictor highly correlated with diversity across 13  
180 taxonomic groups, a finding confirmed for phytoplankton in particular (46). Our results show that  
181 acritarchs are no exception to this rule, and that as far back as the early Paleozoic, the spatial distribution  
182 of phytoplankton diversity was controlled, at least in part, by this abiotic variable.

183 Salinity is known to affect the distribution patterns of marine organisms at local (e.g. 47) and  
184 sometimes at regional scales (48), but its influence on global distribution patterns of diversity seems to be  
185 weak (45, 49). Regarding early Paleozoic acritarchs, Kendall's tests reveal a positive correlation between  
186 diversity and both mean annual sea-surface salinity ( $SSS_{an}$ ) and squared  $SSS_{an}$  ( $SSS^2$ ) during the Cambrian  
187 stage 4 ( $\tau = 0.44$ ,  $p < 0.01$ ; Table 2), and  $SSS^2$  also appears as a predictor of diversity with the GLM  
188 ( $169.95 < AICc < 171.28$ ,  $R^2=0.58$ ; Table 1). For the Darriwilian,  $SSS_{an}$  and  $SSS^2$  appear, respectively, as  
189 positive and negative predictors of diversity using a GLM ( $AICc=186.59$ ,  $R^2=0.61$ ; Table 1). For the  
190 Hirnantian, only the GLM shows that  $SSS^2$  positively predicts the latitudinal distribution of acritarch  
191 diversity ( $AICc=133.83$ ,  $R^2=0.88$ ; Table 1). A relationship thus seems to exist between the early Paleozoic  
192 acritarch diversity and salinity. However, given that SSS values remain quite stable in the inter-tropical  
193 zone from the Cambrian stage 4 to the Hirnantian (*SI Appendix*, Fig. S3d) while a major shift of diversity  
194 is recorded in this area during the Early Ordovician, we argue that temperature was a more limiting factor  
195 of acritarch diversity, because the colonization of the inter-tropical zone by acritarchs during the Floian is  
196 not associated with a change in SSS, but much more likely with a diminution in SST (42).

197 The third abiotic factor investigated here, i.e. continental shelf area (CSA), has often been found to be  
198 related to marine diversity (50), but it should not be considered *a priori* as a bias. Indeed, during  
199 transgression events, flooded continental areas increase, offering more niche space and opportunities for  
200 diversification, and impacting the production of sediments, which provides a general explanation for the  
201 covariation between fossil marine biodiversity and the amount of marine sedimentary rocks (51).

202 However, this signal varies among groups of organisms, spatial scales and time intervals (52). Regarding  
203 acritarchs, CSA is significantly correlated with their diversity for the Cambrian stage 4 using Kendall's  
204 test ( $\tau=0.47$ ,  $p < 0.01$ ; Table 2), and it appears as a positive predictor of diversity for the Darriwilian and  
205 the Hirnantian when analyzed through GLM (AICc = 186.59 and 133.83;  $R^2=0.61$  and 0.88, respectively;  
206 Table 1, *SI Appendix*). This relationship is in fact almost inevitable for Paleozoic marine organisms.  
207 Indeed, because the Paleozoic oceanic crust has long been recycled in subduction zones, the vast majority  
208 of deposits accessible today were located on continental shelves at that time. Furthermore, the fact that  
209 modern dinoflagellates are most diverse in marine shelf areas compared to oceanic and lacustrine  
210 environments, and that organic-walled cyst production is most common in shelf areas (53), supports the  
211 genuine nature of this relationship for acritarchs.

212 Assuming that the diversity of early Paleozoic acritarchs is concentrated on continental shelves, we  
213 compared their empirical LDGs with the LDGs obtained by modeling species distribution on continental  
214 shelves only using the METAL model of Beaugrand et al. (10, 35, 36). Validated for modern plankton,  
215 fish and cetaceans (36), the METAL model shows that the primary cause of LDGs in the oceans lies in the  
216 interaction between species thermal tolerance and both seasonal and year-to-year fluctuations in  
217 temperature, together with the generation of a mid-domain effect in the ecological niche space. For the  
218 Cambrian stage 4 and the Darriwilian, modeled LDGs are bimodal with two peaks of diversity located  
219 respectively at 37.5°S and 42.5°N, and 32.5°S and 32.5°N, when averaged by 5° latitudinal bands (Fig. 2).  
220 The northern peak of diversity is smaller than the southern one for both stages (Fig. 2). For the Hirnantian,  
221 the gradient is steeper and unimodal with a plateau of maximum diversity ranging from ~22.5°S to 27.5°N  
222 (Fig. 2). The three modeled LDGs end around 30°N for each stage because no continental shelf existed  
223 above this latitude during the early Paleozoic, the Northern Hemisphere being essentially covered by the  
224 Panthalassa Ocean. Modeled and empirical LDGs are significantly correlated for the Darriwilian  
225 (Kendall's  $\tau = 0.40$ ,  $p < 0.05$ ), but not for the Cambrian stage 4 and the Hirnantian ( $\tau = 0.05$ ,  $p = 0.72$  and  
226  $\tau = 0.04$ ,  $p = 0.83$ , respectively). Although the Southern Hemisphere peaks of diversity of the modeled and  
227 empirical LDGs are located at close latitudes during the first two stages, some important differences can

228 be observed: modeled LDGs are bimodal during the first two stages while empirical LDGs are unimodal,  
229 and the Hirnantian modeled LDG shows a plateau of equal diversity centered at the equator, while the  
230 empirical LDG shows a diversity peak located around 27.5°S. The change from a bimodal to a unimodal  
231 modeled LDG between the Darriwilian and the Hirnantian does not match our observations, but the fact  
232 that the peak of diversity moves towards lower latitudes during this interval in both cases (i.e. modeled  
233 and empirical; Fig. 1) shows the influence of the climate cooling on the latitudinal distribution of  
234 diversity, allowing taxa to colonize lower latitudes. Bimodal gradients are very common for extant marine  
235 organisms (21–25). They have been documented for marine taxa as varied as bivalves (54), brachiopods  
236 (55), bryozoans (56), foraminifers (10, 21), seaweeds (57) and copepods (10, 44). However, bimodal  
237 LDGs have never been observed for Paleozoic organisms (13, 18, 19). This marked difference may result  
238 either from the fact that modern LDGs are controlled by different factors than early Paleozoic LDGs, or  
239 that the early Paleozoic fossil record is biased and the LDGs one reconstructs are distorted images of the  
240 original ones. The fact that LDGs modeled here are bimodal, and that empirical unimodal LDGs centered  
241 on the mid latitudes of the Southern Hemisphere are characteristic of Paleozoic organisms, supports the  
242 second hypothesis. This seems all the more likely for acritarchs since the LDGs of extant pelagic  
243 organisms (16) and dinoflagellates in particular (58), as well as modeled LDGs of virtual planktic species  
244 (10, 23, 59), are also bimodal. Therefore, we argue that rather than being an atypical unimodal gradient  
245 centered on the mid-latitudes of the Southern Hemisphere, the early Paleozoic acritarch LDG probably  
246 corresponds to a truncated bimodal gradient whose Northern peak of diversity cannot be recovered or  
247 never existed. Either it cannot be recovered because of a reduced sediment and/or specimen preservation,  
248 and/or a smaller sampling effort in the Northern Hemisphere (e.g. absence of data from Siberia); or it  
249 never existed because some habitat-related factors essential for survival of acritarchs but not accounted for  
250 in the model were lacking in most of the Northern Hemisphere because of the small extent of landmasses.

251 This first quantitative analysis of the latitudinal distribution of early Paleozoic acritarch diversity  
252 shows that (i) the earliest representatives of marine phytoplankton were characterized by a LDG already  
253 since the Cambrian Explosion, (ii) this LDG corresponded to a truncated bimodal rather than a unimodal

254 gradient, (iii) variation in the shape of this LDG through time can be attributed to both long-term climate  
255 cooling characterizing the early Paleozoic and plate tectonics, and (iv) the latitudinal distribution of  
256 acritarch diversity was influenced by SST and its seasonal fluctuations, but also to a lesser extent by  
257 salinity and the available area of continental shelf. These results strongly question the unimodal nature of  
258 other LDGs found for Paleozoic organisms, such as brachiopods and bryozoans (13, 18). We strongly  
259 support the combined use of empirical data and modelling approaches of both climate and diversity in the  
260 Past, as this could be the key to understanding still debated macroecological patterns.

261

262

## 263 **Material and Methods**

264

265 **Fossil Occurrence Data.** The dataset we used, initially created as part of the Phytopal project by Mullins  
266 et al. (unpublished), consists of 1503 species of acritarchs belonging to 287 genera and distributed among  
267 328 fossil localities (*SI Appendix*, Table S1 & Fig. S4). Temporal resolution is at the series level for the  
268 Cambrian and at the stage level for the Ordovician. Geographic coordinates of fossil localities were  
269 recovered and their paleocoordinates were calculated by rotating their present-day coordinates with the  
270 software GPlates (60) version 2.0.0 using the rotation file supplied by Scotese (61) for each Cambrian  
271 series and Ordovician stage.

