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Spécialité: Géosciences, Ecologie, Paléontologie et Océanographie

par

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La biodiversité du phytoplancton du Paléozoïque

Thèse dirigée par

Thomas SERVAIS

et

Claude MONNET

Date de soutenance prévue le 06 décembre 2019

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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

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Thomas SERVAIS

and

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Public defense scheduled for the 06th December 2019

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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_2 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

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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_2 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, micropalaéontologie, phytoplancton, acritarches, prasinophytes, Paléozoïque, biodiversité, paléogéographie, paléoécologie, taxonomie, biostratigraphie

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Table of contents

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

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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

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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 cyle. 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_2 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_2 in the upper ocean layers, the absorption of CO_2 from the atmosphere is faciliated by the generation of a steeper CO_2 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_2/O_2 balance since the early Precambrian, with decreasing CO_2 and increasing O_2 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_2, 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

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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_2 levels. It is estimated that marine ecosystems account for nearly one third of the anthropogenic CO_2 emissions being removed from the atmosphere (Hader et al., 2014). Increases of atmospheric CO_2 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_2 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_2, which is also observed during algal blooms, leading to significantly lower CO_2 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, coccolitiophorids and cyanobacteria (Dutkiewicz et al., 2015). While some studies concern the effects of elevated CO_2 concentrations on phytoplankton growth rates and photosynthesis, the conclusions are divergent: While Hein & SandJensen (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_2 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 phytoplanktic 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 exosystems, 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 event and, major extinctions. The early Palaeozoic atmosphere had much higher concentrations of CO_2, 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.

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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 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, wether 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;

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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, decended 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 & Moczydłowska, 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 occured 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 melanocyrillid (vase-shaped) forms appear during this time (Vidal, 1984). A second major radiation is known from the early Cambrian (e.g., Moczydłowska & Zang, 2005; Moczydłowska, 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.

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1.6 Acritarchs – affinities and biology

The term 'acritarch' is derived from the greek words ἄκριτος, 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 tread 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 resistent 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

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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 extanct 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 4α-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 phycomata, 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 zygnematacean 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.

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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 ± 1.0 Ma to the Permian/Triassic boundary at 251.902 ± 0.024 Ma). The era is devided 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 ± 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 ± 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 ± 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 ± 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 ± 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 *Streptogrnathodus isolatus* at the Aidaralash section marks the GSSP at the Carboniferous/Permian boundary (298.9 ± 0.15 Ma) (Davydov et al., 1998). The GSSP for the Palaeozoic/Mesozoic boundary (251,902 ± 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.

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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 ecosytems, 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 where 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, Carolinia, 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

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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 Midde–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 del-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_2 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

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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_2 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 &

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Reyre, 1974; Tappan, 1980): The Sphaeromorphitae comprise forms without processes or crests. These are usually spherical or ellipsoidal with smooth or ornamented vesicle walls. Acritarchs from the Herkomophitae subgroup display crests, which devide the vesicle surface into polygonal fields. The subgroup Acanthomorphitae 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 Diacromorphitae. The Netromorphitae 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 Oomorphitae. Acritarchs of the Polygonomorphitae subgroup show a polygonal vesicle and mostly simple processes. The Prismatomorphitae 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 succesfull. 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.

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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*), *Pyxidinopsis 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 *Spiniferitis 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 vancampoae*, 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 thatmany 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), *Arkonia–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), *Crassiangulina* 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

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(Martin, 1996) *Liliosphaerdium* 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* Vanguestaine 1973 (and "*Dasydiacrodium*" *caudatum* Vanguestaine 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 exagerated. 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 forth 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

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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; Sepsoski & 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).

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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 Hérissé & Gourvennec, 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 & Dìez, 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

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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 Hérissé & Gourvennec, 1995; Le Hérissé et al., 1997). The different biofacies were controlled by depositional environment rather than biogeography (Le Hérissé & Gourvennec, 1995). Le Hérissé & Gourvennec (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 Hérissé et al., 1997), acritarch assemblages contained a higher amount of cosmopolitan taxa (Le Hérissé 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.

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Article I

Biodiversity of Palaeozoic phytoplankton

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Biodiversity of Palaeozoic phytoplankton

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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_2.

Keywords: phytoplankton, acritarchs, Palaeozoic, biodiversity, palaeoecology

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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 transfered to green algal classes (Chlorophyceae, Prasinophyceae, Zygnemataphyceae; e.g., Wall, 1962, Tappan, 1980; Le Hérissé, 1984; Guy-Ohlson, 1996; Martin et al., 2008; Kaźmierczak & Kremer, 2009; Moczydłowska, 2010). Prasinophytes, the reproductive phycomata 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 & Moczydlowska, 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

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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 & Moczydłowska-Vidal (1997). Moczydłowska (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). Moczydłowska (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 zygnemaaceans. 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.

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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 illegimitate, 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 infered 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

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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

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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 diversites 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 Homerian 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 Homerian/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

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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 extend 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.

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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 higherst diversity in the Ordovician, and the late Palaeozoic exhibit very low numbers. The Silurian in Loeblich & Tappan (1973) shows a smaller

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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 Moczydłowska (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 Moczydłowska (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 Moczydłowska (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 Moczydłowska (2011), a global diversity curve based on Grey (2005), Moczydlowska (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. Moczydłowska (2011) addresses this change, refering it to as the 'early-middle Cambrian taxonomic turnover' (see also Moczydłowska, 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 sudies 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). Similarily, the diveristy in Stage 10 is at a low in our study, but increasing in

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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 decling 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. Similarily, the global diversity changes of chitinozoans in the Ordovician

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(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_{28} steranes were prevailing before the euxinic interval, C_{29} sterane became predominant after this interval. An increase in C_{27} 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_{29} sterane-producing phytoplanktic organisms remain the dominant throughout the Palaeozoic until another shift happens at the Devonian–Carboniferous boundary (Schwark & Empt, 2006). C_{28} 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

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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 $\delta^{13}C$ 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 disturbations of the carbon cycle. The relation between Early to Middle Palaeozoic $\delta^{13}C$ 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 $\delta^{13}C_{carb}$ 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 Hérissé, 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 $\delta^{13}C_{carb}$ and $\delta^{18}O$ values (Brenchley et al., 1995; Paris et al., 2000). This decrease comes after a pronounced positive $\delta^{13}C_{carb}$ excursion. While no direct indication is known from the fossil record, these high $\delta^{13}C_{carb}$ 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.

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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 cylce (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 resent 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 phosphor 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 $\delta^{13}C$ positive excursion recorded in the Palaeozoic. Here again, the extinctions occurred stepwise, with benthic preceeding 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 $\delta^{13}C$ 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 $\delta^{13}C$ excursion, indicating reduced primary production. Moreover, it has been argued, that the extreme amplitude of the Ludfordian $\delta^{13}C$ positive excursion is too high to be

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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 $\delta^{13}C$ values correspond to arid conditions, with low terrestrial input resulting in decreases in phytoplankton productivity. Humid episodes show low $\delta^{13}C$ 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 nesessarily 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 μm). Therefore, such forms are lost in standard palyological preparation techniques using sieves with a mesh size of 20 μm. A distinct increase in the C_{28}/C_{29}-sterane ratio is observed by Schwark & Empt (2006) coinciding with the Hangenberg Event, with values remaining permanently higher after this event. This implies a shift from more primitive phytoplankic organisms, which poduce mainly C_{29}-steranes, to more modern forms, producing C_{28}-steranes. Before this event, short-term increases in the C_{28}/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 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 C_{28}/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 & Empt, 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 C_{28}/C_{29}-sterane ratios. This shift coicides with the appearance of euspondyle and metaspondyle Dasycladales in the Tournaisian/Mississippian (Roux, 1985; 1986) and the global spread of filamentous Codiacea (Siphonales) (Schwark & Empt, 2006). It should be noted, that the prasinophytes, which showed short-term abundance increases in anoxia-related extinction events, also

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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_2 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_2 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

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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 prenascence 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

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("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 phytoplankon 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; Sepsoski & 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 detachement of terranes, such as Avalonia, Canderia, Carolinia 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

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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 (Silurain) 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 Hérissé (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 occuring during a sea-level highstand.

Fig. 8 near here

In general, our phytoplankton diversity curves are roughly paralleling the Palaeozoic gobal sea-level curve (e.g., Haq & Shutter, 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

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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}Sr, as opposed to ^{86}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 $^{87}Sr/^{86}Sr$ 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

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phytoplankton diversity trends than the $^{87}Sr/^{86}Sr$ 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 run-off 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 phytosynthetic 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 atmospherical oxygen concentrations during the early to middle Palaeozoic were lower. Therefore, it is possible that the higher availability of iron has faciliated 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.

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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_2 concentrations

The effects of increased CO_2 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_2 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_2 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_2 concentrations (e.g., Berner, 2008; Royer, 2014), coinciding with high phytoplankton diversity. Middle to late Palaeozoic CO_2 trends are mirroring the diversity curves, with declinging CO_2 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_2 concentrations had an impact on the phytoplankton (compare Strother et al., 2010). Particularly, a relation between the marked decrease in atmospheric CO_2 and the corresponding decrease in biodiversity in the Late Devonian is probable. Therefore, the development of terrestrial plants consuming atmospheric CO_2 and sequestrating 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_2 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_2 from the atmosphere.

Fig. 10 near here

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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 $^{87}Sr/^{86}Sr$ 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 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. CO_2 availability might have facilitated diversification of the phytoplankton on the one hand, but inceasing phytoplankton biomass might have reduced atmospheric CO_2 concentrations on the other.

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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 (RTexS). 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 prenascence.

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 $^{87}Sr/^{86}Sr$ ratios (after Prokoph et al., 2008), and terrestrial sediment influx (after Flögel et al., 2000).

Fig. 10. Comparison of phytoplankton diversity with changes in atmosphaeric CO_2 concentrations (after Berner & Kothavala, 2001; Royer et al., 2004).

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Figure 1

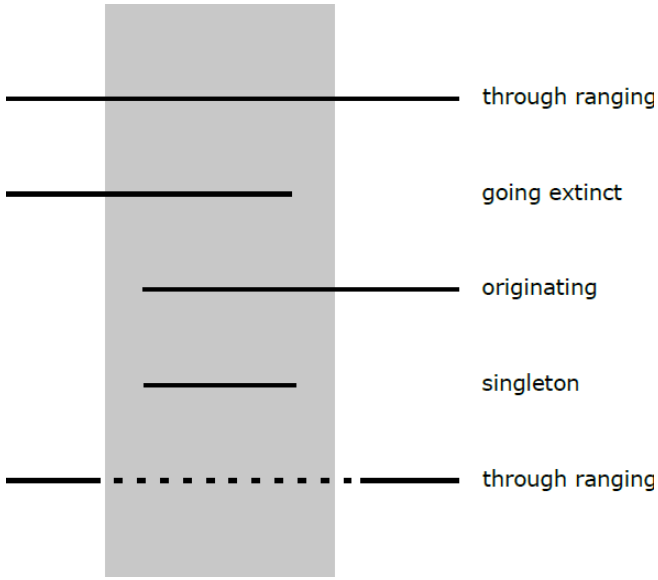

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Figure 2

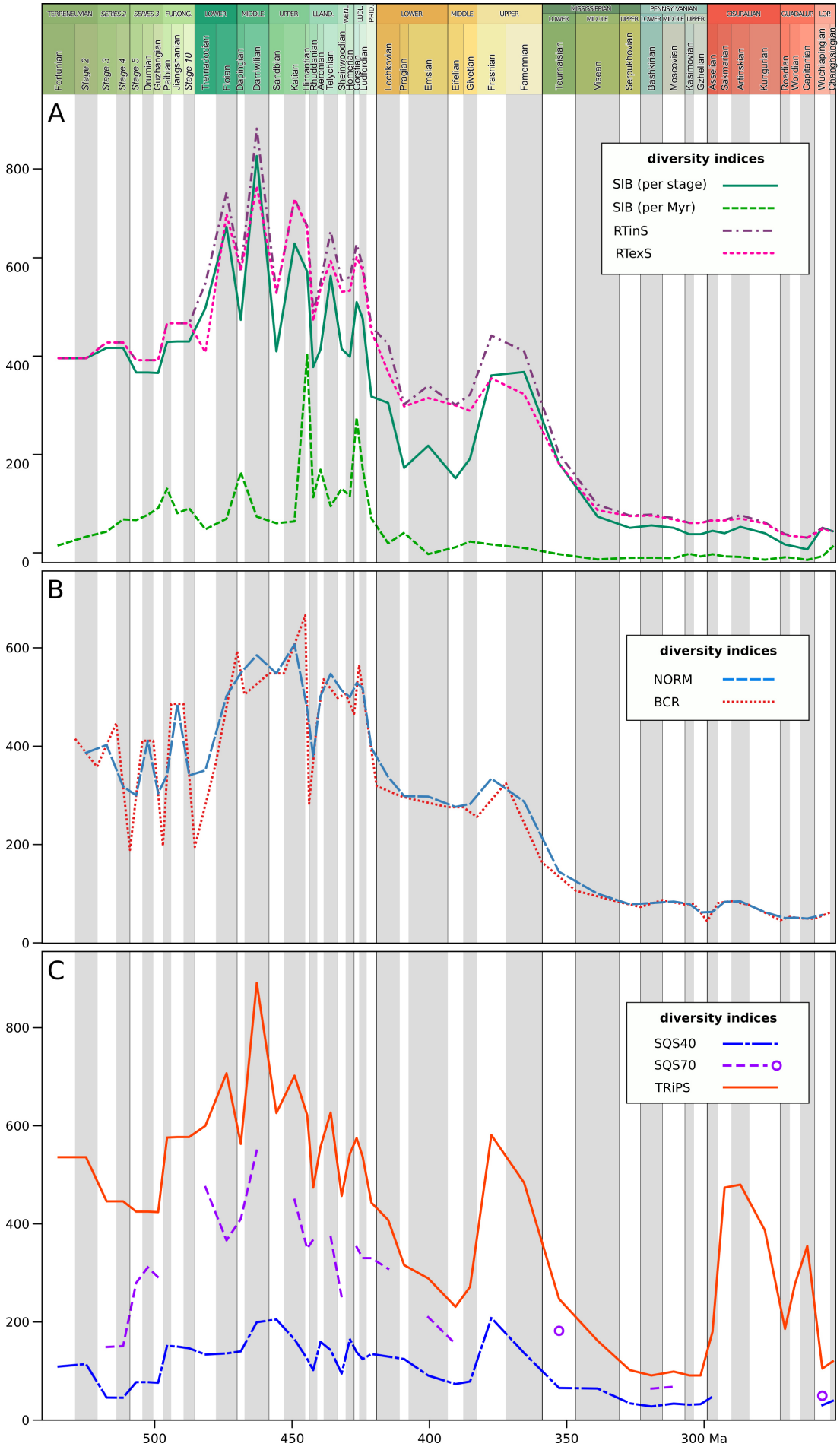

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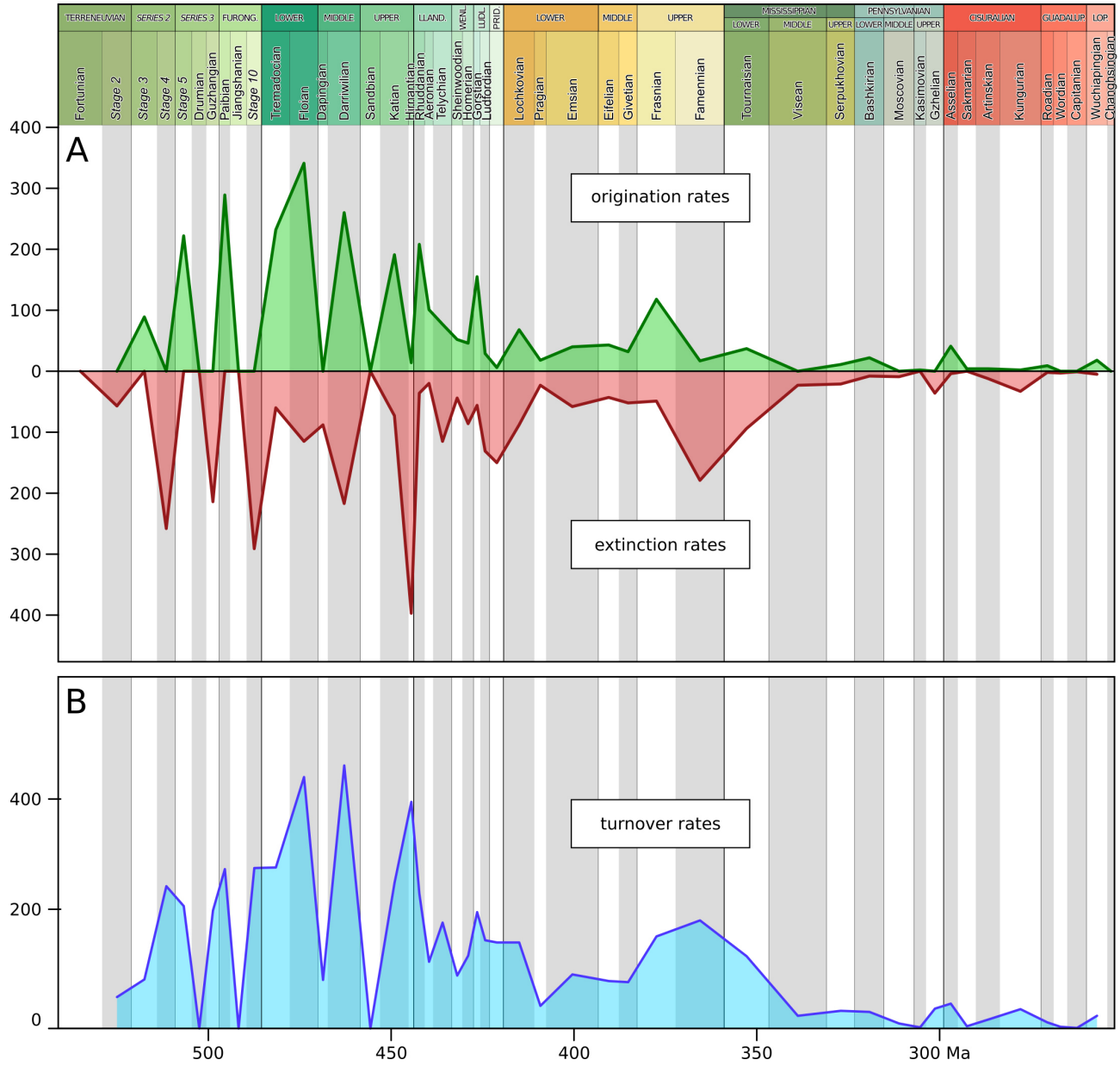
Figure 3