272 **Latitudinal Diversity Gradient.** We tested for the existence of a LDG by calculating the  
273 paleobiodiversity of acritarchs by 5° latitudinal bands at the genus level, because it is considered more  
274 robust than the species level for such analyses (see *SI Appendix*). We estimated the taxonomic richness by  
275 means of two ‘range-through’ indices (see review of Alroy, 62) including or excluding single-interval  
276 taxa: *RTinS* and *RTexS*, respectively. Range-through indices account for every taxon known to occur in a  
277 latitudinal band (i.e. real occurrence), as well as every taxon inferred to be present (i.e. recorded south and  
278 north of the considered latitudinal band). We conducted the diversity analyses at the series level for the  
279 Cambrian and at the stage level for the Ordovician.



280 **Correlation With Abiotic Factors.** We tested the relationships between acritarch diversity and abiotic  
281 factors (continental shelf area, sea-surface temperature and salinity) for three key stages, i.e. the Cambrian  
282 stage 4, the Darriwilian and the Hirnantian. We simulated paleoenvironmental conditions using the Fast  
283 Ocean Atmosphere Model (FOAM) version 1.5 (see *SI Appendix*), with the continental reconstructions of  
284 Scotese and Wright (37). Continental shelf area was derived from the paleogeographical reconstructions,  
285 and values of sea-surface temperature and salinity were extracted from the climatic simulations. We tested  
286 the relationships between these abiotic factors and the latitudinal distribution of acritarch diversity  
287 (*RTextS*) using two approaches (see *SI Appendix* for details): (i) the non-parametric Kendall's rank  
288 correlation coefficient applied between the LDG and each abiotic factor separately, and (ii) a generalized  
289 linear model (GLM, see *SI Appendix*) with a response variable (i.e. diversity) following a Poisson  
290 distribution by means of a log link function, applied to all abiotic factors together, using the R packages  
291 'MuMIn' (63) and 'MASS' (64).

292 **Species Distribution Model.** We modeled species diversity for the Cambrian stage 4, the Darriwilian and  
293 the Hirnantian using a model based on the MacroEcological Theory on the Arrangement of Life (METAL;  
294 see *SI Appendix* and 10, 35-36) forced with the SST values simulated using the climate model on the  
295 paleogeographical reconstructions of Scotese and Wright (37). We created pseudo-species having each a  
296 unique thermal niche with distinct degrees of eurythermy and thermophily (10, 35). We allowed pseudo-  
297 species to colonise any given region of the global ocean provided they could withstand the local monthly  
298 thermal regime. To estimate pseudo-species diversity, we randomly selected 10,000 among 101,397  
299 possible pseudo-species and repeated the procedure 1,000 times. We integrated the number of pseudo-  
300 species for each 5° latitudinal bands and compared this modelled species diversity to the empirical genus  
301 acritarch diversity we observed.

302

303

304 **Acknowledgements**

305 The authors thank the Région Hauts-de-France, the Ministère de l'Enseignement Supérieur et de la  
306 Recherche (CPER Climibio), the European Fund for Regional Economic Development, and the  
307 Leverhulme Trust for their financial support. We sincerely thank Anne Duputié (University of Lille) for  
308 her help with GLM computation, and Bert Van Bocxlaer (University of Lille) for his constructive and  
309 helpful comments on a preliminary version of the manuscript. G. M. thanks Malgorzata Moczydlowska-  
310 Vidal for her guidance on Cambrian taxa when establishing the database. A. P. thanks the CEA/CCRT for  
311 providing access to the HPC resources of TGCC under the allocation 2014-012212 made by GENCI and  
312 the European Union's Horizon 2020 research and innovation programme (Marie Skłodowska-Curie grand  
313 agreement No 838373). This paper is a contribution to the International Geoscience Programme (IGCP)  
314 Project 653 – The onset of the Great Ordovician Biodiversification Event.

315

## 316 **References**

- 317 1. S. L. Chown, K. J. Gaston, Areas, cradles and museums: the latitudinal gradient in species richness.  
318 *Trends in Ecology & Evolution* **15**, 311–315 (2000).
- 319 2. H. Hillebrand, On the Generality of the Latitudinal Diversity Gradient. *The American Naturalist*  
320 **163**, 192–211 (2004).
- 321 3. J. H. Brown, Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22 (2014).
- 322 4. J. H. Brown, *Macroecology* (University of Chicago Press, Chicago, 1995).
- 323 5. Robert. K. Colwell, D. C. Lees, The mid-domain effect: geometric constraints on the geography of  
324 species richness. *Trends in Ecology & Evolution* **15**, 70–76 (2000).
- 325 6. D. J. Currie, Energy and Large-Scale Patterns of Animal- and Plant-Species Richness. *The American*  
326 *Naturalist* **137**, 27–49 (1991).
- 327 7. J. T. Kerr, L. Packer, Habitat heterogeneity as a determinant of mammal species richness in high-  
328 energy regions. *Nature* **385**, 252–254 (1997).
- 329 8. D. Jablonski, K. Roy, J. W. Valentine, Out of the Tropics: Evolutionary Dynamics of the Latitudinal  
330 Diversity Gradient. *Science* **314**, 102–106 (2006).

- 331 9. E. E. Saupe, *et al.*, Non-random latitudinal gradients in range size and niche breadth predicted by  
332 spatial patterns of climate. *Global Ecology and Biogeography* **28**, 928–942 (2019).
- 333 10. G. Beaugrand, I. Rombouts, R. R. Kirby, Towards an understanding of the pattern of biodiversity in  
334 the oceans: The pattern of biodiversity in the oceans. *Global Ecology and Biogeography* **22**, 440–  
335 449 (2013).
- 336 11. A. Z. Krug, D. Jablonski, J. W. Valentine, K. Roy, Generation of Earth’s First-Order Biodiversity  
337 Pattern. *Astrobiology* **9**, 113–124 (2009).
- 338 12. P. D. Mannion, P. Upchurch, R. B. J. Benson, A. Goswami, The latitudinal biodiversity gradient  
339 through deep time. *Trends in Ecology & Evolution* **29**, 42–50 (2014).
- 340 13. M. G. Powell, The Latitudinal Diversity Gradient of Brachiopods over the Past 530 Million Years.  
341 *The Journal of Geology* **117**, 585–594 (2009).
- 342 14. M. L. Rosenzweig, *Species diversity in space and time* (Cambridge University Press, 1995).
- 343 15. J. Alroy, *et al.*, Phanerozoic Trends in the Global Diversity of Marine Invertebrates. *Science* **321**,  
344 97–100 (2008).
- 345 16. M. G. Powell, V. P. Beresford, B. A. Colaianne, The latitudinal position of peak marine diversity in  
346 living and fossil biotas. *Journal of Biogeography* **39**, 1687–1694 (2012).
- 347 17. J. D. Marcot, D. L. Fox, S. R. Niebuhr, Late Cenozoic onset of the latitudinal diversity gradient of  
348 North American mammals. *Proc Natl Acad Sci USA* **113**, 7189–7194 (2016).
- 349 18. E. B. Naimark, A. V. Markov, Northward shift in faunal diversity: a general pattern of evolution of  
350 Phanerozoic marine biota. *Biology Bulletin Reviews* **1**, 71–81 (2011).
- 351 19. T. R. A. Vandenbroucke, *et al.*, Epipelagic chitinozoan biotopes map a steep latitudinal temperature  
352 gradient for earliest Late Ordovician seas: Implications for a cooling Late Ordovician climate.  
353 *Palaeogeography, Palaeoclimatology, Palaeoecology* **294**, 202–219 (2010).
- 354 20. B. Kröger, Changes in the latitudinal diversity gradient during the Great Ordovician  
355 Biodiversification Event. *Geology* **46**, 127–130 (2018).

- 356 21. S. Rutherford, S. D'Hondt, P. Warren, Environmental controls on the geographic distribution of  
357 zooplankton diversity. *Nature* **400**, 749–753 (1999).
- 358 22. K. J. Gaston, Global patterns in biodiversity. *Nature* **405**, 220–227 (2000).
- 359 23. A. Brayard, G. Escarguel, H. Bucher, Latitudinal gradient of taxonomic richness: combined outcome  
360 of temperature and geographic mid-domains effects? *Journal of Zoological Systematics and*  
361 *Evolutionary Research* **43**, 178–188 (2005).
- 362 24. A. Clarke, “Temperature and marine macroecology” in *Marine Macroecology*, Witman, J.D. & Roy,  
363 K., (University of Chicago Press, 2009), pp. 250–278.
- 364 25. D. P. Tittensor, *et al.*, Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**,  
365 1098–1101 (2010).
- 366 26. W. R. Evitt, A Discussion and Proposals Concerning Fossil Dinoflagellates, Hystrichospheres, and  
367 Acritarchs, Ii. *PNAS* **49**, 158–164 (1963).
- 368 27. F. Martin, Acritarchs: a review. *Biological Reviews* **68**, 475–537 (1993).
- 369 28. J. M. Moldowan, N. M. Talyzina, Biogeochemical Evidence for Dinoflagellate Ancestors in the  
370 Early Cambrian. *Science* **281**, 1168–1170 (1998).
- 371 29. M. Vecoli, A. Le Hérisse, Biostratigraphy, taxonomic diversity and patterns of morphological  
372 evolution of Ordovician acritarchs (organic-walled microphytoplankton) from the northern  
373 Gondwana margin in relation to palaeoclimatic and palaeogeographic changes. *Earth-Science*  
374 *Reviews* **67**, 267–311 (2004).
- 375 30. T. Servais, T. Danelian, D. A. T. Harper, A. Munnecke, Possible oceanic circulation patterns,  
376 surface water currents and upwelling zones in the Early Palaeozoic. *GFF* **136**, 229–233 (2014).
- 377 31. A. Le Hérisse, M. Al-Ruwaili, M. Miller, M. Vecoli, Environmental changes reflected by  
378 palynomorphs in the early Middle Ordovician Hanadir Member of the Qasim Formation, Saudi  
379 Arabia. *Revue de Micropaléontologie* **50**, 3–16 (2007).

- 380 32. S. G. Molyneux, A. Delabroye, R. Wicander, T. Servais, Chapter 23 Biogeography of early to mid  
381 Palaeozoic (Cambrian-Devonian) marine phytoplankton. *Geological Society, London, Memoirs* **38**,  
382 365–397 (2013).
- 383 33. L. Stricanne, A. Munnecke, J. Pross, T. Servais, Acritarch distribution along an inshore–offshore  
384 transect in the Gorstian (lower Ludlow) of Gotland, Sweden. *Review of Palaeobotany and*  
385 *Palynology* **130**, 195–216 (2004).
- 386 34. R. E. Martin, T. Servais, Did the evolution of the phytoplankton fuel the diversification of the  
387 marine biosphere? *Lethaia* **53**, 5–31 (2019).
- 388 35. G. Beaugrand, E. Goberville, C. Luczak, R. R. Kirby, Marine biological shifts and climate. *Proc. R.*  
389 *Soc. B* **281**, 20133350 (2014).
- 390 36. G. Beaugrand, C. Luczak, E. Goberville, R. R. Kirby, Marine biodiversity and the chessboard of life.  
391 *PLoS ONE* **13**, e0194006 (2018).
- 392 37. C. R. Scotese, N. Wright, PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the  
393 Phanerozoic (2018).
- 394 38. M. V. Lomolino, B. R. Riddle, R. J. Whittaker, J. H. Brown, *Biogeography* (Sinauer Associates,  
395 Sunderland, 2010).
- 396 39. J. A. Trotter, I. S. Williams, C. R. Barnes, C. Lecuyer, R. S. Nicoll, Did Cooling Oceans Trigger  
397 Ordovician Biodiversification? Evidence from Conodont Thermometry. *Science* **321**, 550–554  
398 (2008).
- 399 40. A. Pohl, *et al.*, Glacial onset predated Late Ordovician climate cooling. *Paleoceanography* **31**, 800–  
400 821 (2016).
- 401 41. B. D. Webby, R. J. Elias, G. A. Young, B. E. E. Neumann, D. Kaljo, “Patterns of Ordovician reef  
402 development” in *The Great Ordovician Biodiversification Event*, Webby, B.D., et al., (Columbia  
403 University Press, 2002), pp. 124–146.
- 404 42. B. Kröger, Changes in the latitudinal diversity gradient during the Great Ordovician  
405 Biodiversification Event. *Geology* **46**, 127–130 (2017).

- 406 43. P. M. Sheehan, The Late Ordovician Mass Extinction. *Annu. Rev. Earth Planet. Sci.* **29**, 331–364  
407 (2001).
- 408 44. I. Rombouts, *et al.*, Global latitudinal variations in marine copepod diversity and environmental  
409 factors. *Proc. R. Soc. B* **276**, 3053–3062 (2009).
- 410 45. D. P. Tittensor, *et al.*, Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**,  
411 1098–1101 (2010).
- 412 46. D. Righetti, M. Vogt, N. Gruber, A. Psomas, N. E. Zimmermann, Global pattern of phytoplankton  
413 diversity driven by temperature and environmental variability. *Science advances* **5**, eaau6253 (2019).
- 414 47. I. V. Telesh, V. V. Khlebovich, Principal processes within the estuarine salinity gradient: A review.  
415 *Marine Pollution Bulletin* **61**, 149–155 (2010).
- 416 48. H. Hillebrand, A. I. Azovsky, Body size determines the strength of the latitudinal diversity gradient.  
417 *Ecography* **24**, 251–256 (2001).
- 418 49. J. A. Fuhrman, *et al.*, A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of*  
419 *the National Academy of Sciences* **105**, 7774–7778 (2008).
- 420 50. A. M. Dunhill, M. J. Benton, R. J. Twitchett, A. J. Newell, Testing the fossil record: sampling  
421 proxies and scaling in the British Triassic-Jurassic. *Palaeogeography, Palaeoclimatology,*  
422 *Palaeoecology* **404**, 1–11 (2014).
- 423 51. B. Hannisdal, S. E. Peters, Phanerozoic Earth System Evolution and Marine Biodiversity. *Science*  
424 **334**, 1121–1124 (2011).
- 425 52. A. B. Smith, R. B. J. Benson, Marine diversity in the geological record and its relationship to  
426 surviving bedrock area, lithofacies diversity, and original marine shelf area. *Geology* **41**, 171–174  
427 (2013).
- 428 53. R. A. MacRae, R. A. Fensome, G. L. Williams, Fossil dinoflagellate diversity, originations, and  
429 extinctions and their significance. *Canadian Journal of Botany* **74**, 1687–1694 (1996).
- 430 54. J. A. Crame, The nature and origin of taxonomic diversity gradients in marine bivalves. *Geological*  
431 *Society, London, Special Publications* **177**, 347–360 (2000).

- 432 55. S.-Z. Shen, G. R. Shi, Capitanian (Late Guadalupian, Permian) global brachiopod  
433 palaeobiogeography and latitudinal diversity pattern. *Palaeogeography, Palaeoclimatology,*  
434 *Palaeoecology* **208**, 235–262 (2004).
- 435 56. A. Clarke, S. Lidgard, Spatial patterns of diversity in the sea: bryozoan species richness in the North  
436 Atlantic. *Journal of Animal Ecology* **69**, 799–814 (2000).
- 437 57. J. J. Bolton, Global Seaweed Diversity: Patterns and Anomalies. *Botanica Marina* **37**, 241–245  
438 (1994).
- 439 58. G. Chust, X. Irigoien, J. Chave, R. P. Harris, Latitudinal phytoplankton distribution and the neutral  
440 theory of biodiversity. *Global Ecology and Biogeography* **22**, 531–543 (2013).
- 441 59. A. D. Barton, S. Dutkiewicz, G. Flierl, J. Bragg, M. J. Follows, Patterns of Diversity in Marine  
442 Phytoplankton. *Science* **327**, 1509–1511 (2010).
- 443 60. R. D. Müller, *et al.*, GPlates: Building a Virtual Earth Through Deep Time. *Geochemistry,*  
444 *Geophysics, Geosystems* **19**, 2243–2261 (2018).
- 445 61. C. R. Scotese, *PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program* (2016).
- 446 62. J. Alroy, Fair sampling of taxonomic richness and unbiased estimation of origination and extinction  
447 rates. *The Paleontological Society Papers* **16**, 55–80 (2010).
- 448 63. K. Barton, M. K. Barton, Package ‘MuMIn.’ *Multi-model inference. version 1* (2019).
- 449 64. B. Ripley, *et al.*, Package ‘mass.’ *Cran R* (2019).