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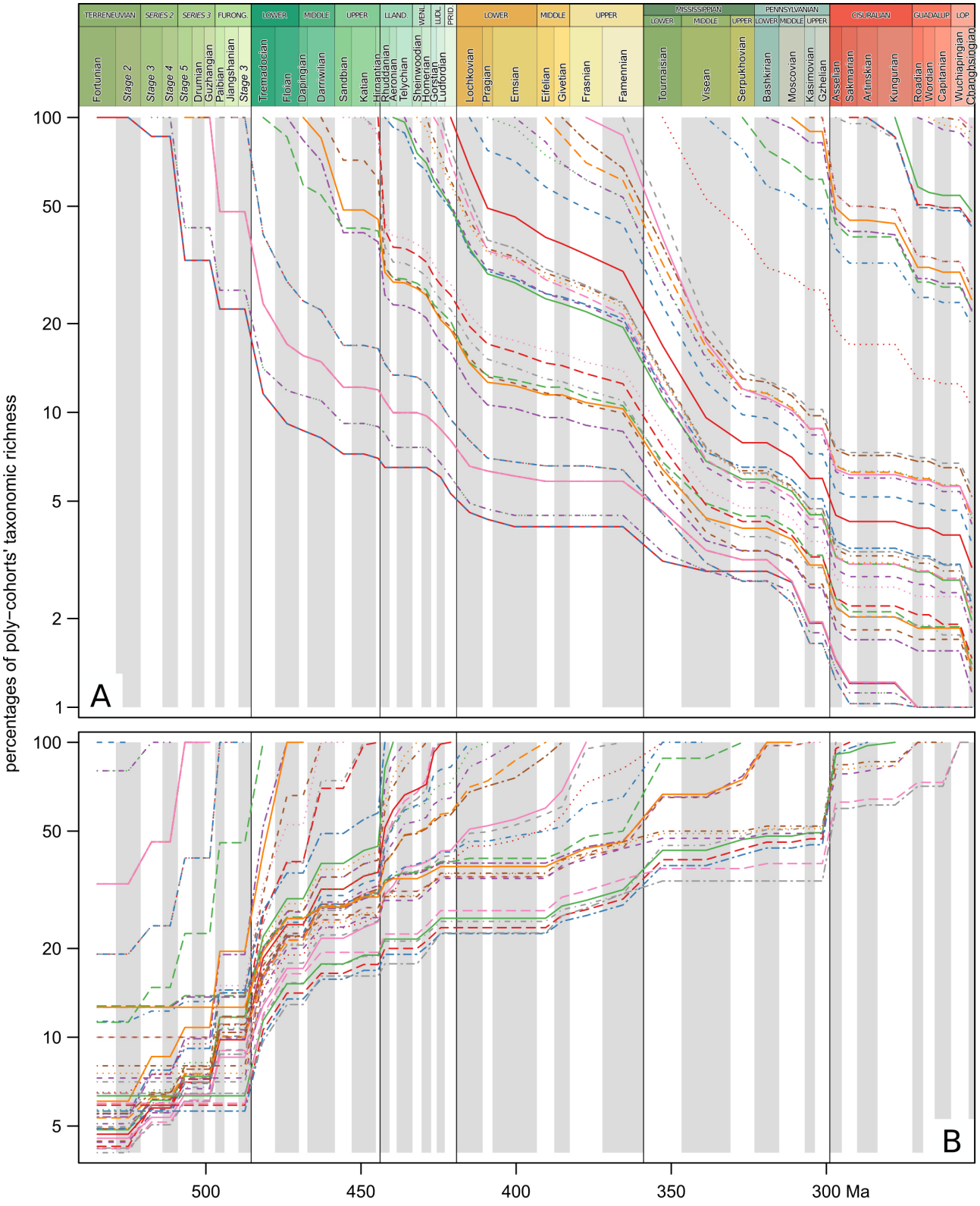

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Figure 5

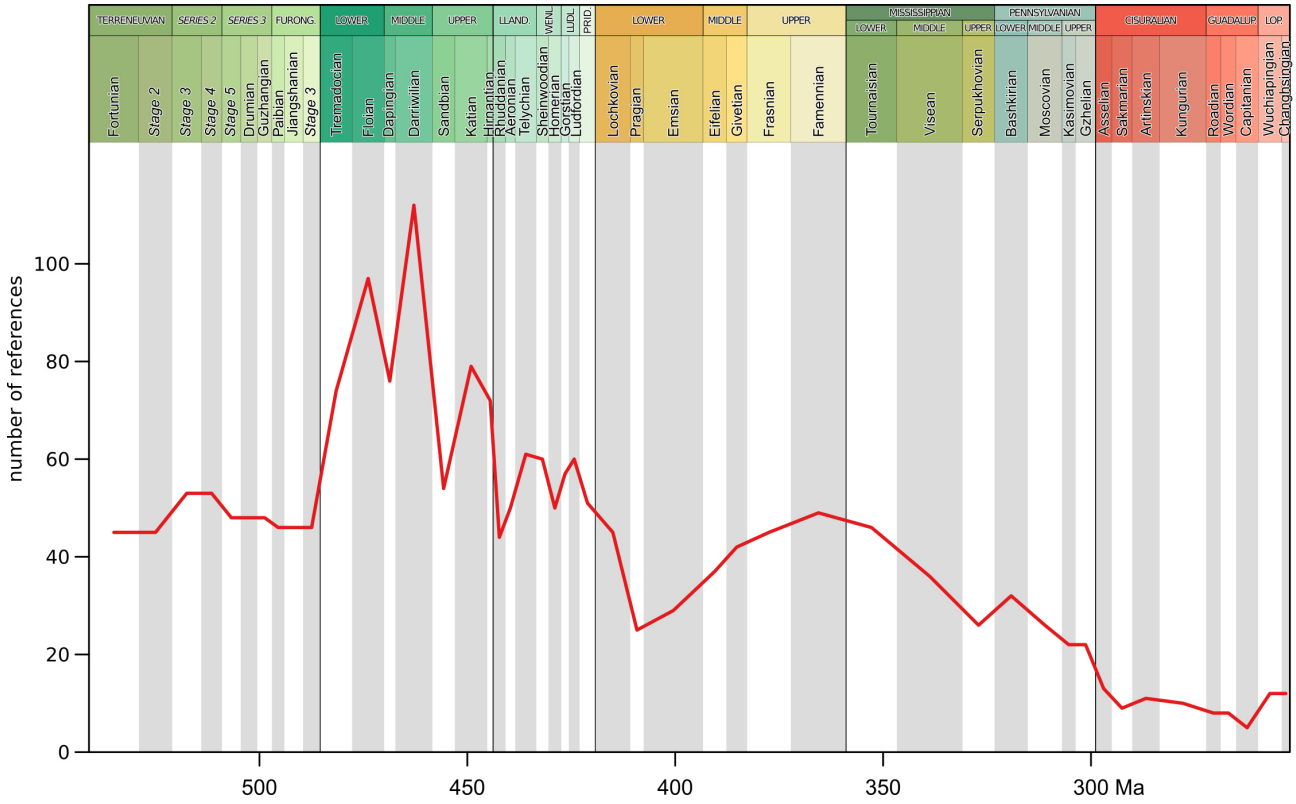

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Figure 6

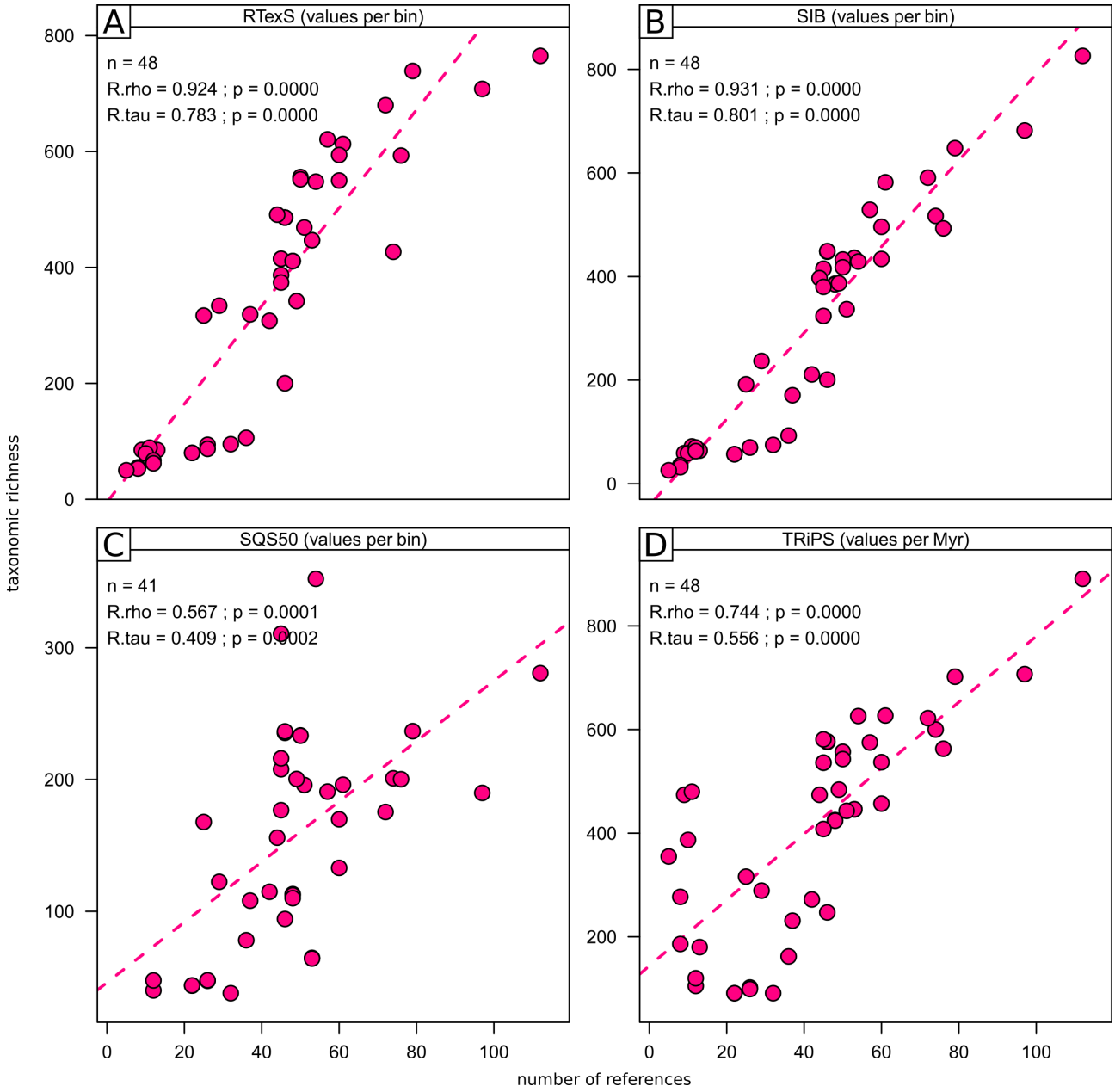

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Figure 7

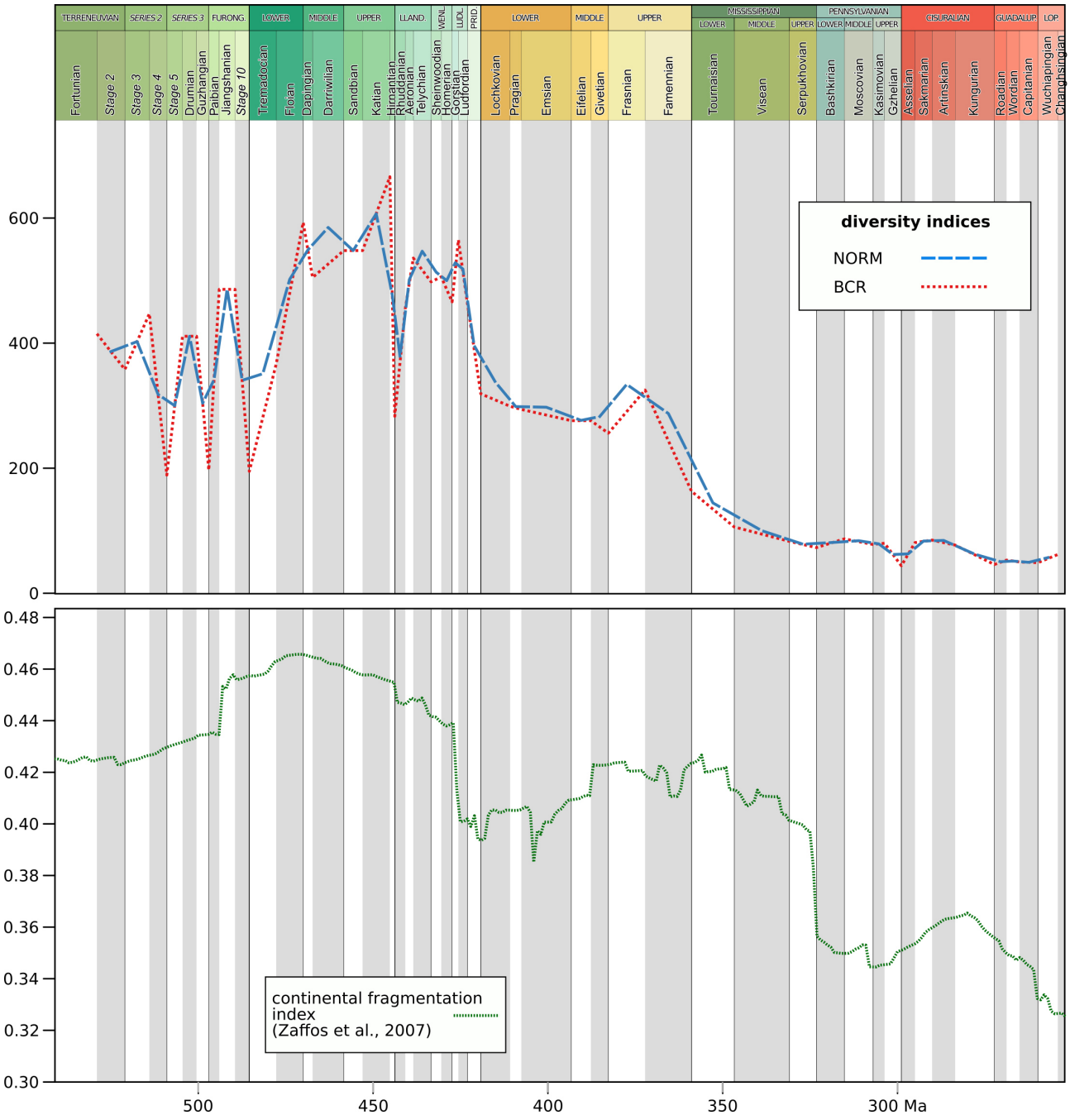

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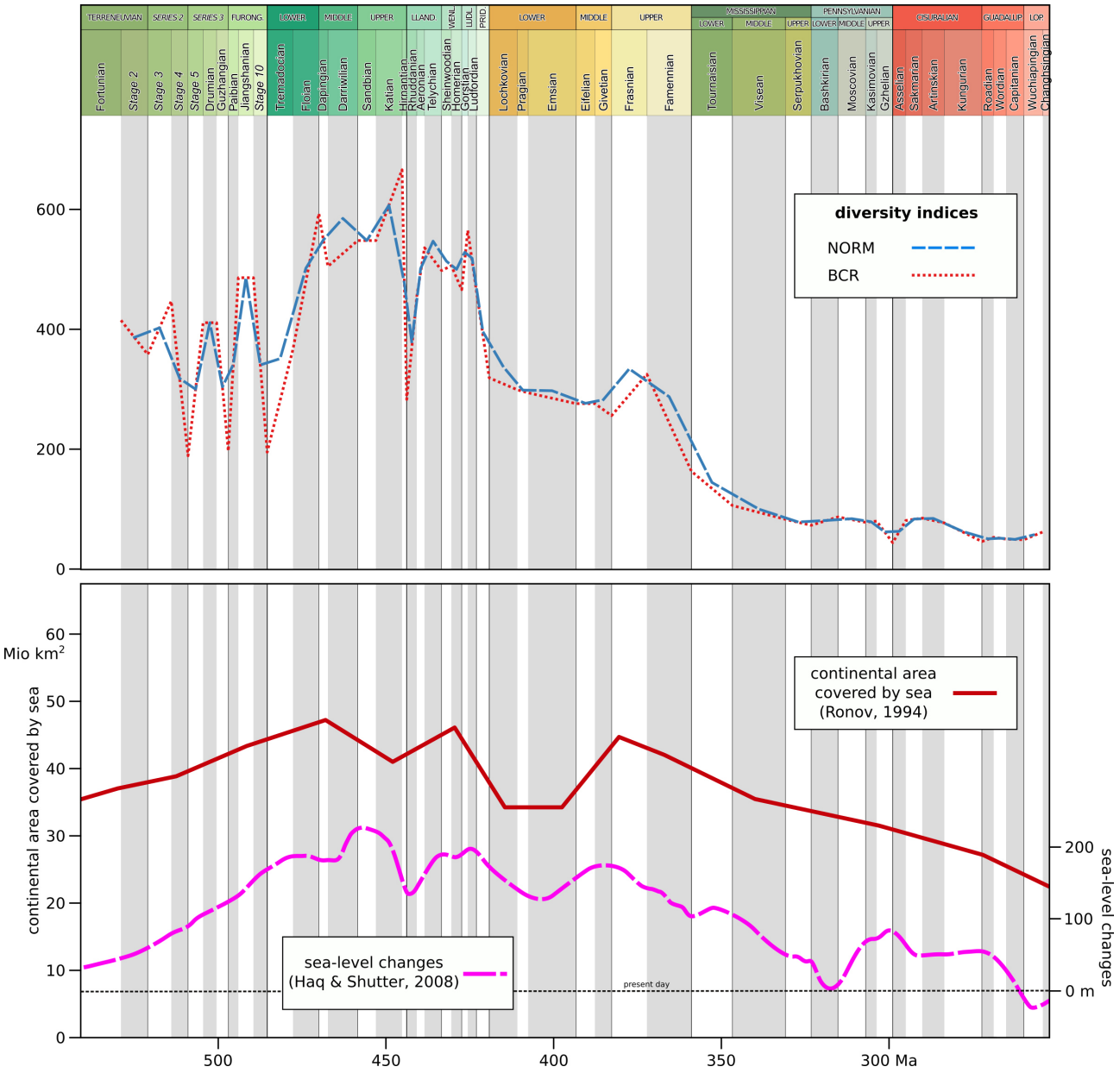
Figure 8