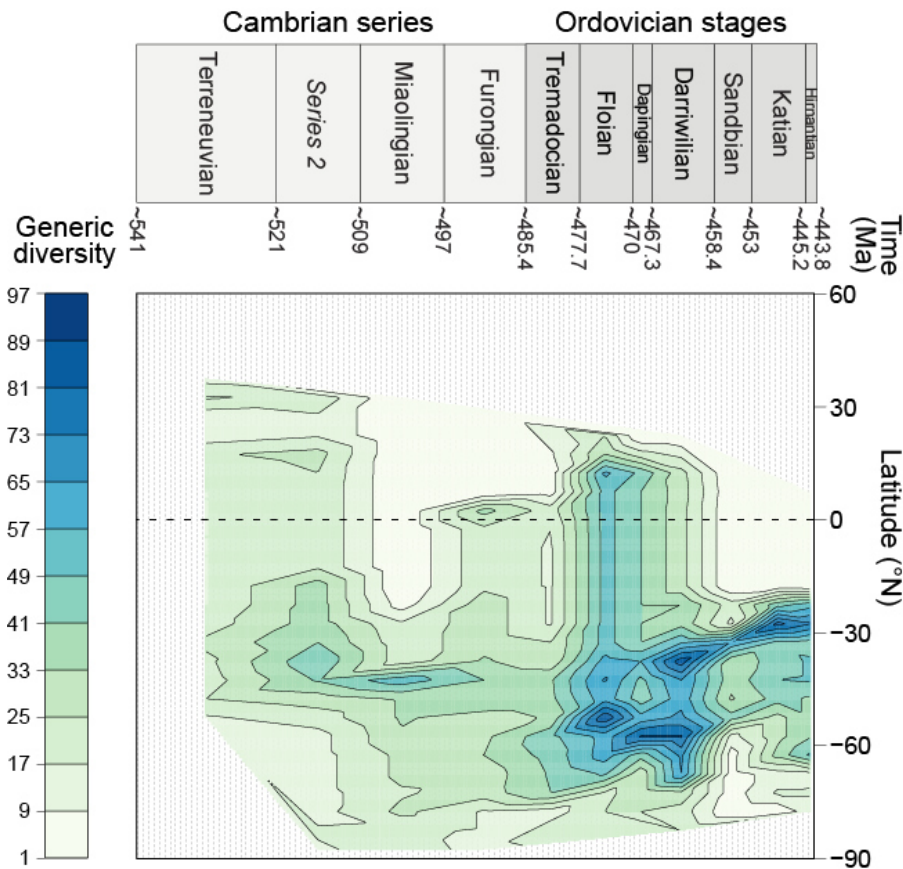
450

451



452 **Figures and Tables**

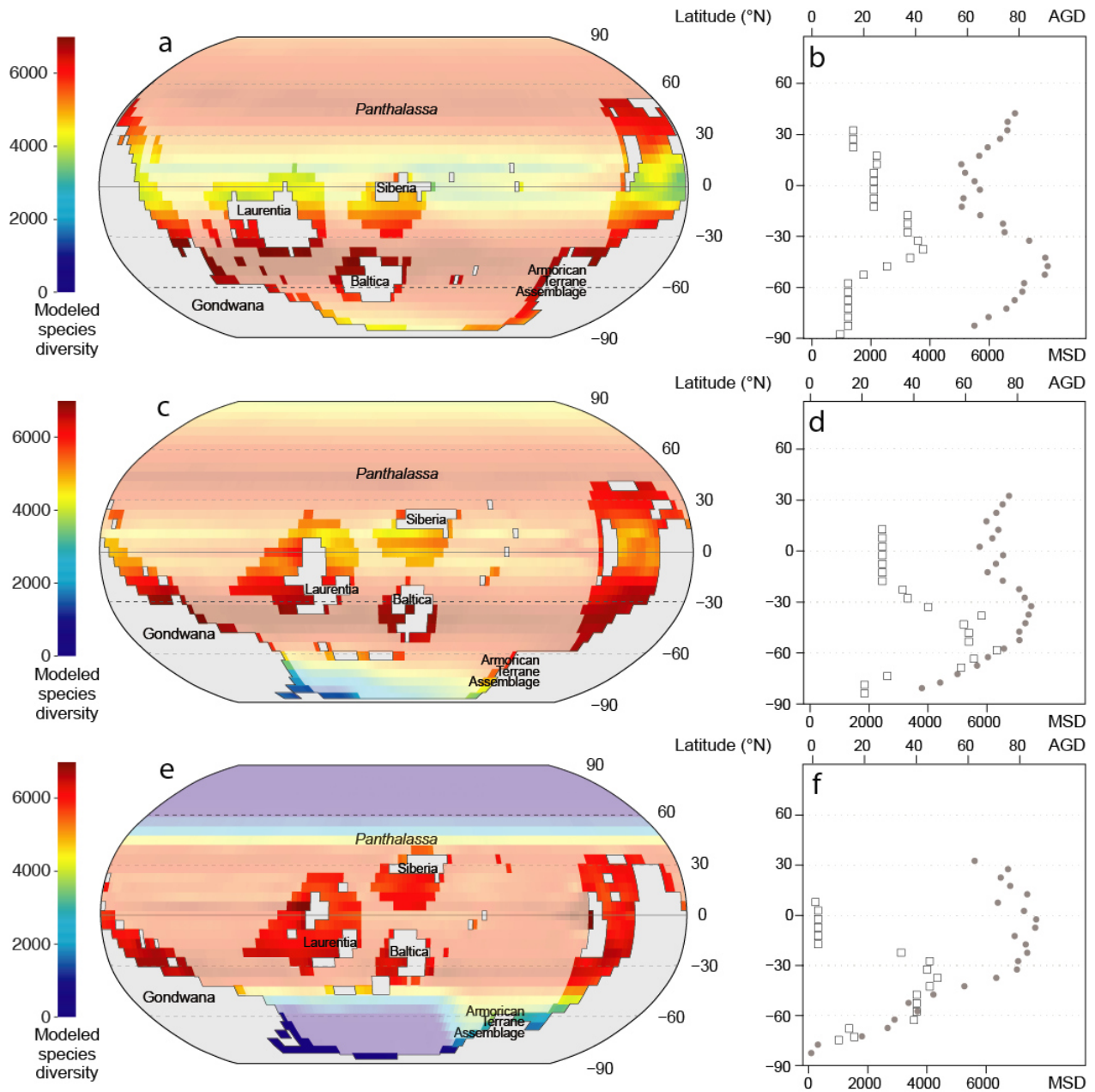
453



454

455 **Figure 1.** Acritarch genus diversity calculated per 5° latitudinal bands with the standard range-through  
 456 approach excluding single-interval taxa (see 62) for each series of the Cambrian and each stage of the  
 457 Ordovician. Note the slight southward drift of peak diversity through the Cambrian, the colonization of  
 458 inter-tropical latitudes during the Early Ordovician and subsequent duplication of the diversity peak. The  
 459 null-diversity observed above ~30°N is a consequence of the particular paleogeography of the early  
 460 Paleozoic, with a Northern Hemisphere mainly constituted by the Panthalassa Ocean. Data are lacking for  
 461 this large area because the vast majority of its oceanic crust has long been recycled in subduction zones.

462



463  
 464 **Figure 2.** Comparison of latitudinal gradient of acritarch generic diversity and modeled species diversity  
 465 for the Cambrian stage 4 (a-b; 510 Ma, 32 PAL, i.e. preindustrial atmospheric level of CO<sub>2</sub>, 1 PAL = 280  
 466 ppm), the Darriwilian (c-d; 460 Ma, 12 PAL), and the Hirnantian (e-f; 445 Ma, 5 PAL). Modeled spatial  
 467 distribution of species diversity corresponds to mean results of 1000 METAL simulations for continental  
 468 shelves (< 200m, bright colors) and ocean surface (<200m, light colors), based on Scotese and Wright's  
 469 (37) maps and SST simulated using the FOAM model, projected on a 5° x 5° spatial grid (a, c, e) and

470 calculated by 5° latitudinal bands (grey dots on b, d, and f plots). Acritarch generic diversity calculated by

471 5° latitudinal bands (white squares on b, d, and f) using the range-through counting approach (62).

472 Abbreviations: AGD, acritarch generic diversity; MSD, modeled species diversity.

473

474 **TABLE 1.** Results of generalized linear models (GLM) for acritarch genus diversity per 5° latitudinal  
 475 band for the Cambrian stage 4, the Darriwilian and the Hirnantian. Only the three best models (i.e. with  
 476 the lowest AICc value and highest Akaike weight) are shown here for each time interval.

Age	Family	Dispersion	R <sup>2</sup>	CSA	SST <sub>an</sub>	SST <sup>2</sup>	SST <sub>diff</sub>	SSS <sub>an</sub>	SSS <sup>2</sup>	SSS <sub>diff</sub>	AICc	Akaike weight
Cambrian stage 4	<i>P</i>	1.793	0.580				0.057		0.003		171.28	0.078
	<i>Quasi P</i>	1.793	0.580				0.057		0.003		∅	∅
	<i>Neg. Bin.</i>	1.119	0.577				0.053		0.003		169.95	∅
Darriwilian	<i>P</i>	4.324	0.733	0.094	-0.118			19.647	-0.281		196.21	0.286
	<i>Quasi P</i>	4.324	0.733	0.094	-0.118			19.647	-0.281		∅	∅
	<i>Neg. Bin.</i>	1.887	0.611	0.118	-0.121			19.916	-0.286		186.59	∅
Hirnantian	<i>P</i>	4.852	0.843	0.252	-0.258		0.259		0.018		158.91	0.331
	<i>Quasi P</i>	4.852	0.843	0.252	-0.258		0.259		0.018		∅	∅
	<i>Neg. Bin.</i>	1.887	0.884	0.295	-0.305		0.282		0.021		133.83	∅

Abbreviations: *P*, Poisson; *Quasi P*, quasi-Poisson; *Neg. bin.*; negative binomial; CSA, continental shelf area (10<sup>6</sup> km<sup>2</sup>), SST<sub>an</sub>, mean annual sea-surface temperature; SST<sup>2</sup>, squared SST; SST<sub>diff</sub>, difference between summer and winter SST; SSS<sub>an</sub>, mean annual sea-surface salinity; SSS<sup>2</sup>, squared SSS; SSS<sub>diff</sub> difference between summer and winter SSS. Dispersion = residual deviance/degrees of freedom, overdispersion when > 1.

477

478

479 **TABLE 2.** Results of Kendall's rank correlation tests between acritarch genus diversity per 5° latitudinal  
 480 band and SST, SSS and CSA.

<b>Temporal interval</b>	<b><i>n</i></b>	<b>CSA</b>	<b>SST<sub>an</sub></b>	<b>SST<sup>2</sup></b>	<b>SST<sub>diff</sub></b>	<b>SSS<sub>an</sub></b>	<b>SSS<sup>2</sup></b>	<b>SSS<sub>diff</sub></b>
Cambrian stage 4	25	0.474**	0.258	0.258	0.007	0.439**	0.439**	0.223
Darriwilian	21	-0.253	-0.253	-0.253	0.531**	-0.045	-0.045	-0.313
Hirnantian	19	-0.089	-0.252	-0.361*	0.402*	0.061	0.061	0.211

Abbreviations: *n*, number of latitudinal bands; CSA, continental shelf area (10<sup>6</sup> km<sup>2</sup>); SST<sub>an</sub>, mean annual sea-surface temperature; SST<sup>2</sup>, squared SST; SST<sub>diff</sub>, difference between summer and winter SST; SSS<sub>an</sub>, mean annual sea-surface salinity; SSS<sup>2</sup>, squared SSS; SSS<sub>diff</sub>, difference between summer and winter SSS. \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05; no symbol = not significant.

481

482

483 **Truncated bimodal latitudinal diversity gradient in early Paleozoic**  
484 **phytoplankton**

485

486 **Supplementary Information**

487

488 Axelle Zacaï<sup>1\*</sup>, Claude Monnet<sup>1</sup>, Alexandre Pohl<sup>2,3</sup>, Grégory Beaugrand<sup>4</sup>, Gary Mullins<sup>5</sup>, David Kröck<sup>1</sup>,  
489 Thomas Servais<sup>1</sup>

490 <sup>1</sup> Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

491 <sup>2</sup> Department of Earth Sciences, University of California, Riverside, CA, USA

492 <sup>3</sup> Biogéosciences, UMR 6282, CNRS, Université Bourgogne Franche-Comté, 6 boulevard Gabriel, F-  
493 21000 Dijon, France

494 <sup>4</sup> Univ. Lille, CNRS, UMR 8187 - Laboratoire d'Océanologie et de Géosciences, F-59000 Lille, France

495 <sup>5</sup> Robertson, a CGG Company, Llandudno, LL30 1SA, UK

496

497 **Latitudinal diversity gradient (LDG).** Analyses of the latitudinal distribution of diversity were  
498 conducted at the genus level because it is considered more robust than an analysis performed at the species  
499 level for three main reasons: (i) genera are easier to identify than species because they are defined by  
500 broader characteristics that remain identifiable when the species is unknown to the author or when  
501 preservation is incomplete (1), (ii) this level suffers less from inconsistent taxonomic treatment among  
502 different workers (2, 3), and (iii) for acritarchs in particular, many species are suspected to be  
503 ecophenotypes rather than different biological species (4), which inevitably leads to an overestimation of  
504 diversity at the species level. The fossil record of acritarchs is therefore assumed to be more preserved,  
505 and their stratigraphic and geographic ranges more accurate, at the genera than at the species level. We  
506 compared sampling effort for these temporal intervals using size-based rarefaction curves (5–7) computed  
507 using R (8) and the package ‘vegan’ (9). The rarefaction curves show that among the four Cambrian series

508 and the seven Ordovician stages, the best sampled intervals are the Cambrian series 2, the Miaolingian  
509 (i.e. Cambrian series 3), the Floian, and the Darriwilian, and the least sampled ones are the Terreneuvian  
510 and the Sandbian (Fig. S2).

511  
512 **Paleoclimatic simulations.** *The FOAM model.* Fields of sea-surface temperature and sea-surface salinity  
513 for the early Paleozoic were simulated using the Fast Ocean Atmosphere Model (FOAM) version 1.5 (10),  
514 a mixed-resolution general circulation model that has been routinely used to study climate in the deep  
515 time. The atmospheric component is a parallelized version of the National Center for Atmospheric  
516 Research's (NCAR) Community Climate Model 2 (CCM2) with radiative and hydrologic physics  
517 upgraded after CCM3 version 3.2 (11). It uses a R15 spectral resolution ( $4.5^\circ \times 7.5^\circ$ ) with 18 levels in the  
518 vertical dimension. The ocean model is the Ocean Model version 3 (OM3). It is a z-coordinate ocean  
519 general circulation model, run at a  $1.4^\circ \times 2.8^\circ$  resolution. Sea ice is simulated based on the  
520 thermodynamic component of the CSM 1.4 sea-ice model, which is based on the Semtner 3-layer  
521 thermodynamic snow/ice model (12). The coupled FOAM model is well designed for paleoclimate  
522 studies. It has no flux correction and its quick turnaround time allows for long millennium-scale  
523 integrations. FOAM has been widely used in paleoclimate studies (13–18).

524 *Boundary conditions.* In terms of boundary conditions, we used the continental configurations of Scotese  
525 and Wright (19) at 510 Ma for the Cambrian Stage 4, 460 Ma for the Darriwilian, and 445 Ma for the  
526 Hirnantian. Time-evolving solar luminosity values were calculated after the model of stellar physics of  
527 Gough (20). Orbital parameters were set to present-day values. We used previous modeling work and  
528 available geological constraints to select atmospheric CO<sub>2</sub> values ( $p\text{CO}_2$ ) providing the most plausible  
529 climatic states for each time period under investigation. For 510 Ma, we used 32 PAL (preindustrial  
530 atmospheric level, 1 PAL = 280 ppm). Hearing et al. (21) demonstrated that the FOAM model simulates  
531 sea-surface temperatures on Avalonia (ca.  $65^\circ$  S) at 510 Ma that satisfactorily match the estimates derived  
532 from the geochemical analysis of fossil biogenic phosphate when simulations are run using this  $p\text{CO}_2$   
533 value. This  $p\text{CO}_2$  level is also in line with the estimate derived from the GEOCARBSULF model (22). For



534 460 Ma (Darriwilian), we used a  $p\text{CO}_2$  of 12 PAL. Such radiative forcing was shown to trigger the growth  
535 of land ice over the South Pole (23), which is in agreement with recent studies suggesting that Ordovician  
536 ice sheets may have developed as early as the Mid Ordovician Darriwilian (24–26). The mean annual,  
537 topical sea-surface temperature simulated at 12 PAL (30.1 °C) corresponds well to the temperature  
538 estimate derived from geochemical analyses for the same period of time (27). For the Hirnantian, we  
539 selected a value of 5 PAL. This value is supported by the study of Pancost et al. (28), who analysed  
540 isotope fractionation between organic and inorganic carbon during photosynthesis ( $\epsilon_p$ ) and calculated a  
541  $p\text{CO}_2$  below ~8 PAL during the Katian. In addition, Pohl et al. (17) demonstrated a climatic instability in  
542 the Ordovician ocean-atmosphere system, which induces a strong global cooling when atmospheric  $\text{CO}_2$  is  
543 lowered below 8 PAL in the FOAM model. They demonstrated that this strong cooling results from the  
544 sudden spread of sea ice to the mid-latitudes. The authors suggested that this instability may explain the  
545 strong cooling documented during the latest Ordovician based on geochemical data (27, 29). They also  
546 showed (23) that the extent of the ice sheet simulated under the cold climatic state matches well the  
547 geological record of glaciation (30), and that associated ocean temperatures are in good agreement with  
548 the climatic belts reconstructed for the Hirnantian by Vandenbroucke et al. (31) based on  
549 micropaleontological data. An analysis of the sea-ice fraction (not shown in the present study, but see  
550 ocean temperatures in Fig. S3 where  $-2$  °C broadly represents the sea-ice extent) confirms that our model  
551 run conducted at 5 PAL using the continental reconstruction of Scotese and Wright (19) belongs to the  
552 cold climatic mode. The mean annual tropical sea-surface temperature in this model run (22.1 °C) is in  
553 agreement with the reconstruction of Trotter et al. (27). Concentrations of other greenhouse gases were  
554 kept to the present-day level. Non-vascular plants started colonizing the continents during the early  
555 Middle Ordovician (32). Vascular plants appeared later, during the Late Ordovician (33). The spatial  
556 coverage of these land plants remains debated (34–36). We therefore imposed a bare soil (rocky desert) at  
557 every land grid point (37, 38).

558 *Initial conditions and model integration.* Simulations were initialized using warm ocean temperatures to  
559 make sure that deep-ocean equilibrium was rapidly reached through oceanic convection. A uniform initial

560 ocean salinity of 35 ‰ was imposed in every model run. Simulations were run until deep-ocean thermal  
561 equilibrium was reached (2000 years). The last 50 years were used to build the monthly climatology files  
562 used for the analyses.

563  
564 **Generalized Linear Model.** To determine the predictor or combination of predictors of acritarch  
565 latitudinal diversity, the best GLM was identified for each stage by the second-order Akaike information  
566 criterion (AICc), which contains a correction for small sample sizes (39, 40). When the first best models  
567 had very close AICc values, we considered as predictors of diversity only the abiotic factors that occurred  
568 in the majority of models. When the best model (i.e. the one with the lowest AICc value) showed an  
569 overdispersion (i.e. residual deviance/degrees of freedom > 1), two alternative models were built by  
570 keeping only the predictors of this best model, and by using a negative binomial and a quasi-Poisson  
571 distribution instead.