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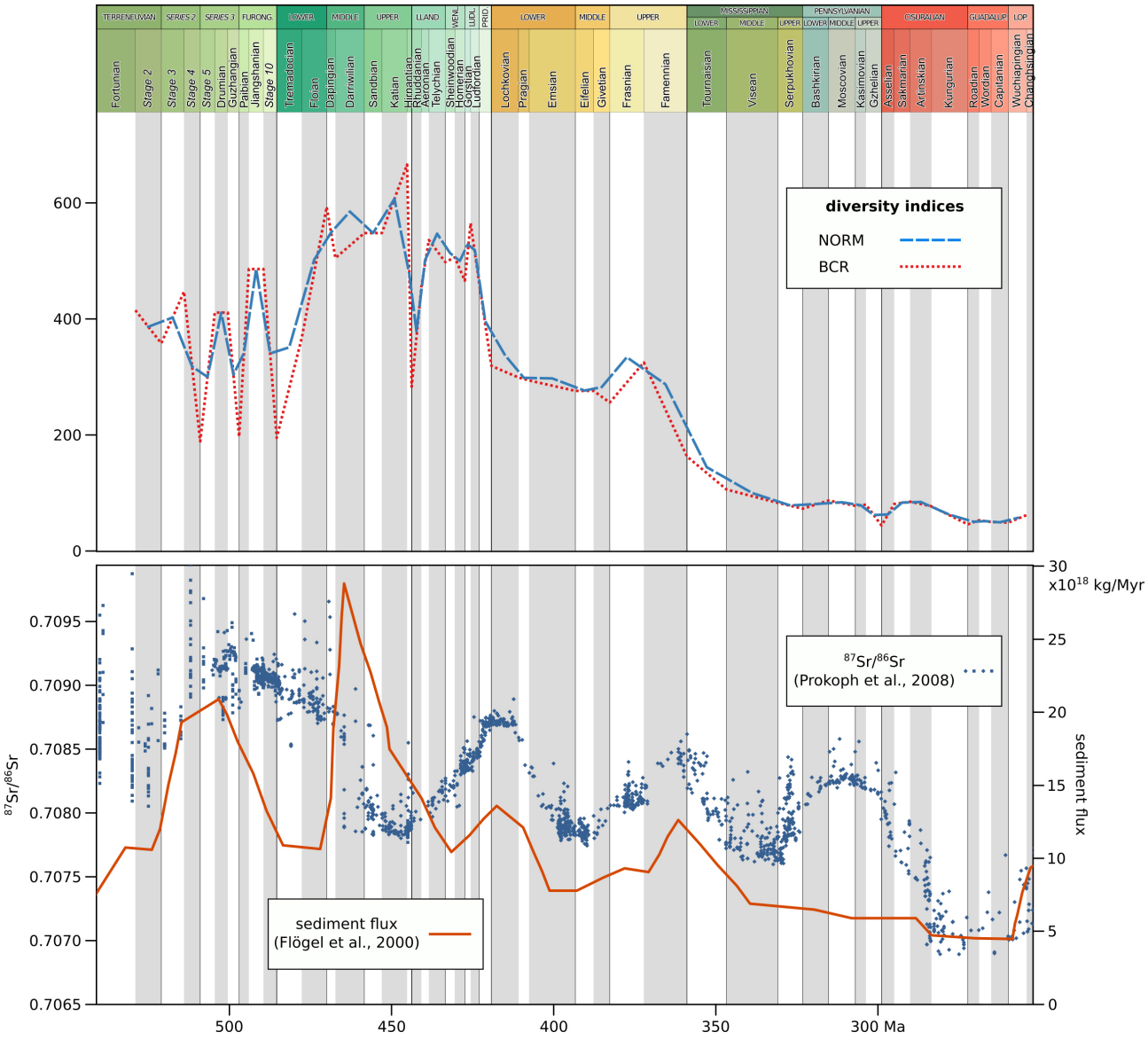

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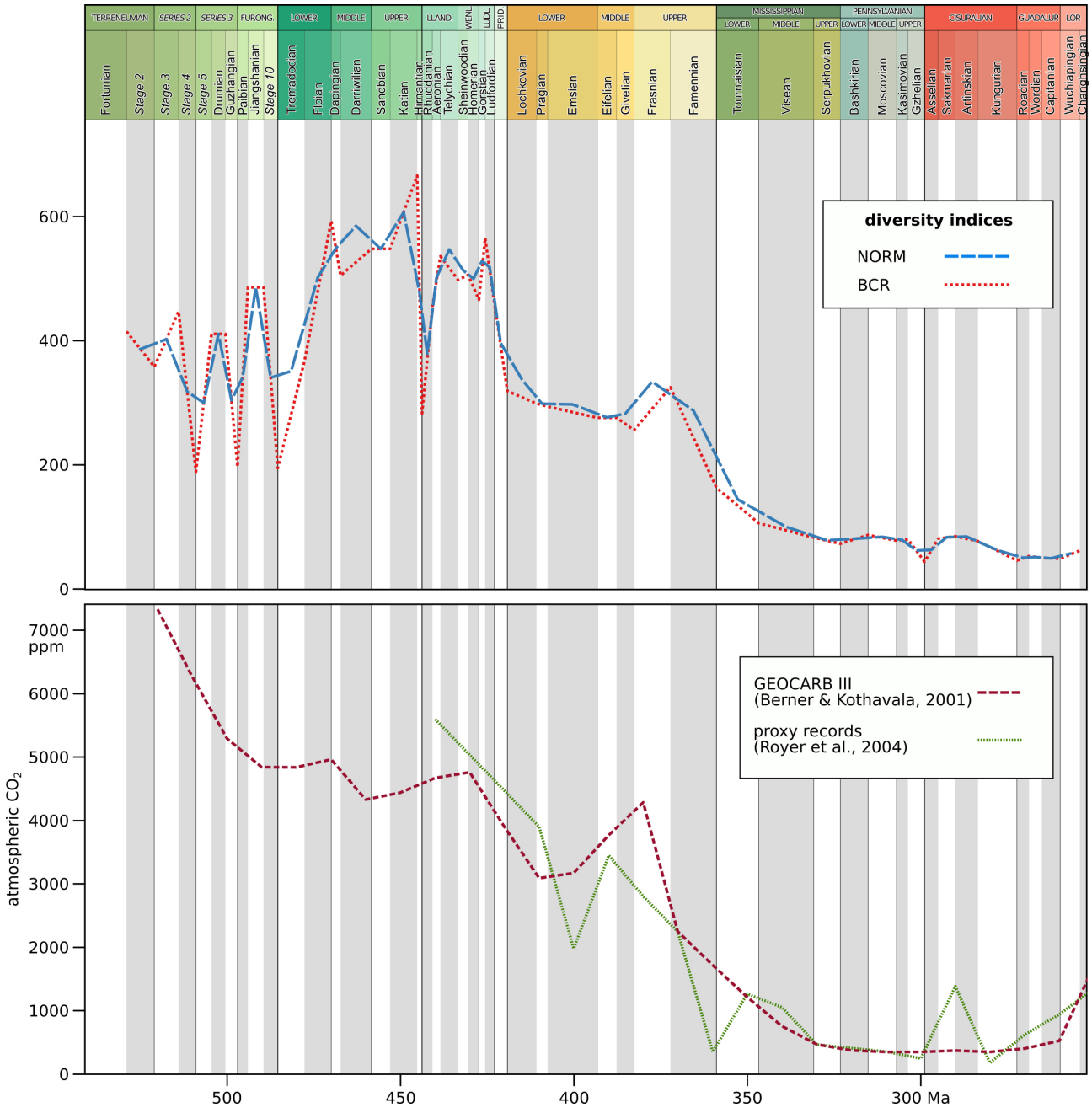
Figure 10



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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 Szcepanik, Thomas Servais

submitted to *Review of Palaeobotany and Palynology.*

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Manuscript Details

Manuscript number	PALBO_2019_125_R2
Title	Revision of the Cambro-Ordovician acritarch genus Vulcanisphaera Deunff, 1961
Article type	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.

Keywords	microphytoplankton; early Palaeozoic; biostratigraphy; palaeogeography; taxonomy; morphometry
Manuscript category	Palaeozoic And Mesozoic Palynological Biostratigraphy And Taxonomy
Corresponding Author	David Kroeck
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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.

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- 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

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

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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

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Keywords: microphytoplankton; early Palaeozoic; biostratigraphy; palaeogeography; taxonomy; morphometry

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1 Introduction

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

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

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

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

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2 Material and methods

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

2.1 Algerian Sahara

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

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

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

Reviews of the literature covering palynological studies in the study area have been provided by Vecoli (1999) and Paris et al. (2000). Palynological investigations of the Nl-2 succession have been carried out by Vecoli et al. (1995), Vecoli (1996, 1999, 2000), Vecoli and Playford (1997), Paris et al. (2000), Stricanne and Servais (2002), Servais et al. (2004), Vecoli and Le Hérissé (2004) and Spina (2015). Vecoli et al. (1995), Vecoli (1996) and Vecoli and Playford (1997) established a palynozonation for the Nl2. Vecoli (2000) interpreted observed changes in the microphytoplankton assemblages in a palaeoenvironmental context. According to him, shallow water conditions prevailed in the Late Cambrian in the study area, followed by a general trend to open marine, offshore conditions in the early Tremadocian, which is interrupted by a regressive event at the Cambrian–Ordovician transition. As stated by Vecoli (2000), the palynomorph assemblages in the Nl-2 borehole point to a proximal, shallow marine environment in the Middle Ordovician and restricted marine conditions in the latest Ordovician.

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

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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 Shineton Shales*, *England*
138
139 The English material is derived from the Tremadocian Shineton 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 Shineton 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 Shineton 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 Shineton 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 Shineton 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 occassional 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

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

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

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

2.3 Eastern Alborz Mountains, Iran

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

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

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

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

2.4 Morphological criteria relevant in the diagnosis of Vulcanisphaera

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

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

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

2.4.2 Morphometric measurements

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

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

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

3 The genus *Vulcanisphaera*

3.1 Historical overview

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

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

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

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

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

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

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

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

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

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

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

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

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

3.2 Systematic palaeontology

Group *Incertae Sedis* ACRITARCHA Evitt, 1963

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

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

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

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

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

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

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

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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 cratershaped 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 unsplitted base
392 of this process. This can be observed in all three species that are retained herein.

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

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

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

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

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

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

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

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

3.3 The species of Vulcanisphaera

3.3.1 List of species described in literature

1961 *Vulcanisphaera africana* Deunff

1961 *V. nebulosa* Deunff

1967 *V. frequens* Górka

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1973 *V. gorgo* Martin

1973 *V.*? *mougnoana* Martin (as *V. mougnoanum*)

1973 *V. lophophora* (Eisenack 1959) Eisenack et al.

1973 *V. tuberata* (Downie 1958) Eisenack et al.

1974 *V. capillata* Jardiné et al.

1974 *V. simplex* Jardiné et al.

1975 *V. flagellum* Martin

1976 *V. britannica* Rasul

1976 *V. cirrita* Rasul

1976 *V. imparilis* Rasul

1976 *V. pila* Rasul

1977 *V. fermosa* Fombella

1978 *V. microspinosa* Tynni nom. nud. (as *V. microspinosum*)

1981 *V. nova* Pöthe de Baldis

1981 *V. turbata* Martin (*in* Martin and Dean)

1986 *V. disjunctospinata* Parsons nom. nud.

1986 *V. rigentisa* Yin

1988 *V. lanugo* by Martin (*in* Martin and Dean)

1991 *V. minor* Uutela and Tynni

1997 *V. ancliforme* (Fombella 1978) Sarjeant and Vavrdová

1997 *V. elliptica* (Cramer and Díez 1977) Sarjeant and Vavrdová

1997 *V.*? *eodigitata* (Fombella 1978) Sarjeant and Vavrdová

1997 *V. eopirifera* (Fombella 1978) Sarjeant and Vavrdová

1997 *V. multipugiunculata* (Cramer and Díez 1977) Sarjeant and Vavrdová

1998 *V. danilovae* Paalits and Heuse nom. nud.

1998 *V. phacelosa* Yuan and Hofmann

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2000 *V. obsoleta* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.

2000 *V. spinulifera* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.

2000 *V. striatula* Volkova *in* Volkova and Sivertseva 1991 comb. nov. Parsons and Anderson, p. 70.

2001 *V. pseudofaveolata* (Fridrichsone 1971) Zang

2015 *V. cantabrica* Palacios

3.3.2 Species excluded from the genus Vulcanisphaera

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

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

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

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

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

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

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

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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 μm 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 *multipugiunculata* (Cramer and Díez, 1977) Sarjeant and Vavrdová, 1997. *V. multipugiunculata*
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 μm) columnar base and secondary
570 branching of the processes on top of these. The diameter of the vesicle is very large (64 μm)
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

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

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

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

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

3.3.3 Species retained in this study

Vulcanisphaera africana Deunff, 1961 emend. nov.

(Plate I, 6–16)

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

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

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

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

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

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

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

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

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

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

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

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

Original diagnosis (translated from Deunff, 1961): Shell light brown of 40 to 45 µm spherical, possessing on the surface small cones carrying processes about 10 µm height, grouped by three, and whose ends are finely branched.

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

Dimensions: (311 specimens measured). Vesicle diameter: 20 µm (39.7 µm) 60 µm. Process length: 2 µm (10.47 µm) 24 µm. Width of process bases: 0.5 µm (2.54 µm) 4.9 µm.

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

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

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

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

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

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

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

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

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

Vulcanisphaera mougnoana (Martin, 1973) emend. nov.

(Plate I, Figs. 1-5)

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

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

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

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

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

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

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

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

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

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

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

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

1991 *R. striatula* Volkova *in* Volkova and Sivertseva, p. 121; pl. ("Рис.") 1, figs. i, l, v (*и*, *л*, *в*); holotype: i, l (*и*, *л*).

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1996 *V. nebulosa* Deunff 1961 Ghavidel-Syooki (incorrect identification)

1999a "Gen. et sp. nov. № 2" Volkova; pl. IV, fig. 8.

1999b *Undosisphaera pilosiuscula* Volkova; p. 75; pl. ("таблице") VIII, fig.1, 2, 6; holotype fig. 1

2000 *V. obsoleta* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.

2000 *V. spinulifera* Volkova 1990 comb. nov. Parsons and Anderson, p. 70.

2000 *V. striatula* Volkova *in* Volkova and Sivertseva, 1991 comb. nov. Parsons and Anderson, p. 70.

2006 *Timofeevia* cf. *T. microretis* Aráoz and Vergel, pl. ("figura") 5, K.

2011 *V.* sp. Jachowicz-Zdanowska, p. 256-257, pl. ("fig.") 10, fig. J.

2015 *V. cantabrica* Palacios, pp. 100, 103; pl. XV, figs. 1–6; holotype fig. 1.

Holotype: Martin, 1973, pl. II, fig. 8.

Original diagnosis (translated from Martin, 1973): Central body globular with a diameter of 45 to 62 μm. Appendages in a number of sixty to eighty and of a length of 11 to 18 μm. Conical shape with single or finely branched distal end. In a polygonal and often hexagonal arrangement, they are isolated or grouped by two or three on the same specimen. Isolated appendages have a broad base of 1.5 to 2 μm; those grouped are thinner, the width of their base is 0.5 to 1 μm.

Emended diagnosis: More or less spherical to ellipsoidal vesicle, sometimes slightly polygonal in outline; psilate to granulate surface; small solid conical process bases with either a simple single tapering solid process or tufts of two to numerous solid processes; processes are of variable length, solid, tapering, erect or curved, with simple, bi-, trifurcated or finely branched distal ends; isolated appendages usually have a broader base than those grouped in tufts; thin ridges between processes forming a polygonal structure on the vesicle surface with the processes appearing where these ridges merge, with smooth or slightly dented tops.