572  
573 **Modeled diversity.** The MacroEcological Theory on the Arrangement of Life (METAL; 41–43) states  
574 that biodiversity is strongly influenced by climate and environment, in a deterministic manner (44). This  
575 influence mainly occurs through the interactions between the species ecological niche and both climatic,  
576 and environmental changes. The theory uses the concept of ecological niche *sensu* Hutchinson (i.e. the  
577 range of a species tolerance when several factors are taken simultaneously) as an elementary emergent  
578 macroscopic process, to predict (i) local changes in abundance (45), species phenology, and biogeographic  
579 range shifts (46) at the species level, and (ii) the arrangement of biodiversity, including the latitudinal  
580 diversity gradient (47), and long-term community/ecosystem shifts, including regime shifts (48), at the  
581 community level. We assume here that the ecological niche integrates the sum of many physiological  
582 processes occurring at both the individual and population levels. This theory offers a way to make testable  
583 ecological and biogeographical predictions to understand how life is organized, and how it responds to  
584 global environmental changes (44–47). Pseudo-species and pseudo-communities (i.e. virtual species and  
585 communities) can be generated throughout the ocean provided that their ecological niche enables them to

586 withstand local changes in the climatic and the environmental regime in time. Actual communities only  
587 represent a subset of the theoretical pseudo-communities because not all niches are occupied in a given  
588 location (48).

589

## 590 **References**

- 591 1. H. Nowak, T. Servais, C. Monnet, S. G. Molyneux, T. R. A. Vandenbroucke, Phytoplankton  
592 dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification  
593 Event: A review of Cambrian acritarch diversity. *Earth-Science Reviews* **151**, 117–131 (2015).
- 594 2. A. Z. Krug, D. Jablonski, J. W. Valentine, K. Roy, Generation of Earth’s First-Order Biodiversity  
595 Pattern. *Astrobiology* **9**, 113–124 (2009).
- 596 3. P. D. Mannion, *et al.*, A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for  
597 Late Cretaceous geographical partitioning: Temperate palaeodiversity peak in dinosaurs. *Global*  
598 *Ecology and Biogeography* **21**, 898–908 (2012).
- 599 4. T. Servais, L. Stricanne, M. Montenari, J. Pross, Population dynamics of galeate acritarchs at the  
600 Cambrian-Ordovician transition in the Algerian Sahara. *Palaeontology* **47**, 395–414 (2004).
- 601 5. S. H. Hurlbert, The Nonconcept of Species Diversity: A Critique and Alternative Parameters.  
602 *Ecology* **52**, 577–586 (1971).
- 603 6. N. J. Gotelli, R. K. Colwell, Quantifying biodiversity: procedures and pitfalls in the measurement  
604 and comparison of species richness. *Ecology Letters* **4**, 379–391 (2001).
- 605 7. A. Chao, L. Jost, Coverage-based rarefaction and extrapolation: standardizing samples by  
606 completeness rather than size. *Ecology* **93**, 2533–2547 (2012).
- 607 8. R Development Core Team, *R: A Language and Environment for Statistical Computing, version*  
608 *3.5.3*. (R Foundation for Statistical Computing, 2019).
- 609 9. J. Oksanen, *et al.*, *Vegan: community ecology package, version 2.5-4* (2019).
- 610 10. R. L. Jacob, “Low frequency variability in a simulated atmosphere ocean system” Doctoral  
611 dissertation, Madison University of Wisconsin-Madison. (1997).

- 612 11. J. T. Kiehl, *et al.*, The National Center for Atmospheric Research Community Climate Model:  
613 CCM3. *Journal of Climate* **11**, 1131–1149 (1998).
- 614 12. A. J. Semtner Jr, A model for the thermodynamic growth of sea ice in numerical investigations of  
615 climate. *Journal of Physical Oceanography* **6**, 379–389 (1976).
- 616 13. G. Dera, Y. Donnadieu, Modeling evidences for global warming, Arctic seawater freshening, and  
617 sluggish oceanic circulation during the Early Toarcian anoxic event. *Paleoceanography* **27**, PA2211  
618 (2012).
- 619 14. Y. Donnadieu, E. Pucéat, M. Moiroud, F. Guillocheau, J.-F. Deconinck, A better-ventilated ocean  
620 triggered by Late Cretaceous changes in continental configuration. *Nature Communications* **7**, 10316  
621 (2016).
- 622 15. J.-B. Ladant, Y. Donnadieu, Palaeogeographic regulation of glacial events during the Cretaceous  
623 supergreenhouse. *Nature Communications* **7**, 12771 (2016).
- 624 16. C. J. Poulsen, R. T. Pierrehumbert, R. L. Jacob, Impact of ocean dynamics on the simulation of the  
625 neoproterozoic “snowball Earth.” *Geophys. Res. Lett.* **28**, 1575–1578 (2001).
- 626 17. A. Pohl, Y. Donnadieu, G. Le Hir, J.-F. Buoncristiani, E. Vennin, Effect of the Ordovician  
627 paleogeography on the (in)stability of the climate. *Clim. Past* **10**, 2053–2066 (2014).
- 628 18. E. Nardin, *et al.*, Modeling the early Paleozoic long-term climatic trend. *Geological Society of*  
629 *America Bulletin* **123**, 1181–1192 (2011).
- 630 19. C. R. Scotese, N. Wright, PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the  
631 Phanerozoic (2018).
- 632 20. D. O. Gough, Solar interior structure and luminosity variations. *Physics of Solar Variations* **74**, 21–  
633 34 (1981).
- 634 21. T. W. Hearing, *et al.*, An early Cambrian greenhouse climate. *Science Advances* **4**, eaar5690 (2018).
- 635 22. R. A. Berner, Inclusion of the weathering of volcanic rocks in the GEOCARBSULF model.  
636 *American Journal of Science* **306**, 295–302 (2006).

- 637 23. A. Pohl, *et al.*, Glacial onset predated Late Ordovician climate cooling. *Paleoceanography* **31**, 800–  
638 821 (2016).
- 639 24. M. P. Dabard, *et al.*, Sea-level curve for the Middle to early Late Ordovician in the Armorican  
640 Massif (western France): Icehouse third-order glacio-eustatic cycles. *Palaeogeography,*  
641 *Palaeoclimatology, Palaeoecology* **436**, 96–111 (2015).
- 642 25. B. R. Turner, H. A. Armstrong, C. R. Wilson, I. M. Makhlof, High frequency eustatic sea-level  
643 changes during the Middle to early Late Ordovician of southern Jordan: Indirect evidence for a  
644 Darriwilian Ice Age in Gondwana. *Sedimentary Geology* **251**, 34–48 (2012).
- 645 26. C. M. Ø. Rasmussen, *et al.*, Onset of main Phanerozoic marine radiation sparked by emerging Mid  
646 Ordovician icehouse. *Scientific Reports* **6**, 18884 (2016).
- 647 27. J. A. Trotter, I. S. Williams, C. R. Barnes, C. Lecuyer, R. S. Nicoll, Did Cooling Oceans Trigger  
648 Ordovician Biodiversification? Evidence from Conodont Thermometry. *Science* **321**, 550–554  
649 (2008).
- 650 28. R. D. Pancost, *et al.*, Reconstructing Late Ordovician carbon cycle variations. *Geochimica et*  
651 *Cosmochimica Acta* **105**, 433–454 (2013).
- 652 29. S. Finnegan, *et al.*, The magnitude and duration of Late Ordovician–Early Silurian glaciation.  
653 *Science* **331**, 903–906 (2011).
- 654 30. J.-F. Ghienne, D. P. Le Heron, J. Moreau, M. Denis, M. Deynoux, “The Late Ordovician Glacial  
655 Sedimentary System of the North Gondwana Platform” in *Glacial Sedimentary Processes and*  
656 *Products*, M. J. Hambrey, P. Christoffersen, N. F. Glasser, B. Hubbard, Eds. (Blackwell Publishing  
657 Ltd., 2009), pp. 295–319.
- 658 31. T. R. A. Vandenbroucke, *et al.*, Polar front shift and atmospheric CO<sub>2</sub> during the glacial maximum  
659 of the Early Paleozoic Icehouse. *Proceedings of the National Academy of Sciences* **107**, 14983–  
660 14986 (2010).