Dimensions: (280 specimens measured). Vesicle diameter: 30 μm (43.75 μm) 60 μm. Process length: 1.24 μm (11 μm) 20.36 μm. Width of process bases: 0.8 μm (1.7 μm) 3.8 μm.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

(Plate II, 1-16)

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

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

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

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

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

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

Original diagnosis (translated from Jardiné et al., 1974): Spherical vesicle with almost polygonal outline due to the strong expansion of the process bases; complex appendages with conical base, ending in a tuft of two to four fine branches, rather short, with a simple end or bifurcated in tenuous elements. Body diameter: 30-50 μm; height of the undivided process base ("basal cone"): 3-10 μm; length of branches: 3-7 μm.

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

Dimensions: (280 specimens measured). Vesicle diameter: 18 μm (26.7 μm) 45.47 μm. Process length: 1.27 μm (8 μm) 20 μm. Width of process bases: 1.0 μm (2.7 μm) 5.1 μm.

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

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

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

3.4 Statistical analysis

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

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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

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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 Newfounfland, 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 Vanguestaine, 1993; Brück and Vanguestaine, 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

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

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

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

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

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

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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

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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 contintental 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 prefered 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

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4.2.1 Gondwana

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

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

4.2.2 Avalonia

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

4.2.3 Baltica

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

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

4.2.4 North Kara Terrane

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

4.2.5 Laurentia

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

5 Discussion

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

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

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

6 Conclusions

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

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

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

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

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

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

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

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

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

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

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

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

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

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12. Shineton Shales B15/1; EF: R27/1. **13.** Shineton Shales C10/1; EF: K27/1. **14.** Shineton Shales D6/1; EF: E22/2. **Fig. 15.** Shineton Shales D6/1; EF: G26/2**. 16.** Shineton Shales C10/1; EF: K49. Scale bars: 20 μm.

Plate II. **1-16:** *V. simplex.* **1.** Shineton Shales, C10/1; EF: K41/1. **2.** Shineton Shales, D6/1; EF: F34. **3.** Shineton Shales, D6/1; EF: H61/4. **4.** Shineton Shales outcrops, C10/1; EF: K41/2. **5**. Shineton Shales, B8/1; EF: U50/3. **6.** Shineton Shales, B15/1; EF: K26. **7.** Shineton Shales, B15/1; EF: G26. **8.** Shineton Shales, B15/1; EF: U27. **9.** Shineton Shales, B8/1; EF: M50/3. **10.** Shineton Shales, B15/1; EF: Q26/2. **11.** Shineton Shales, C10/1; EF: Q26/4. **12.** Shineton Shales outcrops C10/1; EF: Q27/1. **13.** Shineton Shales outcrops, B8/1; EF: T49/2. **14.** Shineton Shales B8/1; EF: T49/2. **15.** Shineton Shales B8/1; EF: V50/1. **16.** Shineton Shales B8/1; EF: M50/4. Scale bars: 20 μm.