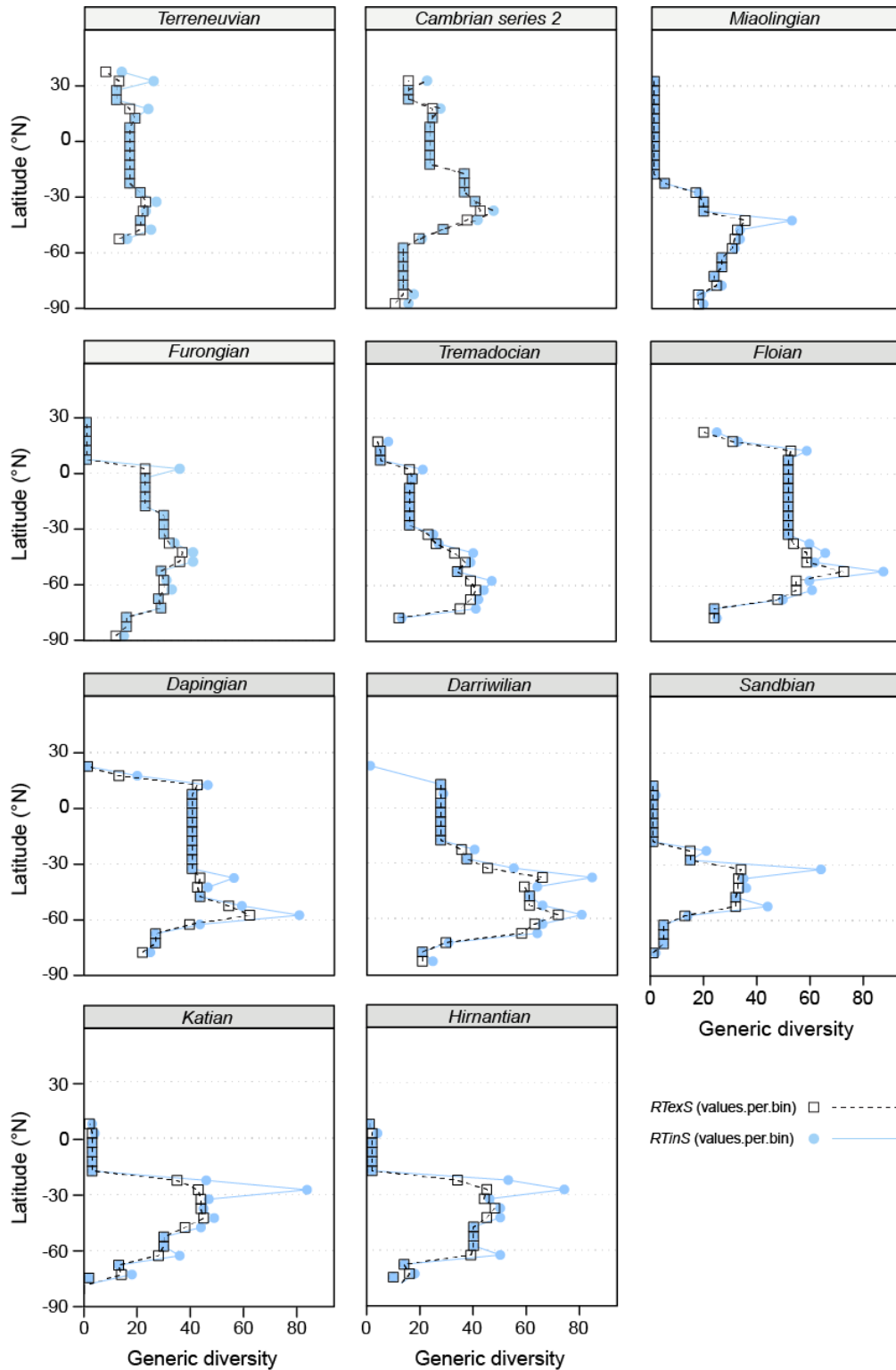
- 661 32. C. V. Rubinstein, P. Gerrienne, G. S. de la Puente, R. A. Astini, P. Steemans, Early Middle  
662 Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist* **188**, 365–  
663 369 (2010).
- 664 33. P. Steemans, *et al.*, Origin and radiation of the earliest vascular land plants. *Science* **324**, 353–353  
665 (2009).
- 666 34. D. Edwards, L. Cherns, J. A. Raven, Could land-based early photosynthesizing ecosystems have  
667 bioengineered the planet in mid-Palaeozoic times? *Palaeontology* **58**, 803–837 (2015).
- 668 35. T. M. Lenton, M. Crouch, M. Johnson, N. Pires, L. Dolan, First plants cooled the Ordovician.  
669 *Nature Geosci* **5**, 86–89 (2012).
- 670 36. P. Porada, *et al.*, High potential for weathering and climate effects of non-vascular vegetation in the  
671 Late Ordovician. *Nature Communications* **7**, 12113 (2016).
- 672 37. A. Pohl, *et al.*, Possible patterns of marine primary productivity during the Great Ordovician  
673 Biodiversification Event. *Lethaia* **51**, 187–197 (2017).
- 674 38. A. Pohl, E. Nardin, T. R. A. Vandenbroucke, Y. Donnadieu, High dependence of Ordovician ocean  
675 surface circulation on atmospheric CO<sub>2</sub> levels. *Palaeogeography, Palaeoclimatology,*  
676 *Palaeoecology* **458**, 39–51 (2016).
- 677 39. H. Akaike, A new look at the statistical model identification. *IEEE Transactions on Automatic*  
678 *Control* **19**, 716–723 (1974).
- 679 40. K. P. Burnham, D. R. Anderson, Multimodel Inference: Understanding AIC and BIC in Model  
680 Selection. *Sociological Methods & Research* **33**, 261–304 (2004).
- 681 41. G. Beaugrand, E. Goberville, C. Luczak, R. R. Kirby, Marine biological shifts and climate. *Proc. R.*  
682 *Soc. B* **281**, 20133350 (2014).
- 683 42. G. Beaugrand, I. Rombouts, R. R. Kirby, Towards an understanding of the pattern of biodiversity in  
684 the oceans. *Global Ecology and Biogeography* **22**, 440–449 (2013).
- 685 43. G. Beaugrand, C. Luczak, E. Goberville, R. R. Kirby, Marine biodiversity and the chessboard of life.  
686 *PLoS ONE* **13**, e0194006 (2018).

- 687 44. G. Beaugrand, Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Phil.*  
688 *Trans. R. Soc. B* **370**, 20130264 (2015).
- 689 45. G. Beaugrand, D. Mackas, E. Goberville, Applying the concept of the ecological niche and a  
690 macroecological approach to understand how climate influences zooplankton: Advantages,  
691 assumptions, limitations and requirements. *Progress in Oceanography* **111**, 75–90 (2013).
- 692 46. G. Beaugrand, E. Goberville, C. Luczak, R. R. Kirby, Marine biological shifts and climate. *Proc. R.*  
693 *Soc. B* **281**, 20133350 (2014).
- 694 47. G. Beaugrand, *Marine biodiversity, climatic variability and global change* (Routledge, 2014).
- 695 48. J. W. Valentine, J. D. Witman, K. Roy, “Overview of marine biodiversity” in *Marine macroecology*,  
696 J. D. Witman, K. Roy, Eds. (University of Chicago Press, Chicago, 2009) pp. 3–28.
- 697 49. R. D. Müller, *et al.*, GPlates: Building a Virtual Earth Through Deep Time. *Geochemistry,*  
698 *Geophysics, Geosystems* **19**, 2243–2261 (2018).
- 699 50. C. R. Scotese, PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program. *PALEOMAP*  
700 *Project* (<http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/>) (2016).