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Figure 1

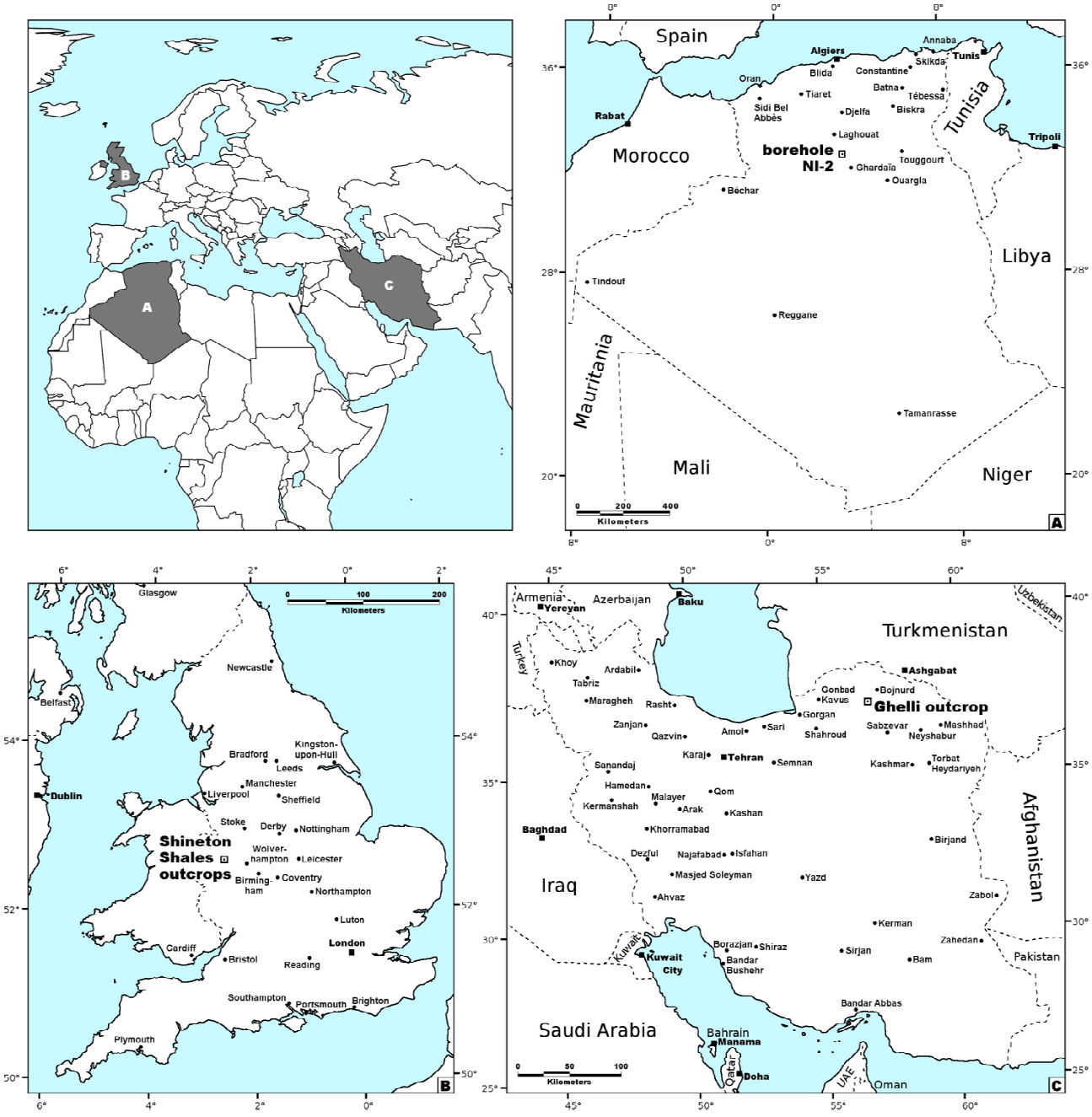

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Figure 2

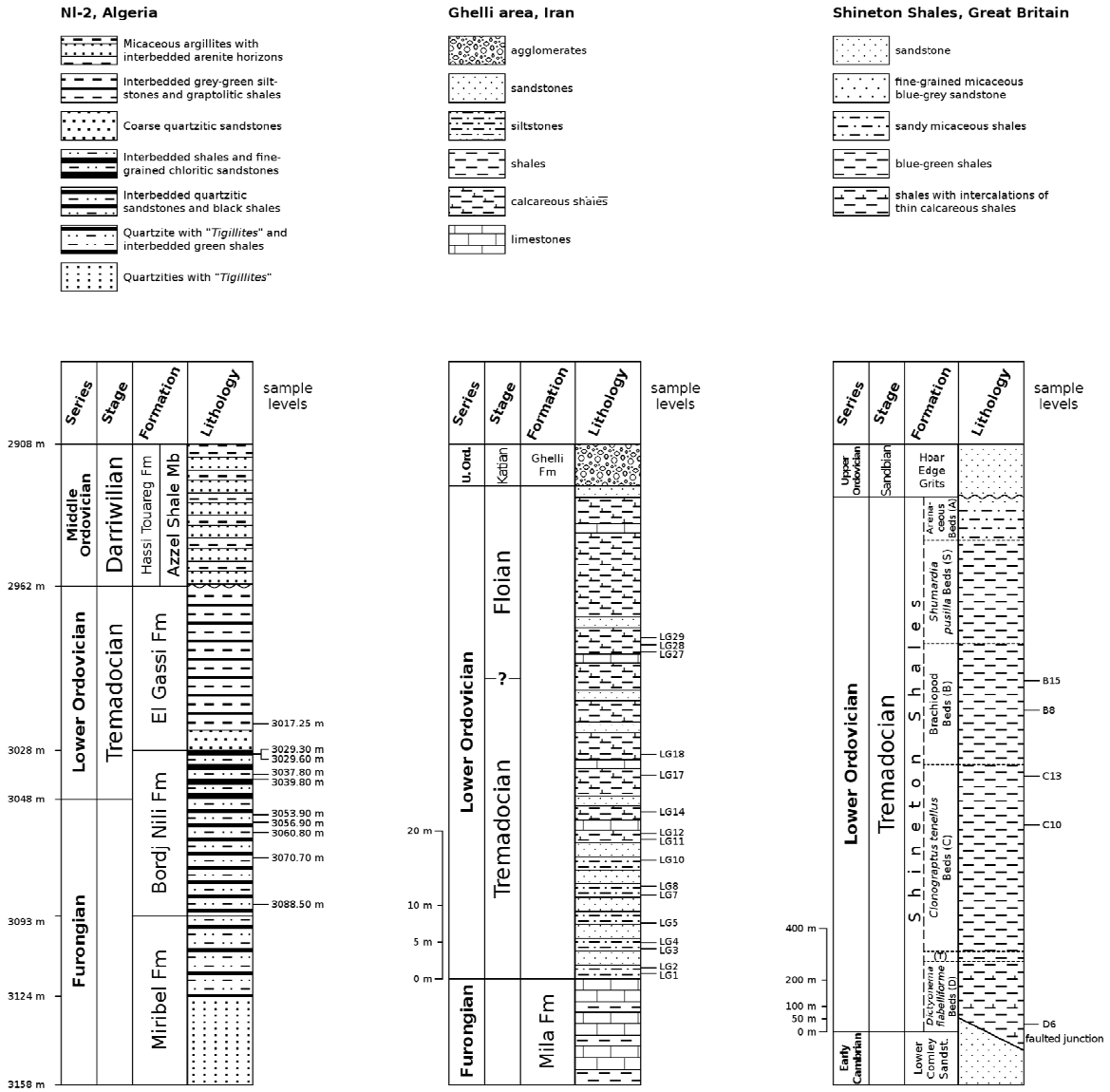

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Figure 3

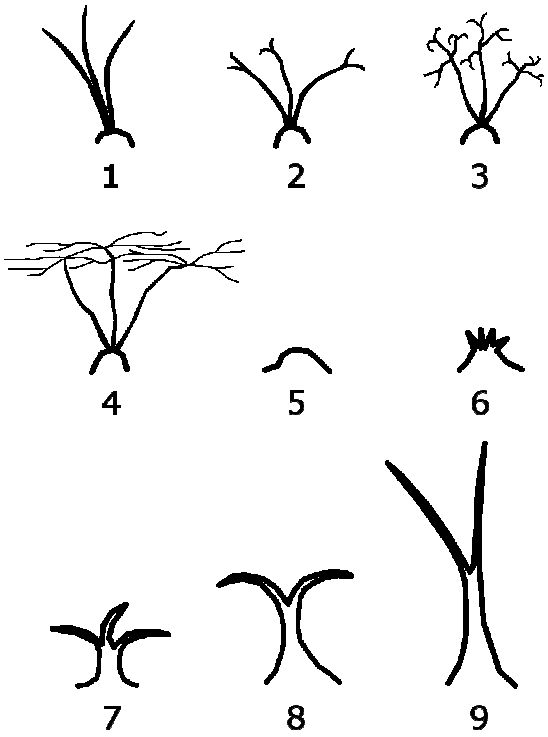

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Figure 4

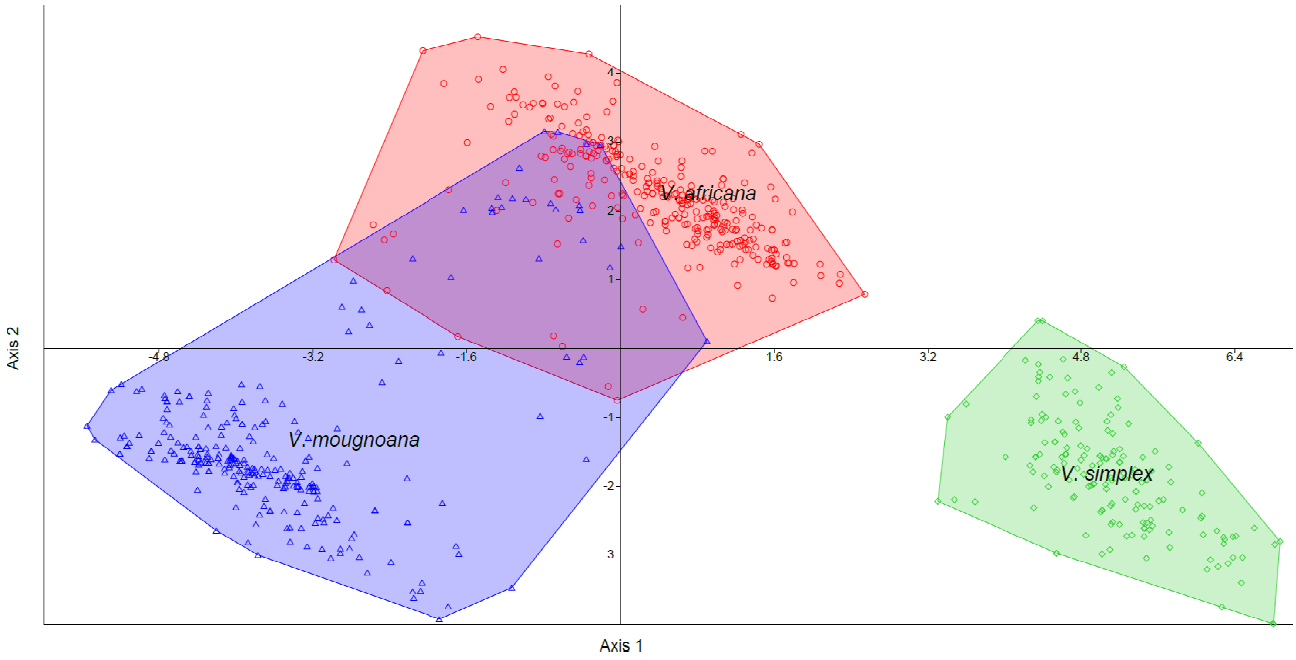

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Figure 5

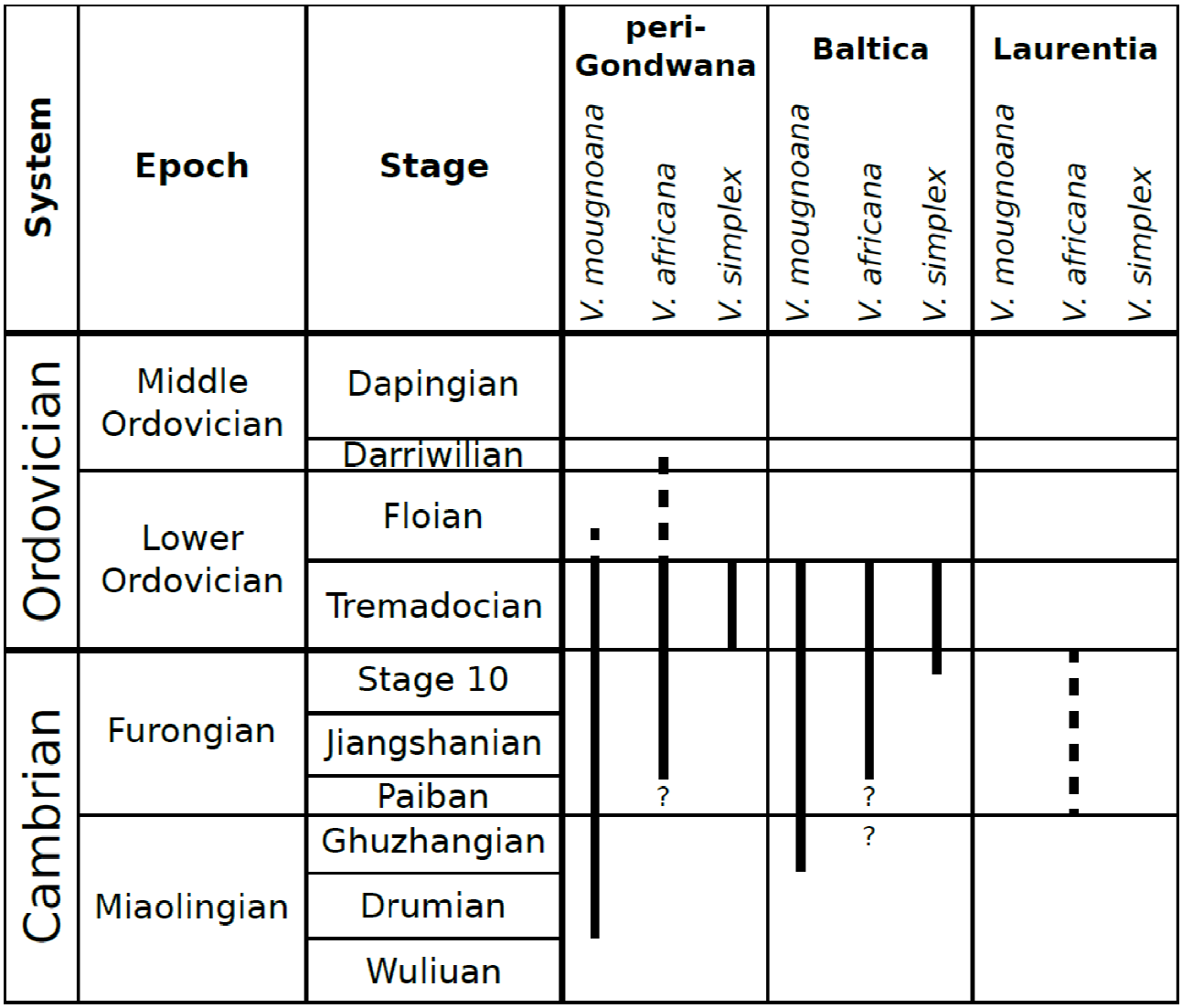

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Figure 6

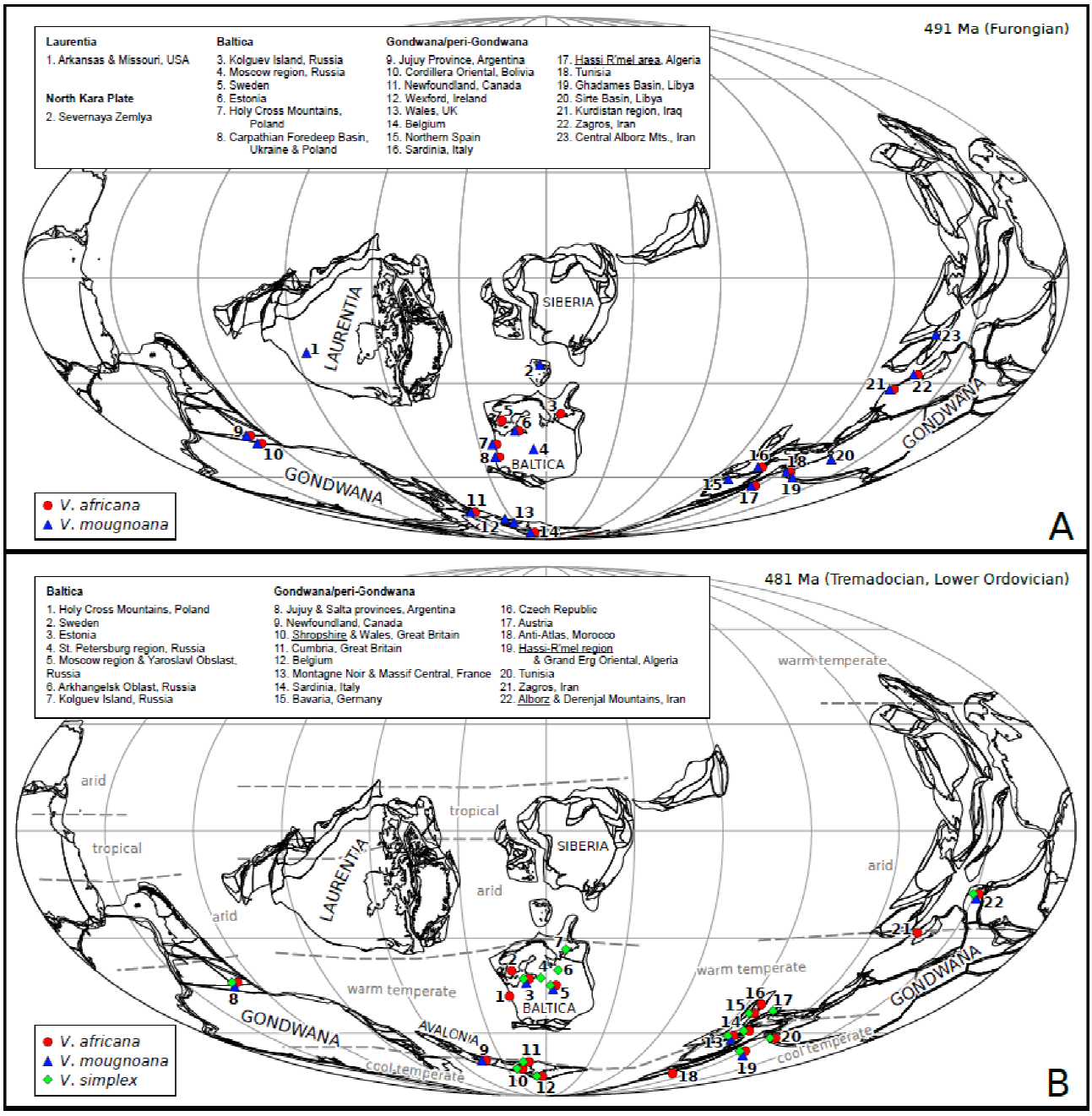

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Plate I

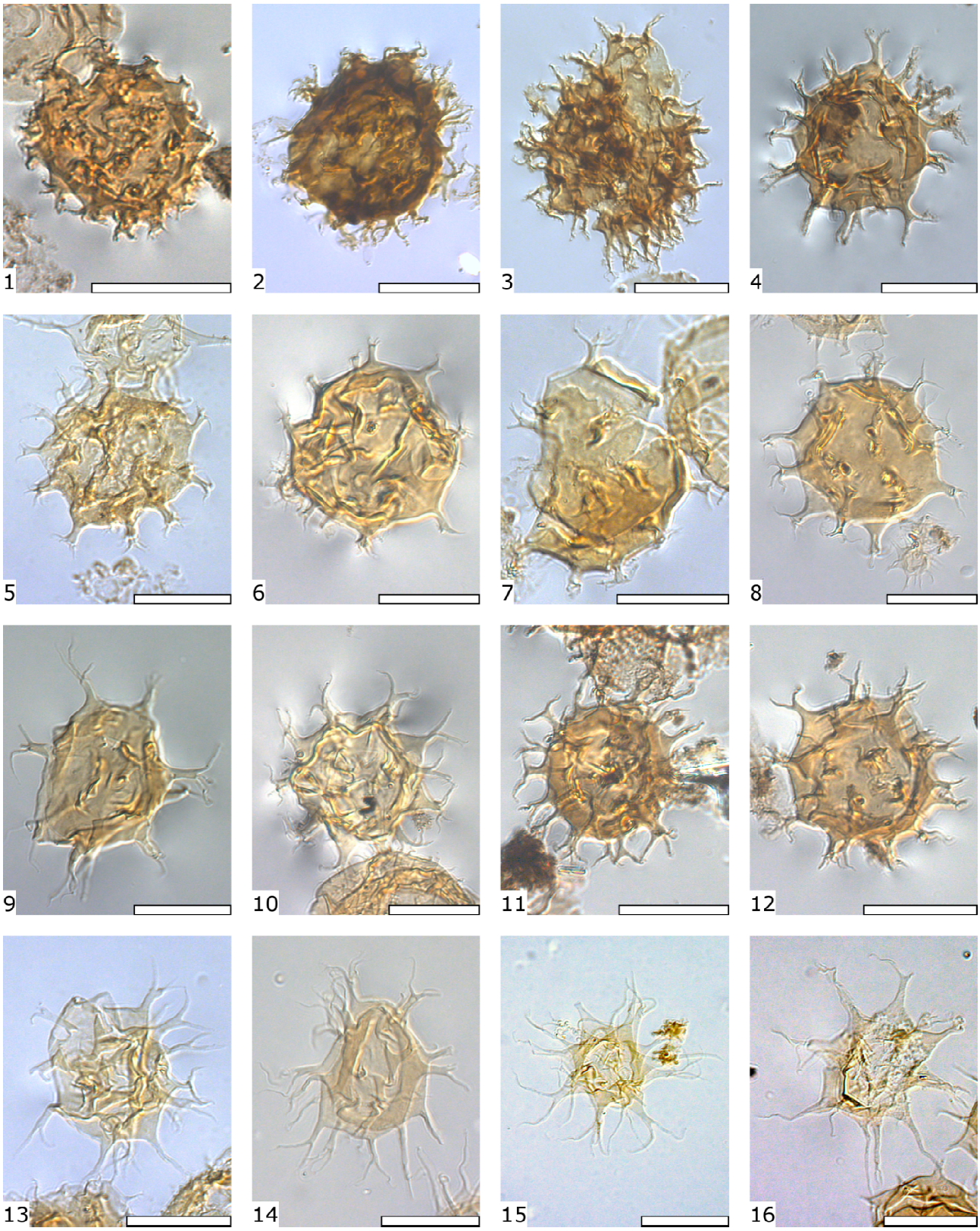

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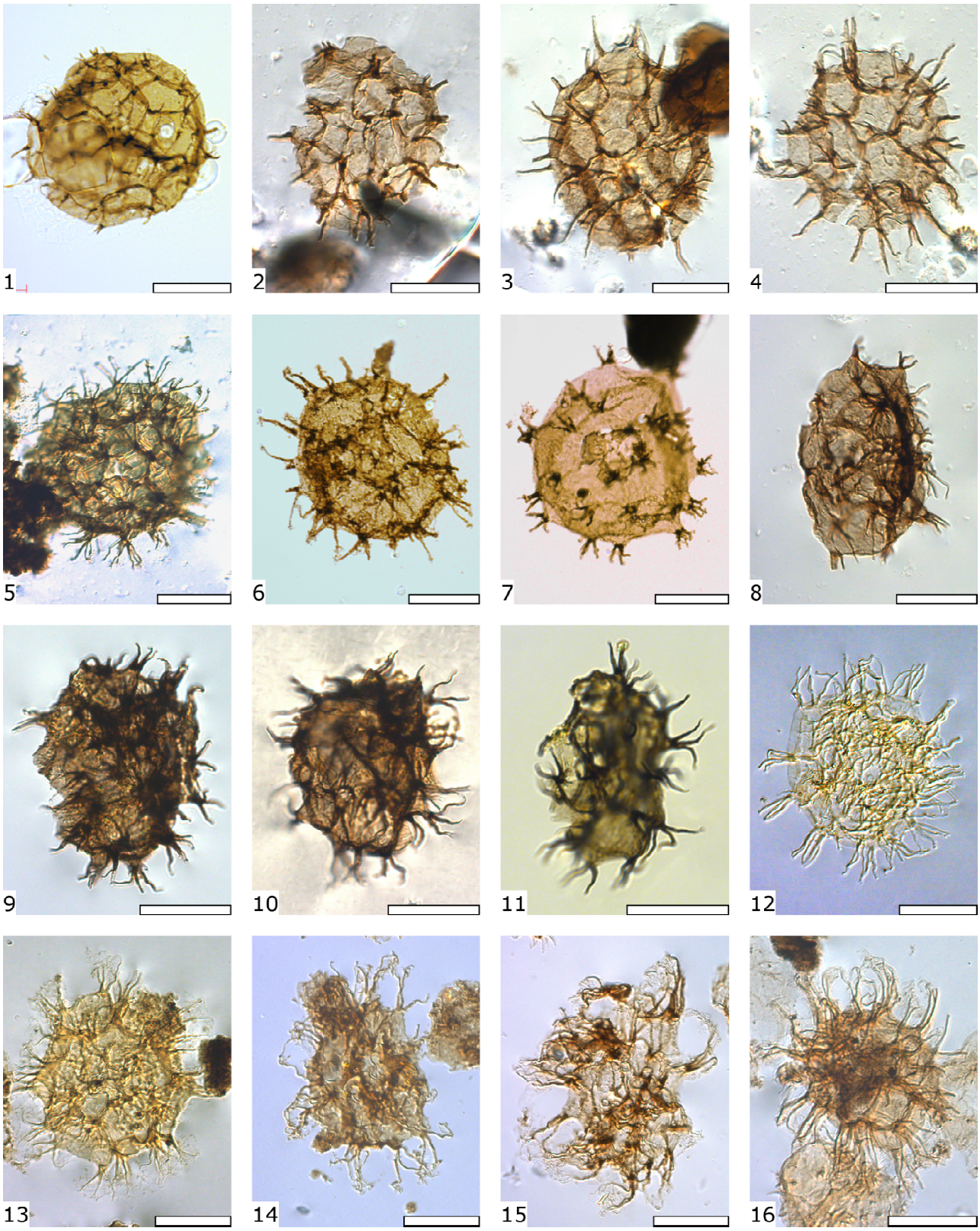
Plate II



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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

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

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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 *varietas* 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.

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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), *Arkonia–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 *Cyclopospaeridium* (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.

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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 μm 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.

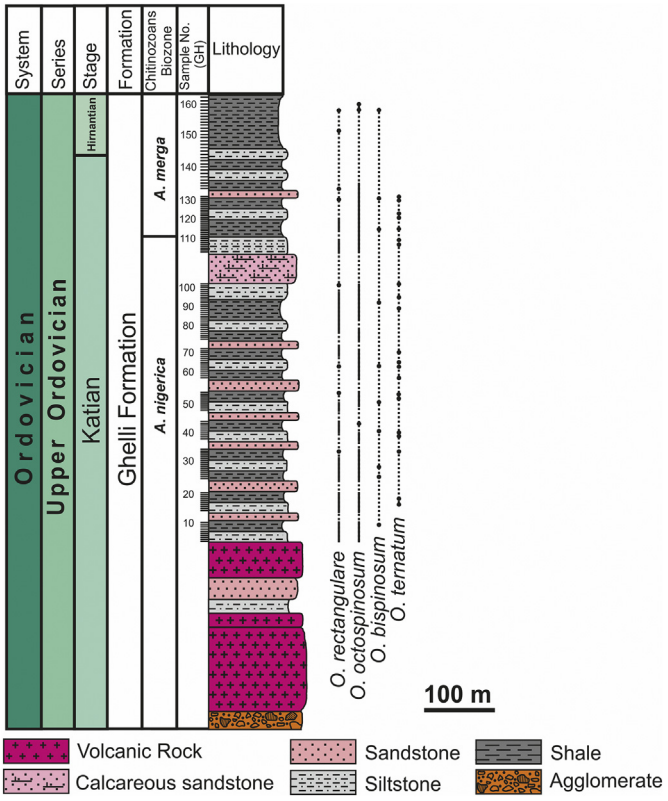

Fig. 2. Synthetic view of the type section of the Ghelli Formation with the position of the investigated samples and the distribution of *Orthosphaeridium* species in the sequence. Chitinozoan biostratigraphy unpublished.

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.

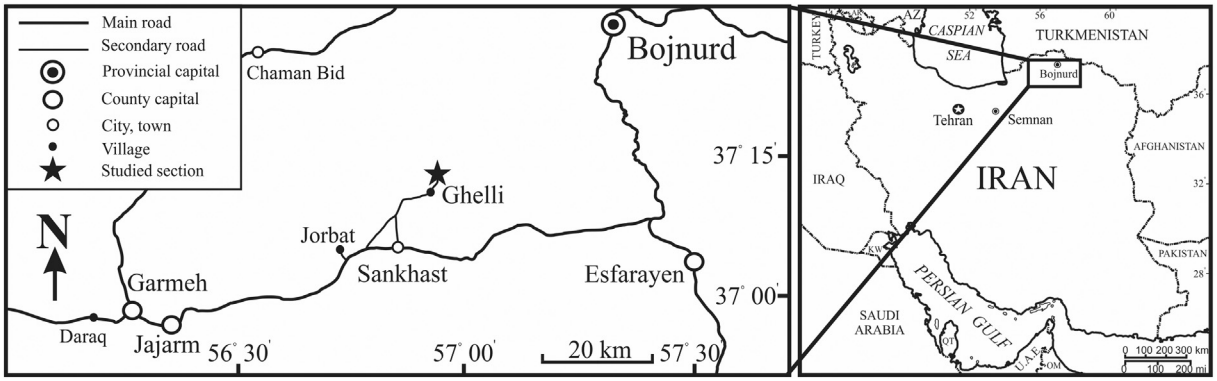

Fig. 1. Geographical map of northeastern Iran showing the location of the study area and the investigated section.

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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
Orthosphaeridium bispinosum	*Orthosphaeridium bispinosum*	Turner (1984)
Orthosphaeridium ternatum	*Baltisphaera ternata*	Burmann (1970)
	Baltisphaera procera	Burmann (1970)
Orthosphaeridium rectangulare	*Baltisphaeridium rectangulare*	Eisenack (1958)
	Orthosphaeridium inflatum	Loeblich (1970)
	Baltisphaera quadrinata	Burmann (1970)
	Baltisphaera transitoria	Burmann (1970)
	Baltisphaera quadricornis	Burmann (1970)
	Baltisphaera abbreviata	Burmann (1970)
	? *Baltisphaera occulata*	Burmann (1970)
	Orthosphaeridium chondrododora	Loeblich and Tappan (1971)
	Orthosphaeridium vibrissiferum	Loeblich and Tappan (1971)
	? *Orthosphaeridium latispinosum*	Uutela and Tynni (1991)
Orthosphaeridium octospinosum	*Orthosphaeridium octospinosum*	Eisenack (1968)
	Orthosphaeridium insculptum	Loeblich (1970)
	Orthosphaeridium densigranosum	Kjellström (1971b)
	Orthosphaeridium densiverrucosum	Kjellström (1971b)
	? *Orthosphaeridium gaspesianum*	Martin (1980)
	Orthosphaeridium insculptum forma *erectum*	Uutela and Tynni (1991)
	? *Orthosphaeridium orthogonium*	Le Hérissé et al. (2015)
Unknown genus *Lusatia dendroidea*	*Orthosphaeridium trabeculatum*	Kjellström (1971a)
	Orthosphaeridium? extensum	Parsons and Anderson (2000)
	Orthosphaeridium? triangulare	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. occultata*, 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 subquadrate 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

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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* Burmann, 1970 emend. Albani et al., 2007 that is a typical acritarch taxon of the Upper Cambrian (Albani et al., 2006, 2007).

Finally, Le Hérissé 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 Hérissé 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 subspherical 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., Burmann, 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 tubercule-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* (Burmann, 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.

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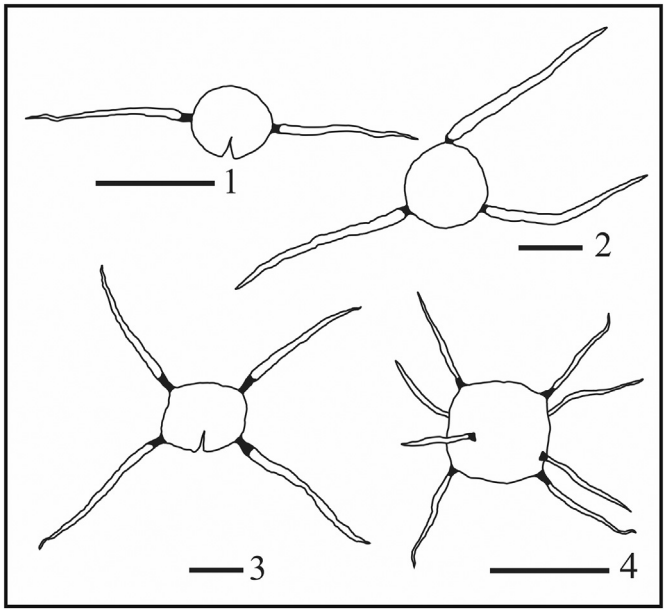

Fig. 3. Idealized line drawings of the four general morphotypes of *Orthosphaeridium* retained herein as species. 1. *Orthosphaeridium bispinosum*, 2. *Orthosphaeridium ternatum*, 3. *Orthosphaeridium rectangulare*, 4. *Orthosphaeridium octospinosum*. Scale bar = 50 μm.

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, subspherical, hollow, thick walled (1.5–2.5 μm); 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 μm) 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 Hérissé, 2004); Middle Ordovician–Caradoc, Poland (Jachowicz, 2005); late Dapingian–early 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

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Germany (Burmann, 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 Hérissé 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 occultata* 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, southeastern Turkey (Steemans et al., 1996); Ashgill, northeastern Missouri, USA (Wicander et al., 1999); Ashgill, "northern" Gondwana (Vecoli and Le Hérissé, 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 Hérissé 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 tubercules. 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 tubercules. 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*

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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 (Burmann, 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 Griffelschiefer 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 (Burmann, 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 (Steemans et al., 1996); Caradoc, England (Molyneux et al., 1996); late Ordovician, southeastern Turkey (Erkmen, 1979); early Caradoc–late Ashgill, "northern" Gondwana (Vecoli and Le Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Katian–Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, central Saudi Arabia (Le Hérissé 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 Hérissé, 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* Burmann, 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* (Burmann, 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 densigranosum* 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 Hérissé, 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. densigranosum* 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 *forma*.

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Thèse de David M. Kroeck, Université de Lille, 2019

The new species *O. orthogonium* Le Hérissé 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 (Steemans 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 Hérissé, 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 densigranosum* 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. densigranosum*, *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–

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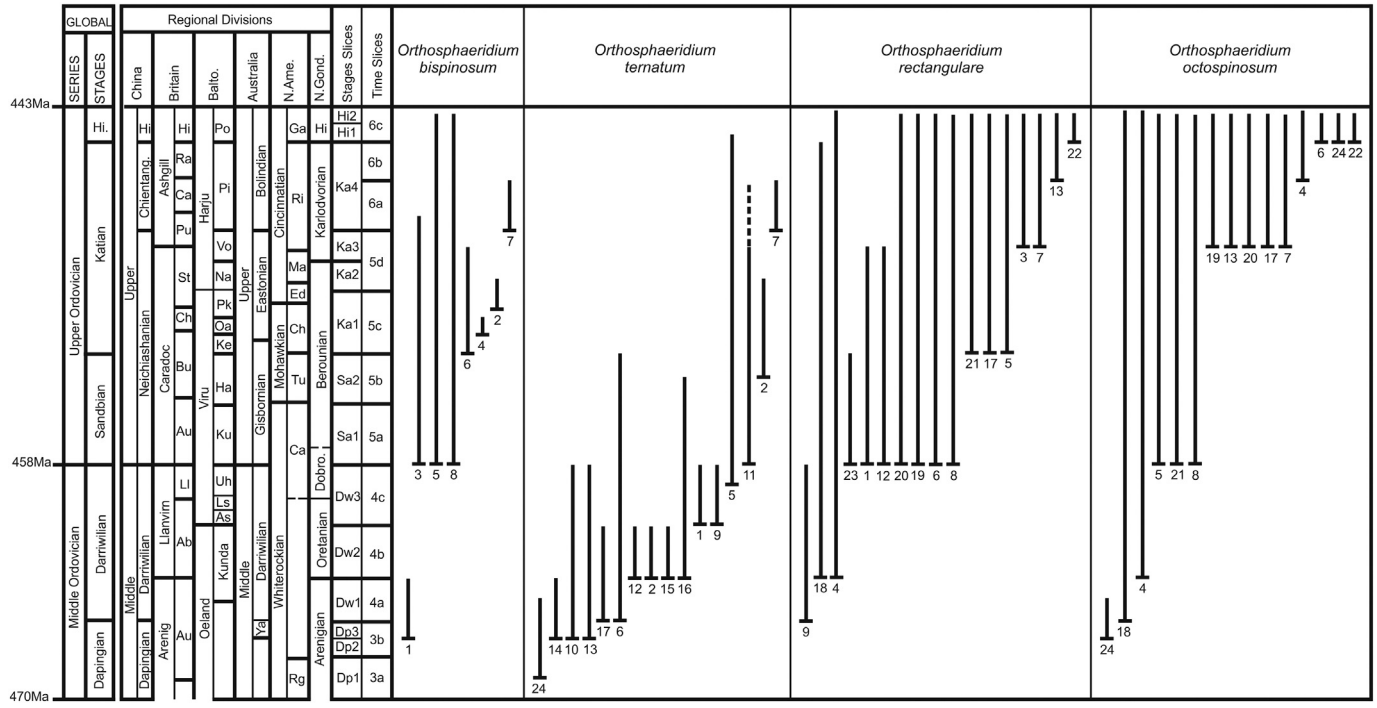

Fig. 4. Global stratigraphical distribution of the four species of *Orthosphaeridium*. Global Series and Stages, regional divisions, stage slices and time slices of the Ordovician, based on Webby et al. (2004) and Bergström et al. (2009). 1. Northern England (Booth, 1979; Downie, 1984; Turner, 1984; 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 et al., 2014; Ghavidel-Syooki and Borji, 2018); 6. Saudi Arabia (Jachowicz, 1995; Miller and Al-Ruwaili, 2007; Le Hérissé et al., 2007, 2015); 7. Libya (Hill and Molyneux, 1988; Abuhamida, 2013); 8. "Northern Gondwana" (Vecoli and Le Hérissé, 2004); 9. Germany (Burmann, 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; Górka, 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,

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Thèse de David M. Kroeck, Université de Lille, 2019

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 chondrodoodora* 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 densigranosum* 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 chondrodoodora* 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 Hérissé, 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 (Burmann, 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 (Steemans et al., 1996); Ashgill, "northern" Gondwana (Vecoli and Le Hérissé, 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 (Burmann, 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 (Steemans 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 Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Caradoc, western Iraq (Al-Ameri, 2010); Katian–Hirnantian, Saudi Arabia (Le Hérissé 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,

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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 (Steemans 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 Arenigian 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 *gibberulus–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 Schwarzburg 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. Paleoecology and paleogeography

5.1. Paleoecology

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

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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 peteinosphaerid–*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 *Ordovicidium*, 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 tubercules 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 phylogenetical 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*,

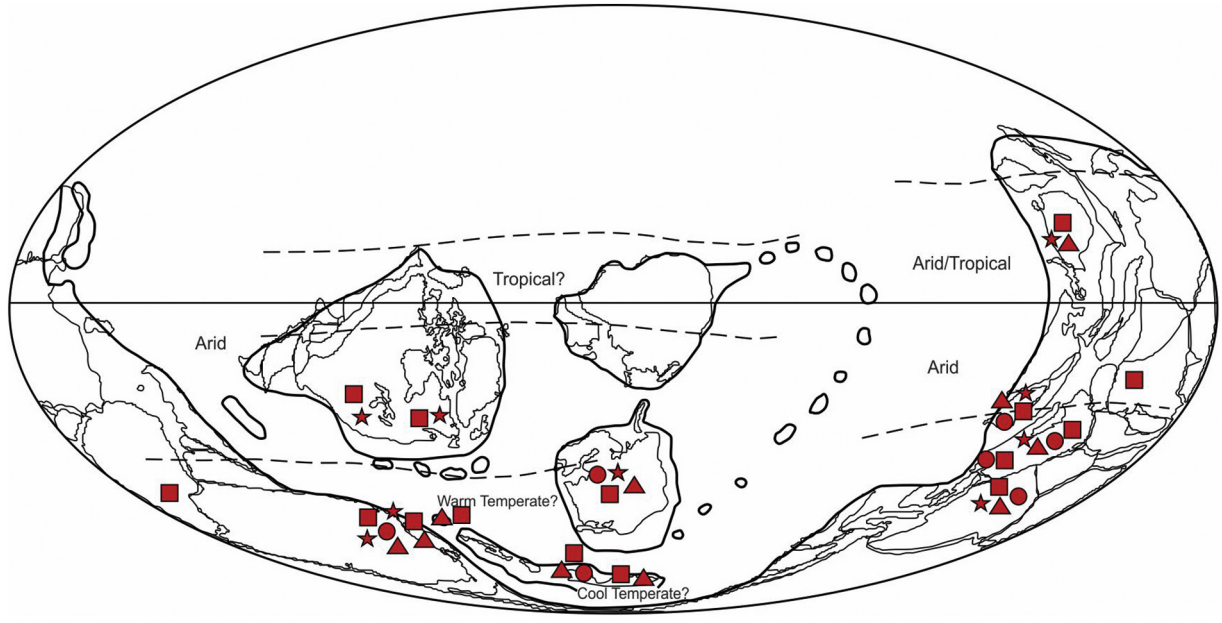

Fig. 5. Paleogeographic distribution of *Orthosphaeridium* in the Middle–Late Ordovician. Paleogeographic reconstruction modified from Boucot et al. (2009). *Orthosphaeridium bispinosum* ●; *Orthosphaeridium ternatum* ▲; *Orthosphaeridium rectangulare* ■; *Orthosphaeridium octospinosum* ★.

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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.

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Plate I

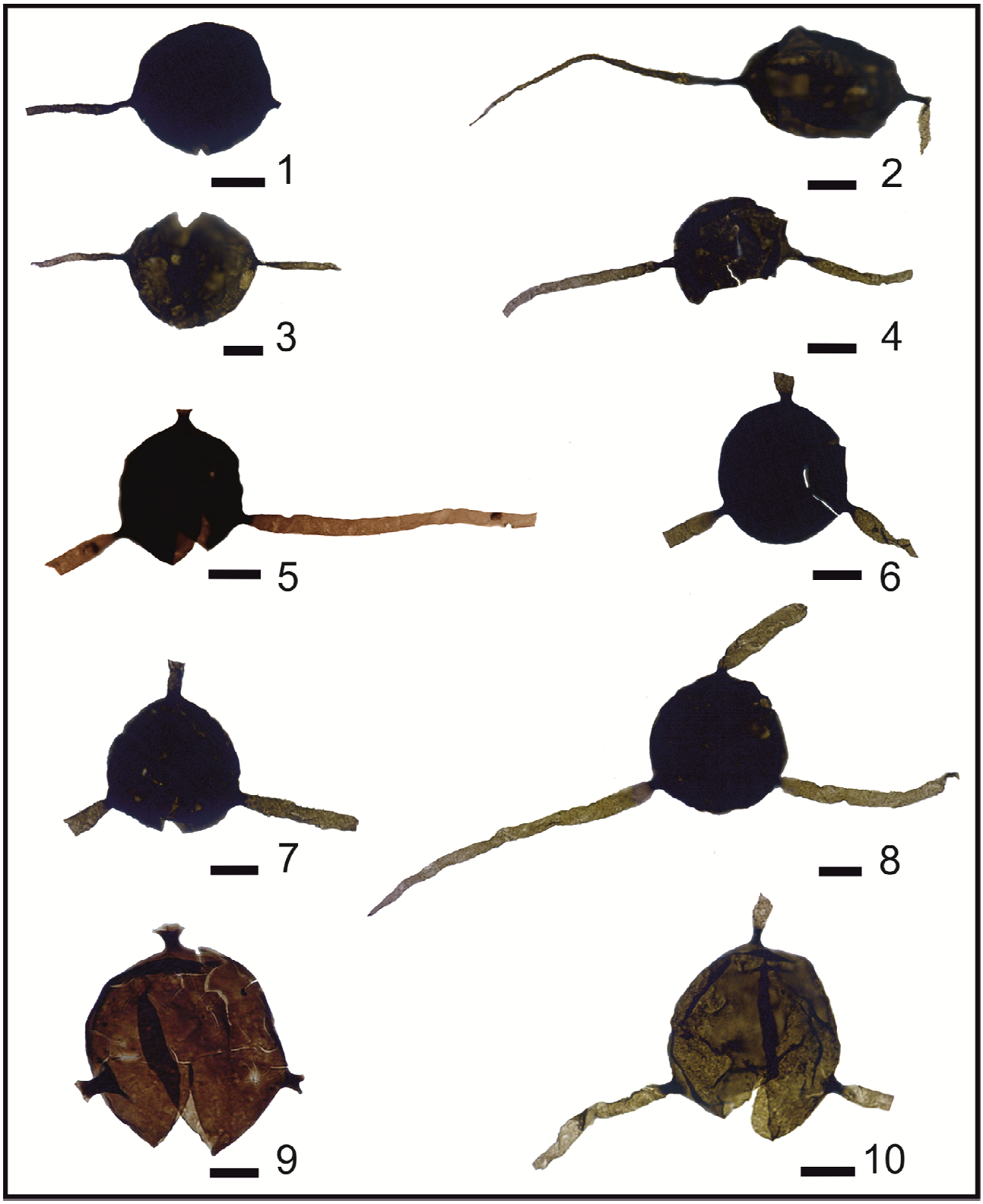

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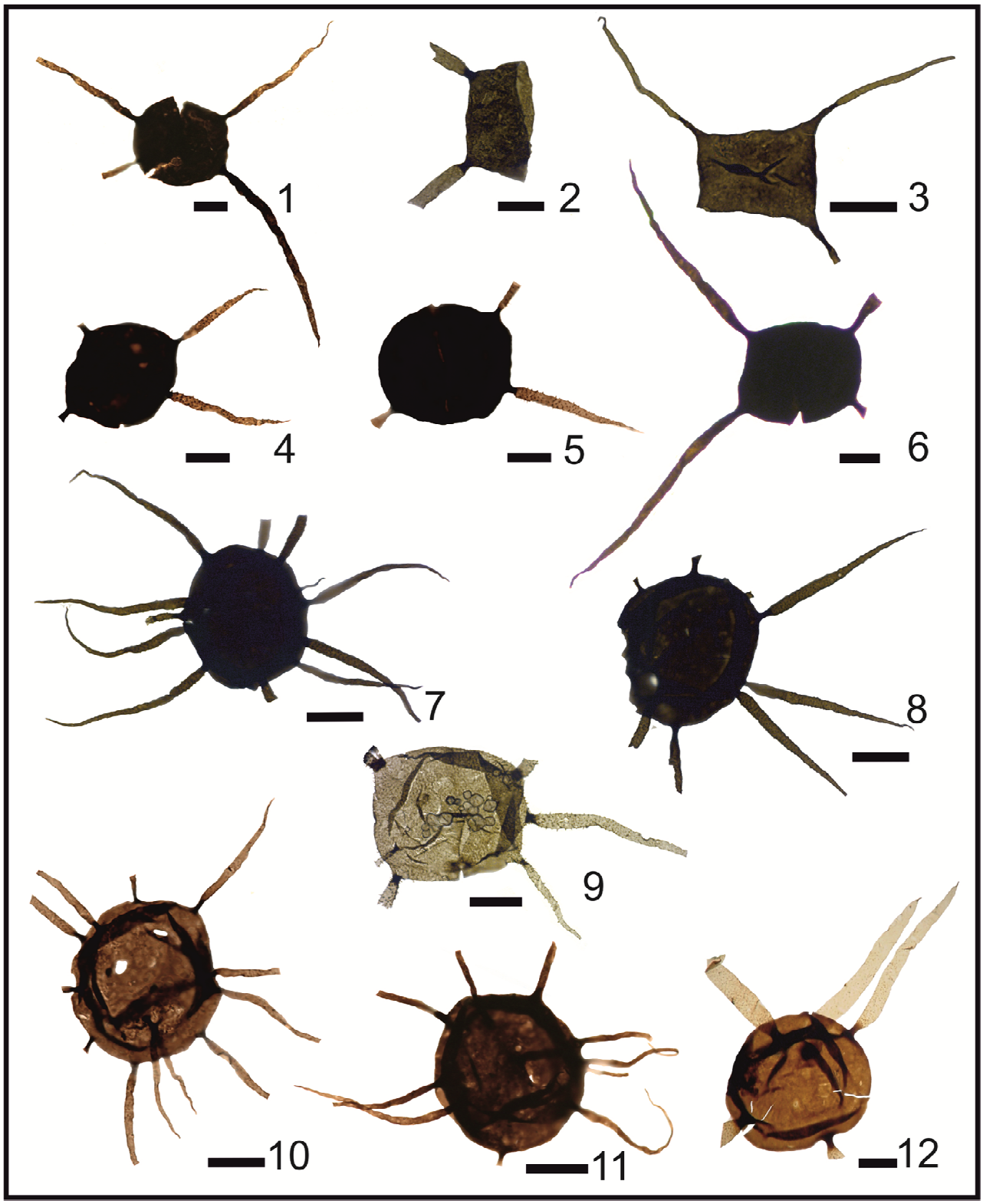
Plate II



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Article IV

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

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

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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*, *Cyclopospheridium* 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.