701

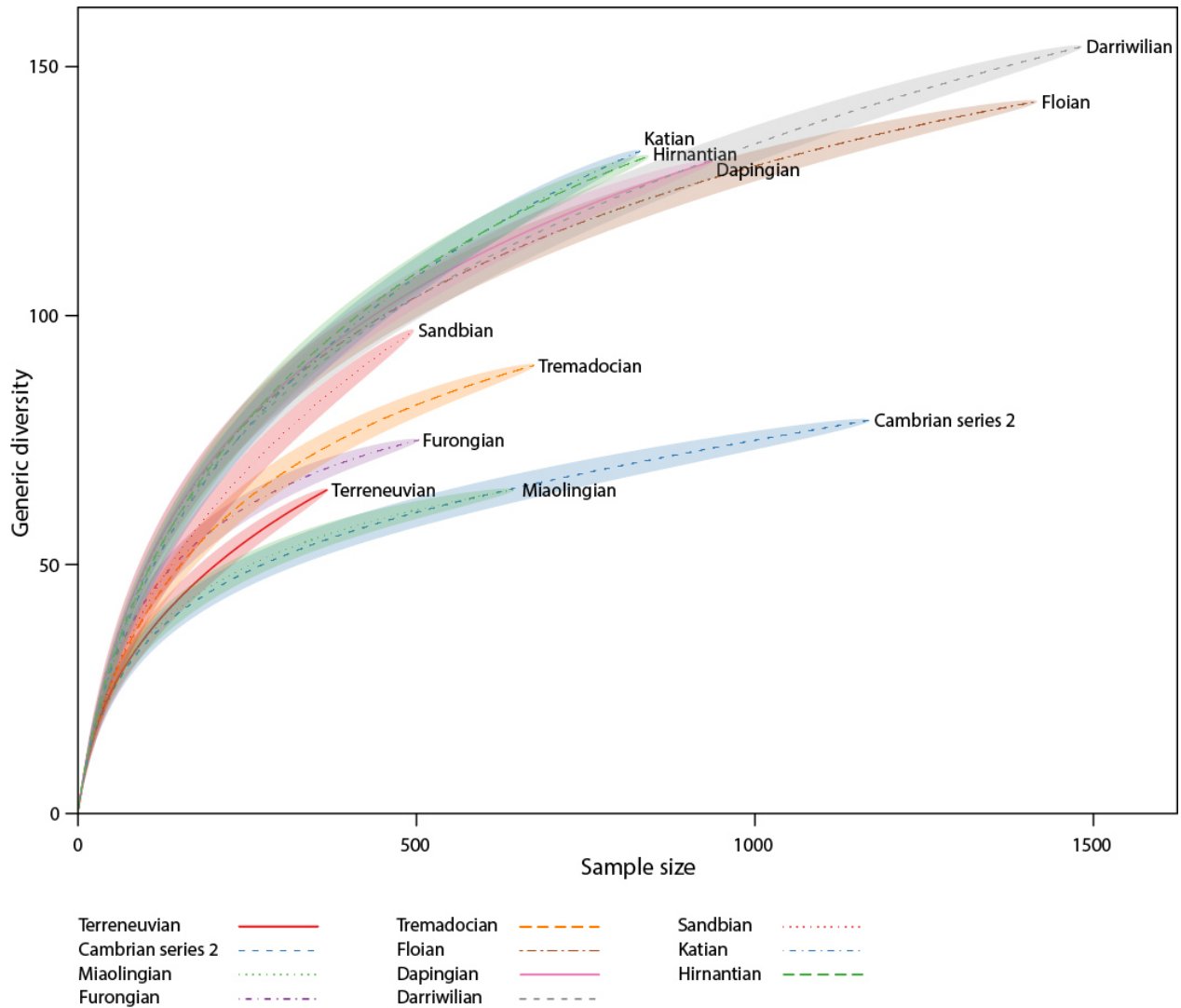
702



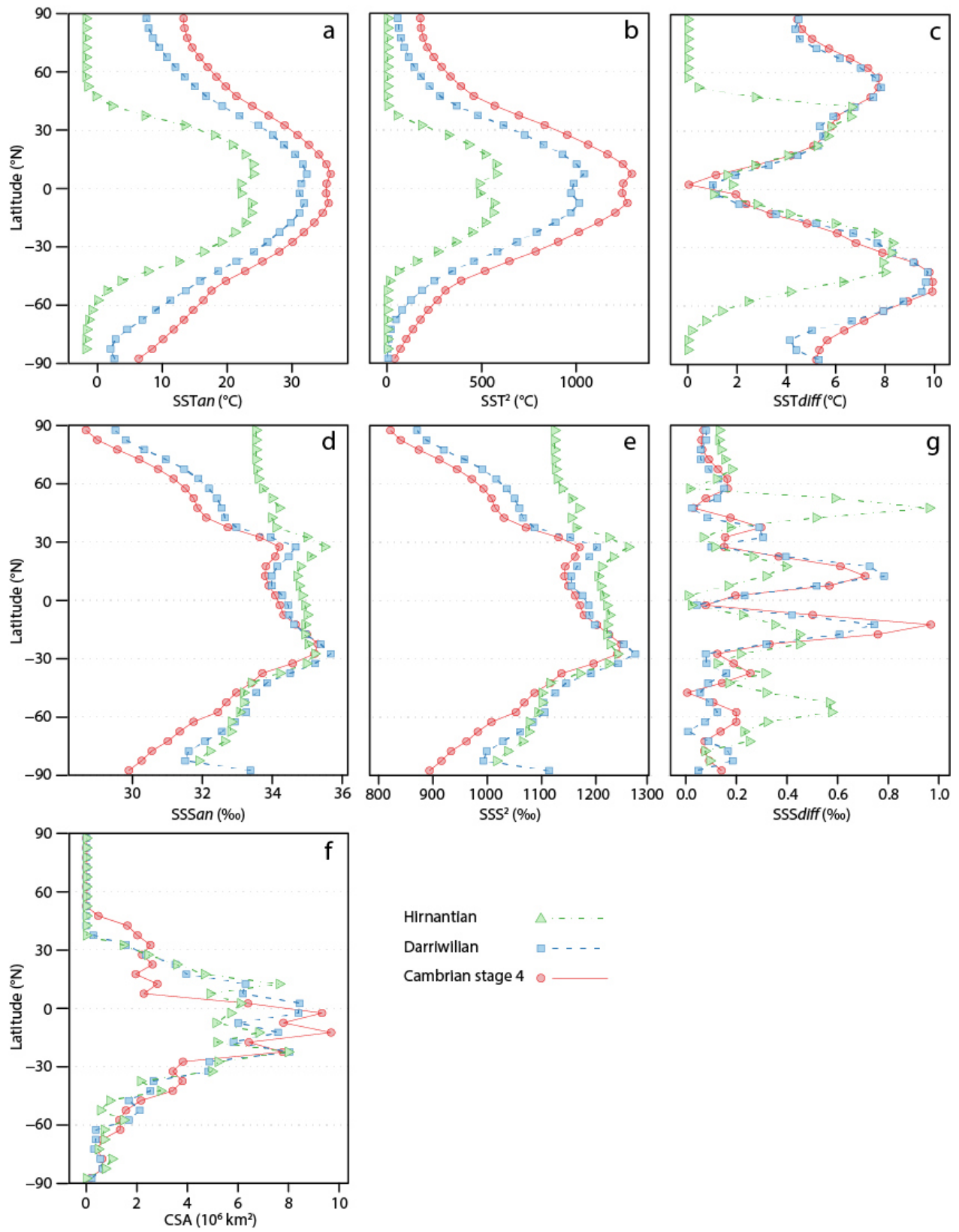


703

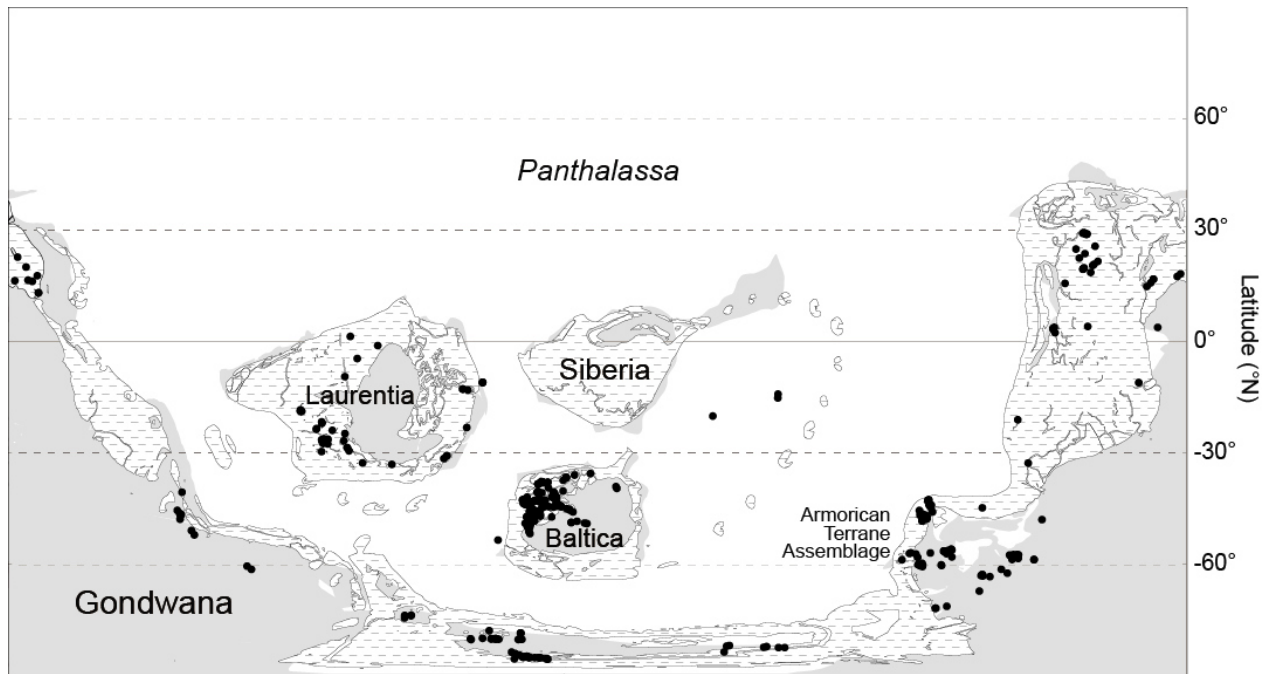
704 **Figure S1.** Acritarch genus diversity calculated per 5° latitudinal bands for each series of the Cambrian  
 705 and each stage of the Ordovician. Diversity was calculated using the standard ‘range-through’ counting  
 706 approach, with and without single-interval taxa (*RTinS* and *RTextS* and indices, respectively).



707  
 708 **Figure S2.** Size-based rarefaction curves and their associated standard deviation for early Paleozoic  
 709 acritarch genera. Each curve corresponds to a Cambrian series or an Ordovician stage. The best sampled  
 710 intervals are the Cambrian series 2, the Miaolingian (Cambrian series 3), the Floian, and the Darriwilian;  
 711 and the least sampled are the Terreneuvian and the Sandbian.  
 712



714 **Figure S3.** Latitudinal distribution of modeled mean annual sea-surface temperature (SST), sea-surface  
715 salinity (SSS) and continental shelf area (CSA, in millions of km<sup>2</sup>) for the Cambrian stage 4 (*p*CO<sub>2</sub>=32  
716 PAL), Darriwilian (12 PAL) and Hirnantian (5 PAL), per 5° latitudinal bands. a) mean annual SST  
717 (SST<sub>an</sub>), b) squared mean annual SST (SST<sup>2</sup>), c) seasonal variation in SST (SST<sub>diff</sub>, i.e. difference  
718 between summer and winter SST), d) mean annual SSS (SSS<sub>an</sub>), e) squared mean annual SSS (SSS<sup>2</sup>), f)  
719 seasonal variation in SSS (SSS<sub>diff</sub>, i.e. difference between summer and winter SSS), g) CSA based on  
720 Scotese and Wright's (19) maps.  
721



722  
 723 **Figure S4.** Paleogeographical context of the early Paleozoic. (a) Paleogeographical reconstruction for the  
 724 mid-early Paleozoic (Jiangshanian, 491.75 Ma) computed with GPlates 2.0.0 (49) using the rotation file of  
 725 Scotese (50), and paleolocation of the 328 fossil localities used in this study (black dots) for this time  
 726 interval. Striped parts correspond to continental shelf areas after Scotese (50).