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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 decribed 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 *Arkonia* 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 prospectives 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

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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 lenght 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. Palaezoic 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 lenghts are the peteinoid acritarchs. Several genera have been attributed to this plexus of forms, including the genera *Peteinosphaeridium* Staplin et al. 1965, *Cyclopospha*eridium 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 *Peteinospaeridium* (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

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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 *Cyclopospha*eridium Uutela & Tynni 1991, and *Liliosphaeridium* Uutela & Tynni 1991. Playford et al. (1995) considered that *Peteinosphaeridium*, *Cyclopospha*eridium 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. *Cyclopospha*eridium 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 *Cyclopospha*eridium, 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)

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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 componant 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 palaoeontolocal 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

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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 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 µm (with few specimens showing vesicles up to 90 µm), but is generally between 40 and 50 µm. The process length is more variable, with short processes (about 7 µm) and long processes (about 35 µm) being present in the Hälludden section. Most processes are about 15 to 25 µm 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 µm. The calyx continuously various from being very short or even absent to having lengths of up to 20 or 25 µm, but usually being around 5 to 10 µm. The distal width of the calyx is also unimodally distributed with values between 5 and 35 µm, but mean widths of 10 to 15 µm.

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 calix 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 specimes 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

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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 peteionoids. 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. brevicalix*, 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. brevicalix* (calyx and stem of equal length) to *L. tintinnabulum* (very long calyx, short stem). Most interestingly, Bagnoli & Ribecai (2001) noted in the discussion paragraph conerning their new species *Liliosphaeridium brevicalix* 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 brevicalix* (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. Similarily, *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,

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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 arbitrarely. 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.

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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 lenght; 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 lenght (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. brevicalix*-type. 13. slide Häll16-2 >51μm, EF: H17/2; 14. slide Häll16-2 >51μm, EF: W6/1. Scale bars = 20 μm.

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Figure 1

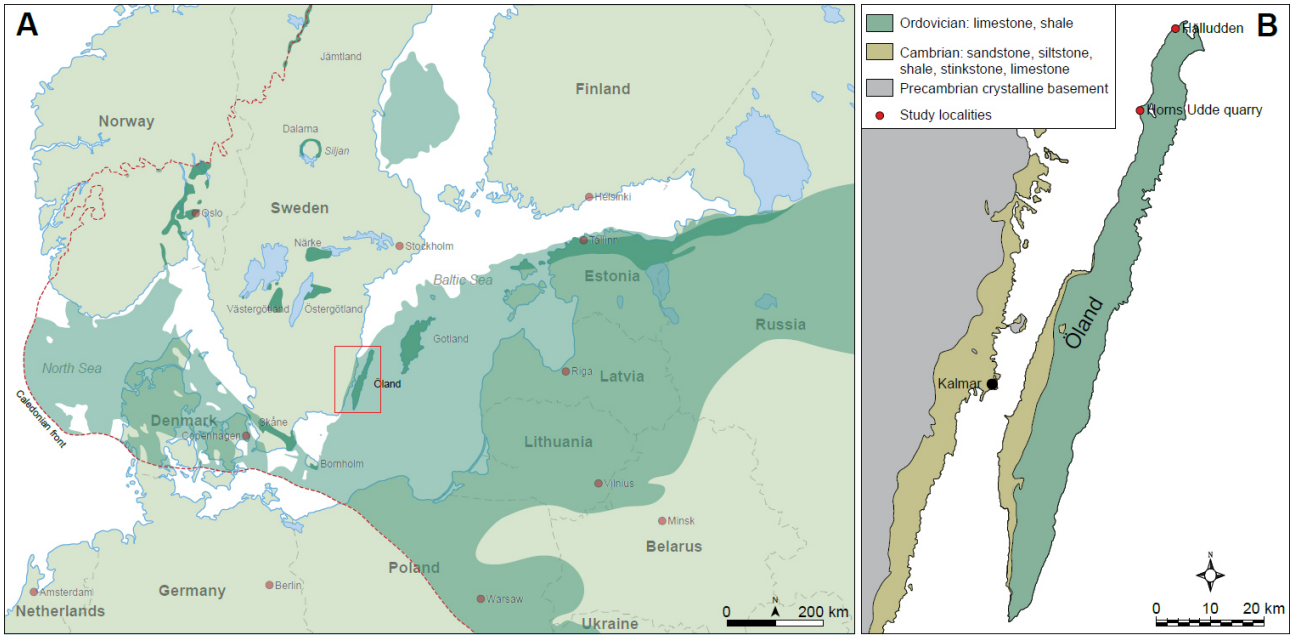

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Figure 2

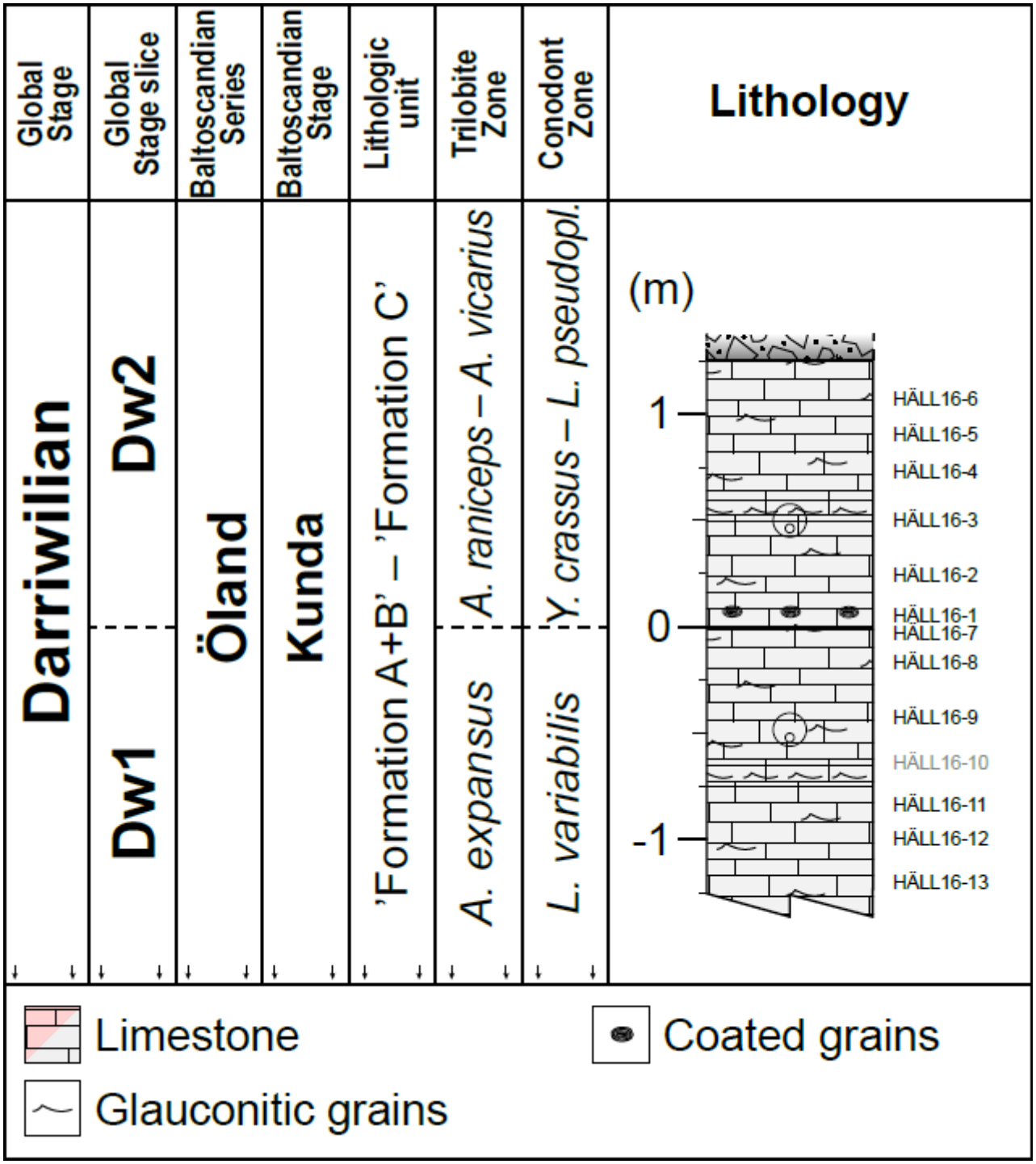

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Figure 3

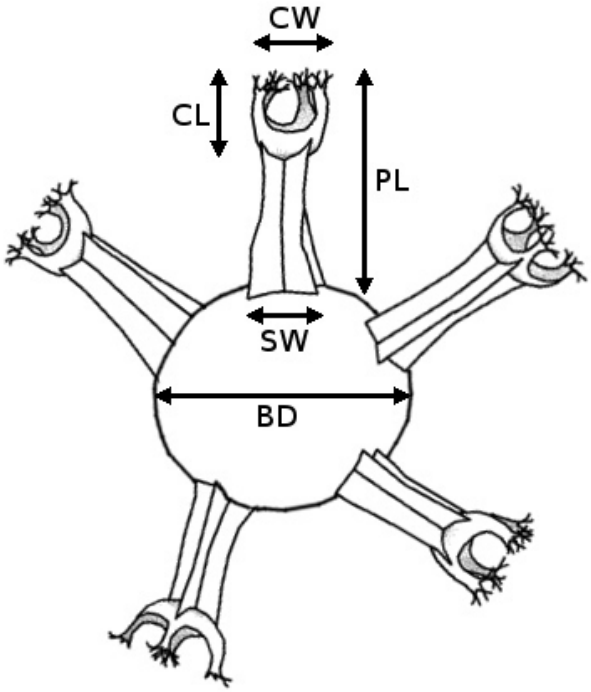

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Figure 4

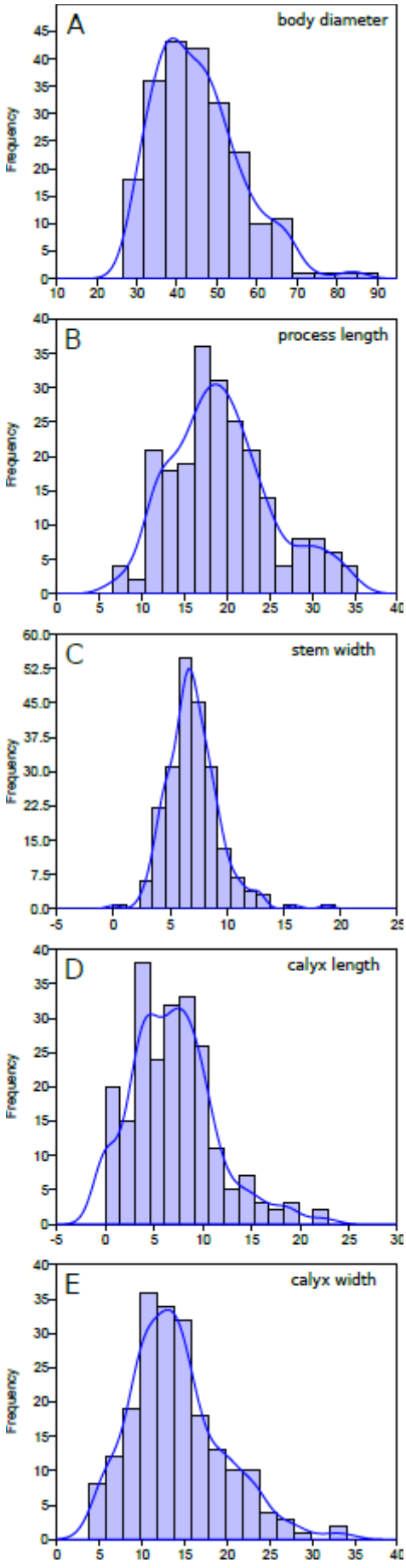

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Figure 5

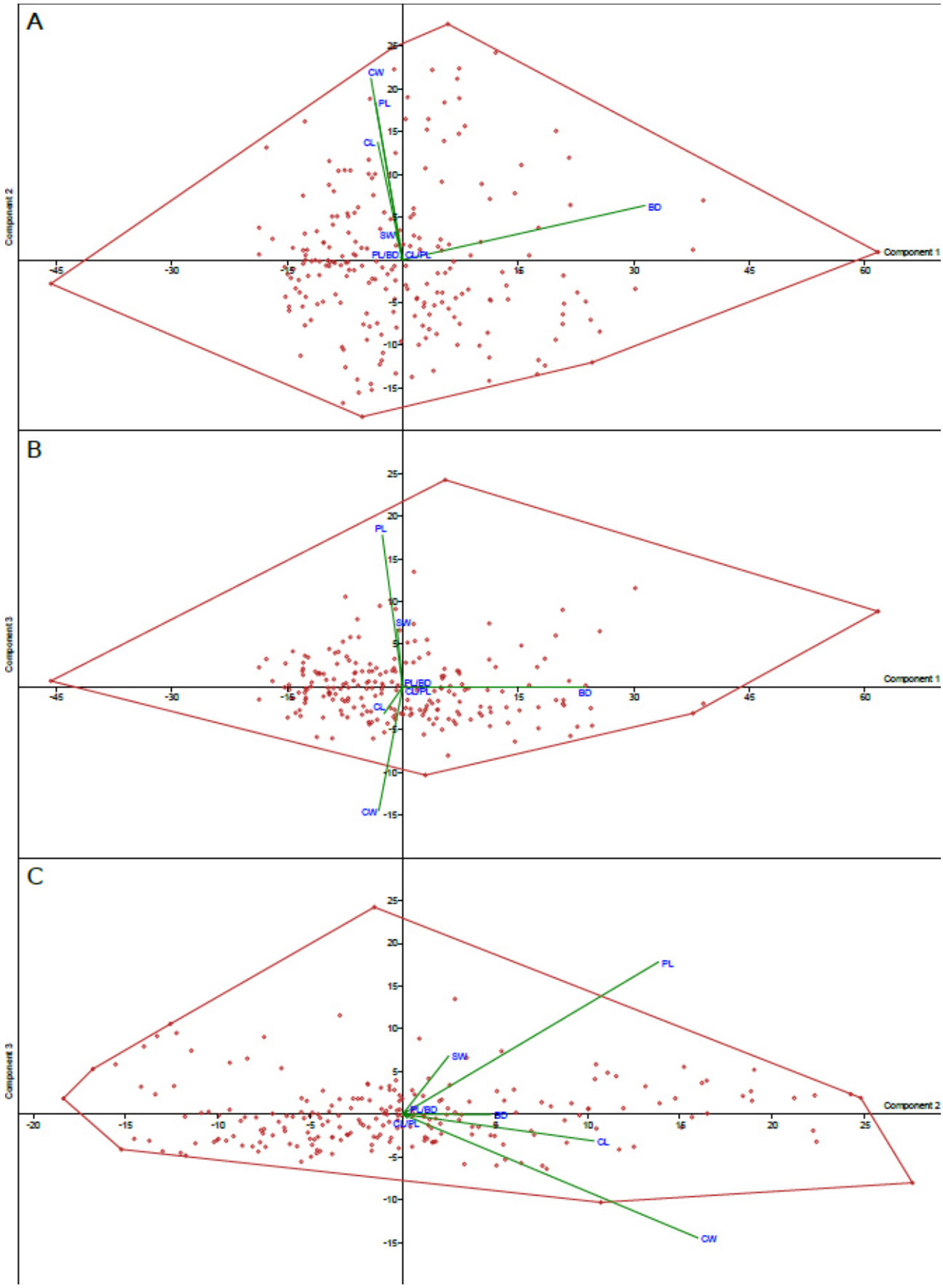

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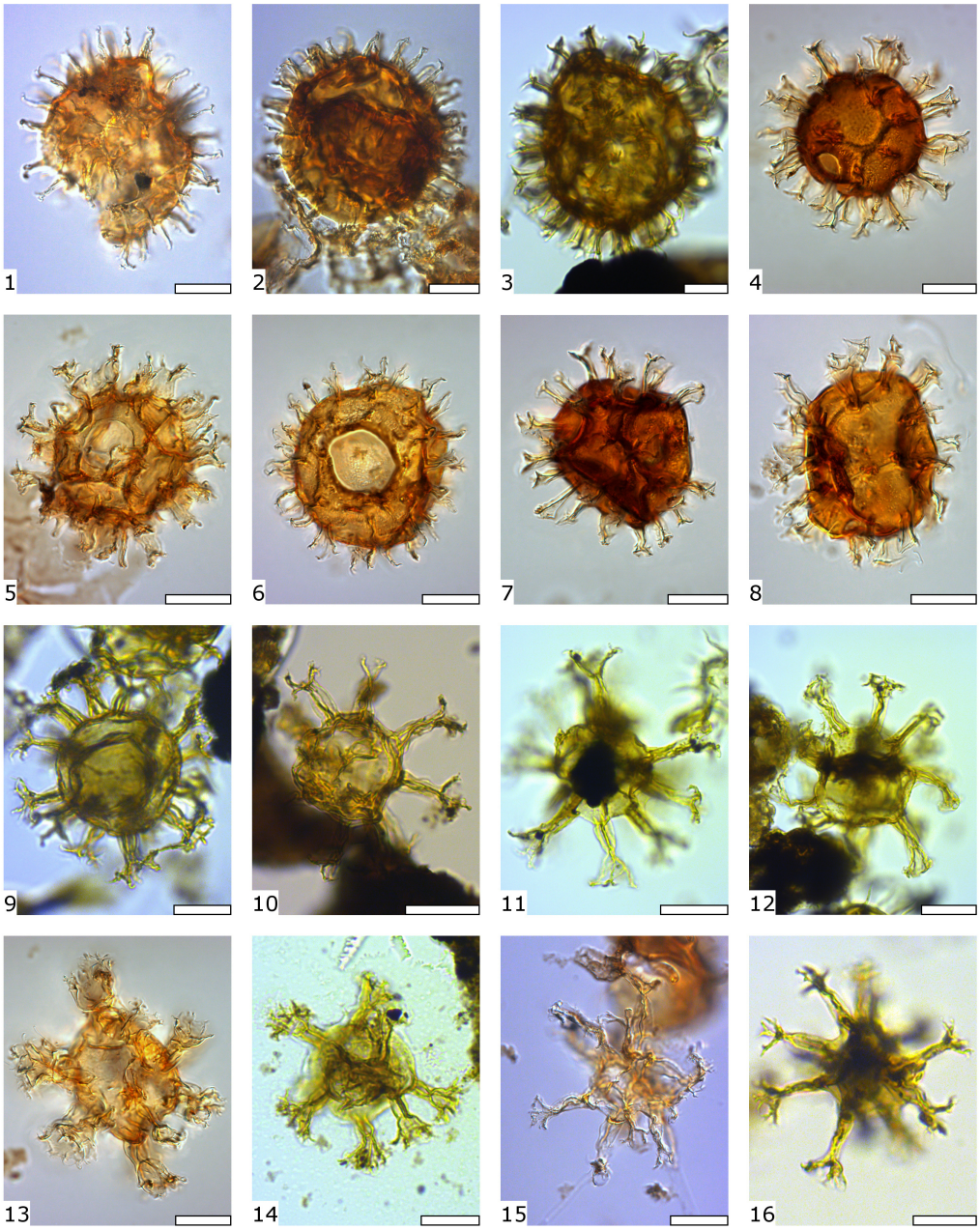
Plate I



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Article V

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

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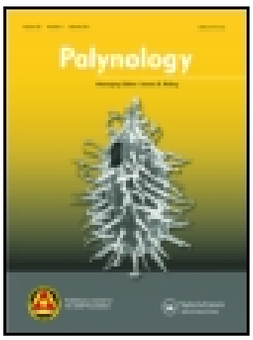

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Peri-Gondwanan acritarchs from the Ordovician of the Llanos Orientales Basin, Colombia

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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 *Dactyolofusa 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^2 (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 Cediel 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.

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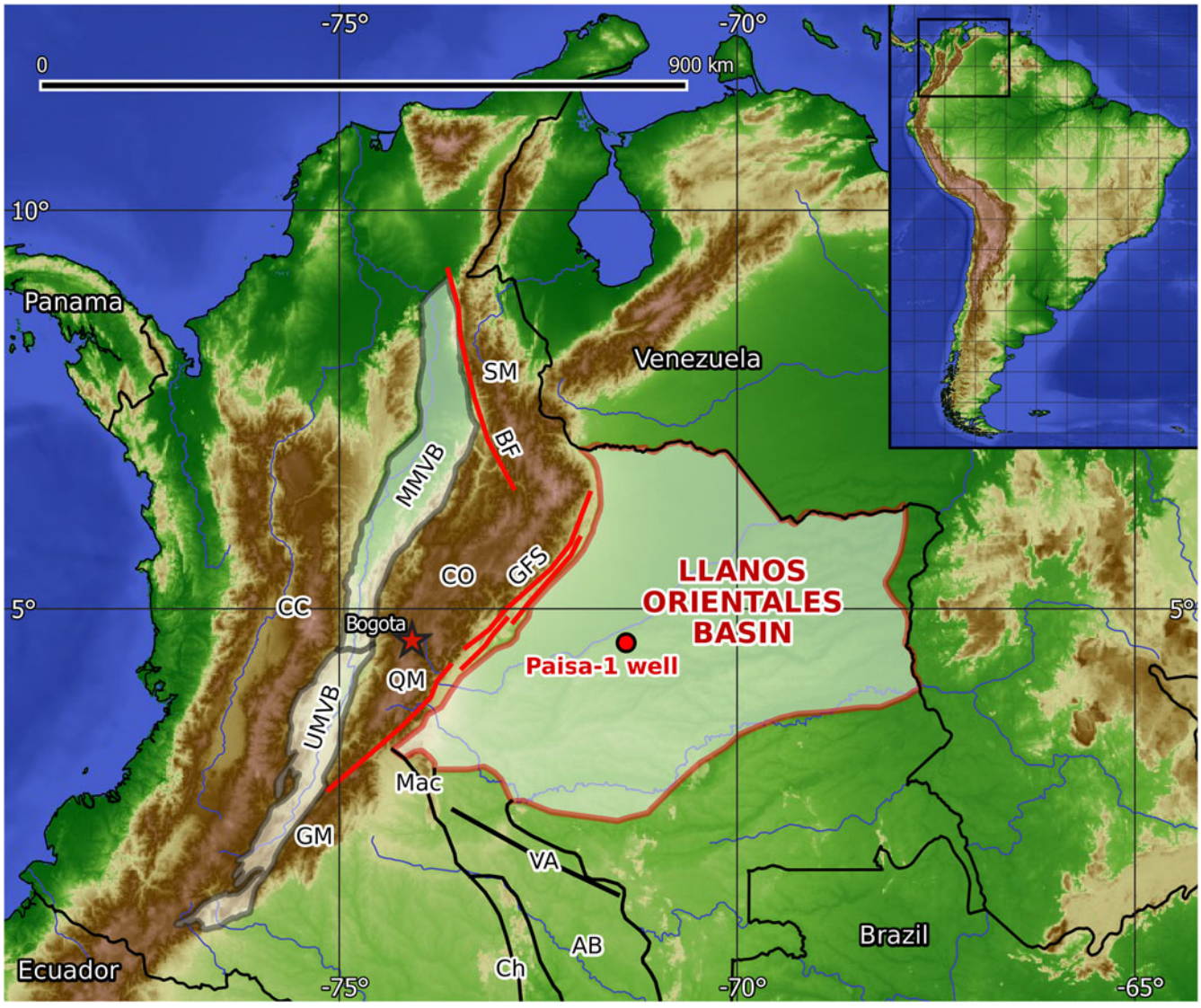

Figure 1. Location of the Llanos Orientales Basin in Colombia and the main geotectonic features. AB: Amazonas Basin; BF: Bucaramanga Fault; CC: Cordillera Central; Ch: Serranía de Chibiriquete; CO: Cordillera Oriental; GFS: Guaicáramo fault system; GM: Garzón Massif; Mac: Serranía de la Macarena; MMVB: Middle Magdalena Valley Basin; QM: Quetame Massif; SM: Santander Massif; UMVB: 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 palaeoenvironmental conditions.

2. Geological setting

The LB is today a sub-Andean foreland basin, limited to the west by the Andean Cordillera Oriental (Guaicáramo 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

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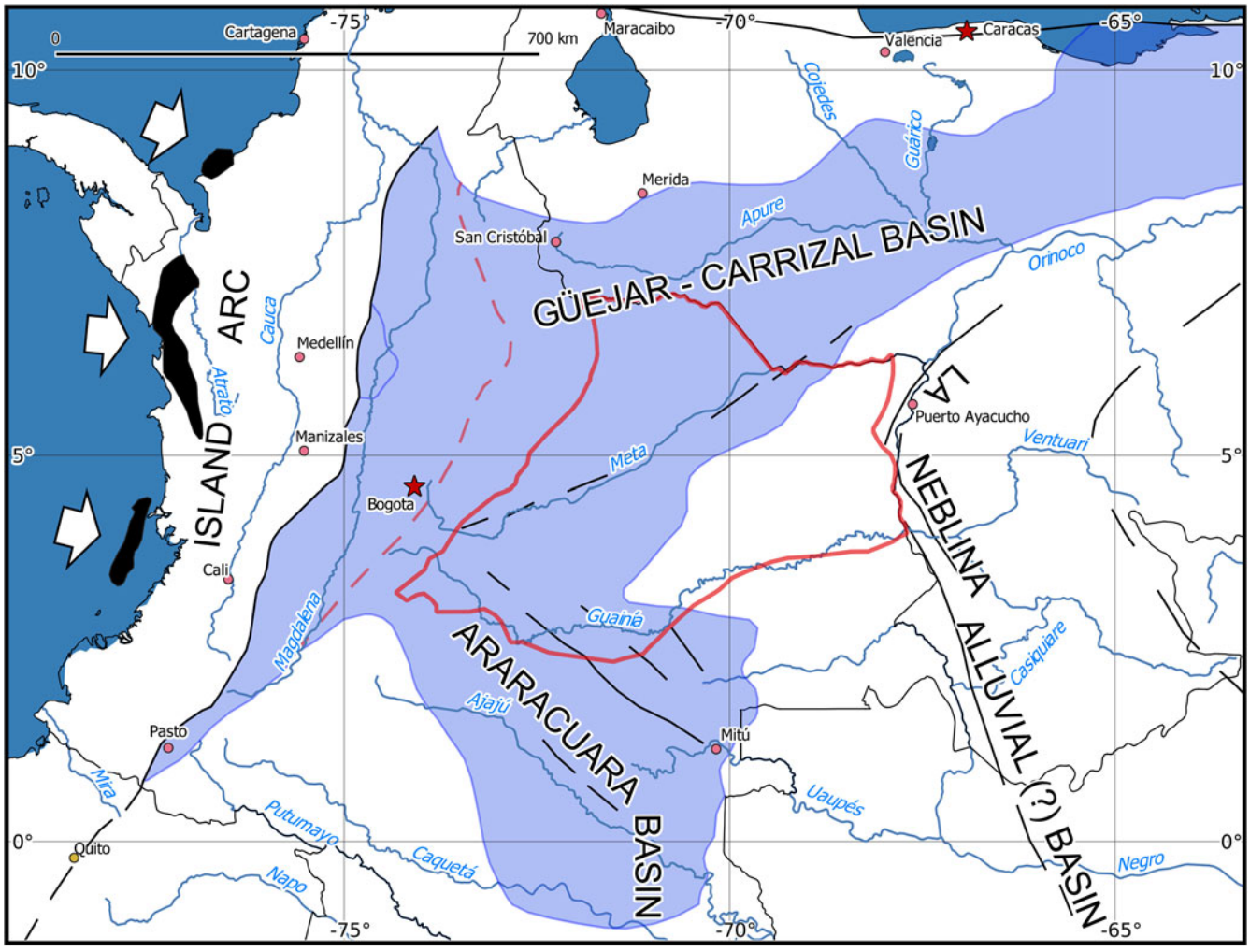

Figure 2. Depositional basins in north-western South America during the Cambrian–Ordovician. Dashed line: basement boundary between Chicamocha Terrane in the west and the Guyana Shield in the east. Based on Cediel et al. (2011).

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; Cediel et al. 2011; Cediel 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 disconformity (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). Cediel (2019, fig. 1.23) shows intertidal coastal swamp deposition in the north-western LB area near the foothills in his palaeogeographical interpretation for the

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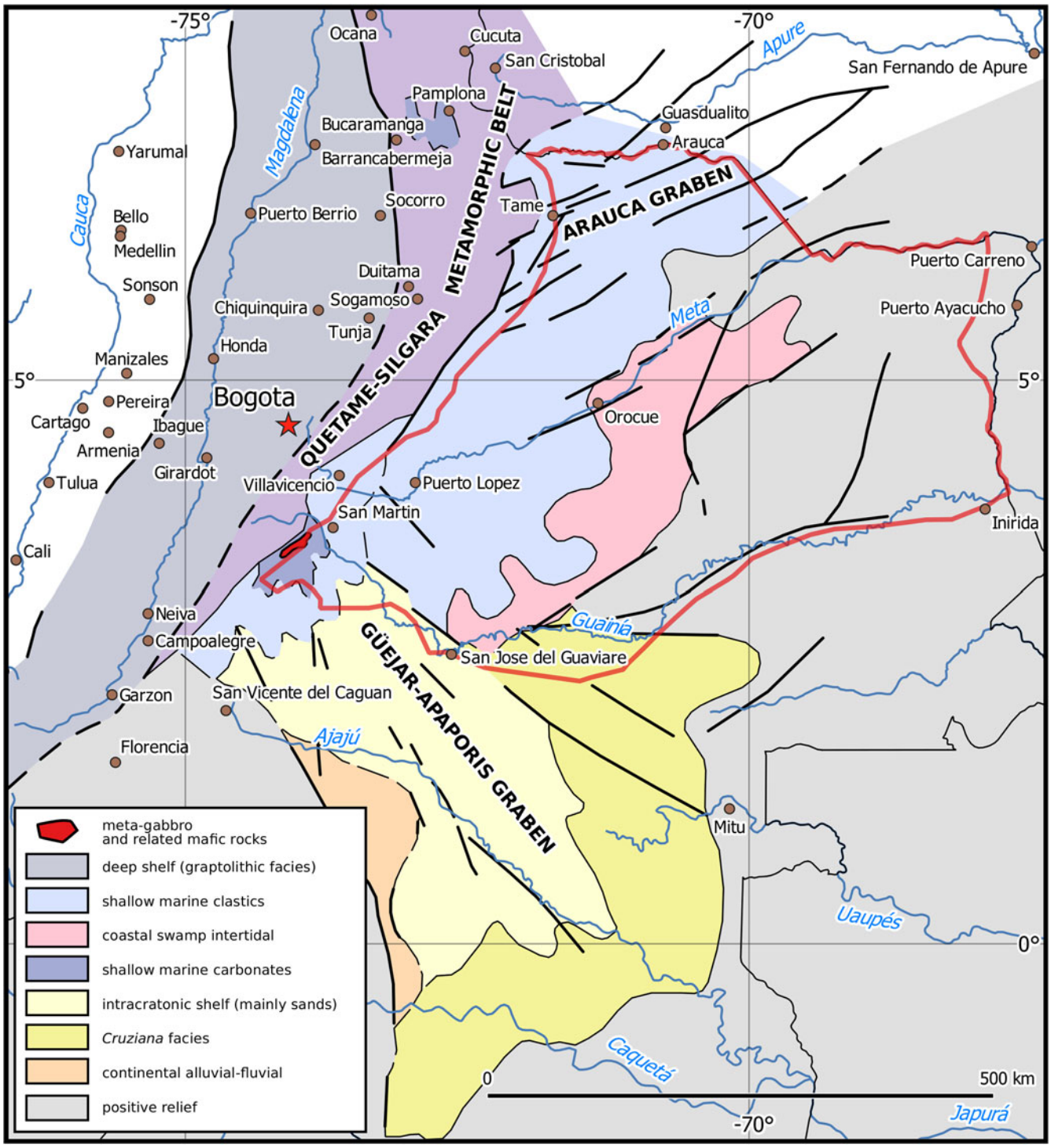

Figure 3. Sedimentary facies distribution in the eastern lower Palaeozoic basins of Colombia. Modified after Cediel (2019).

Devonian (cf. Cediel 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

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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

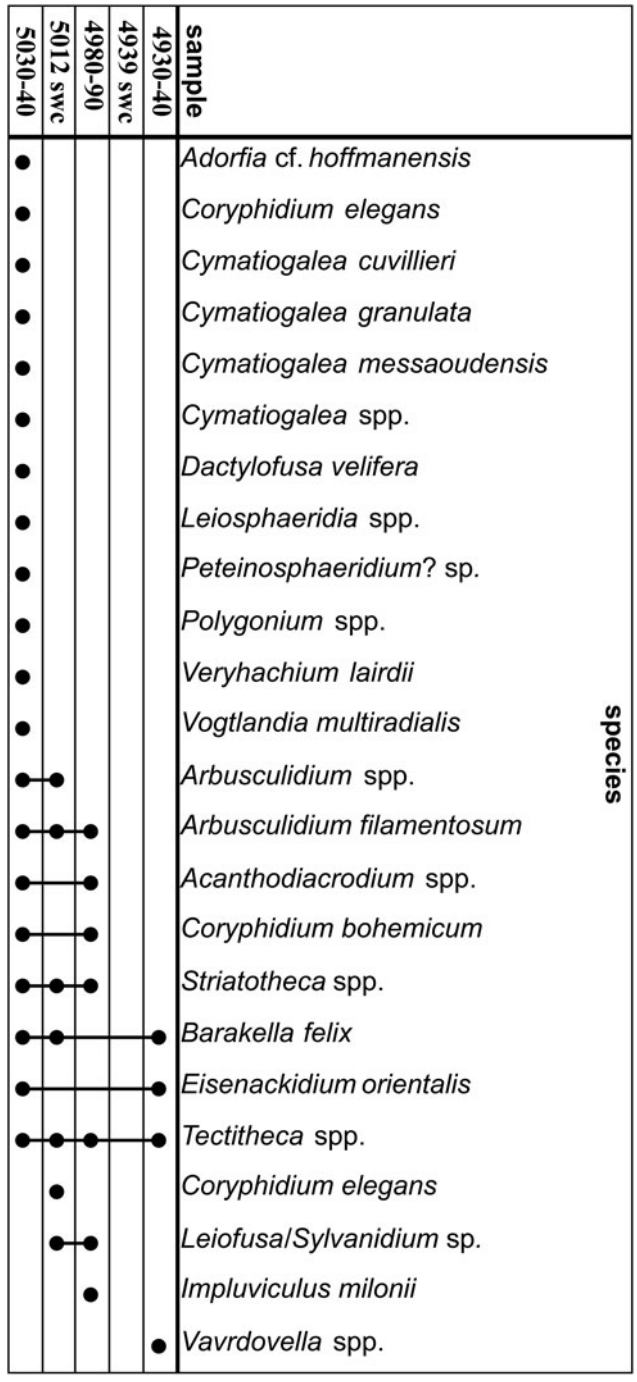

Figure 4. Distribution by sample of acritarch taxa from the Paisa-1 well in the Llanos Orientales Basin in Colombia.

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

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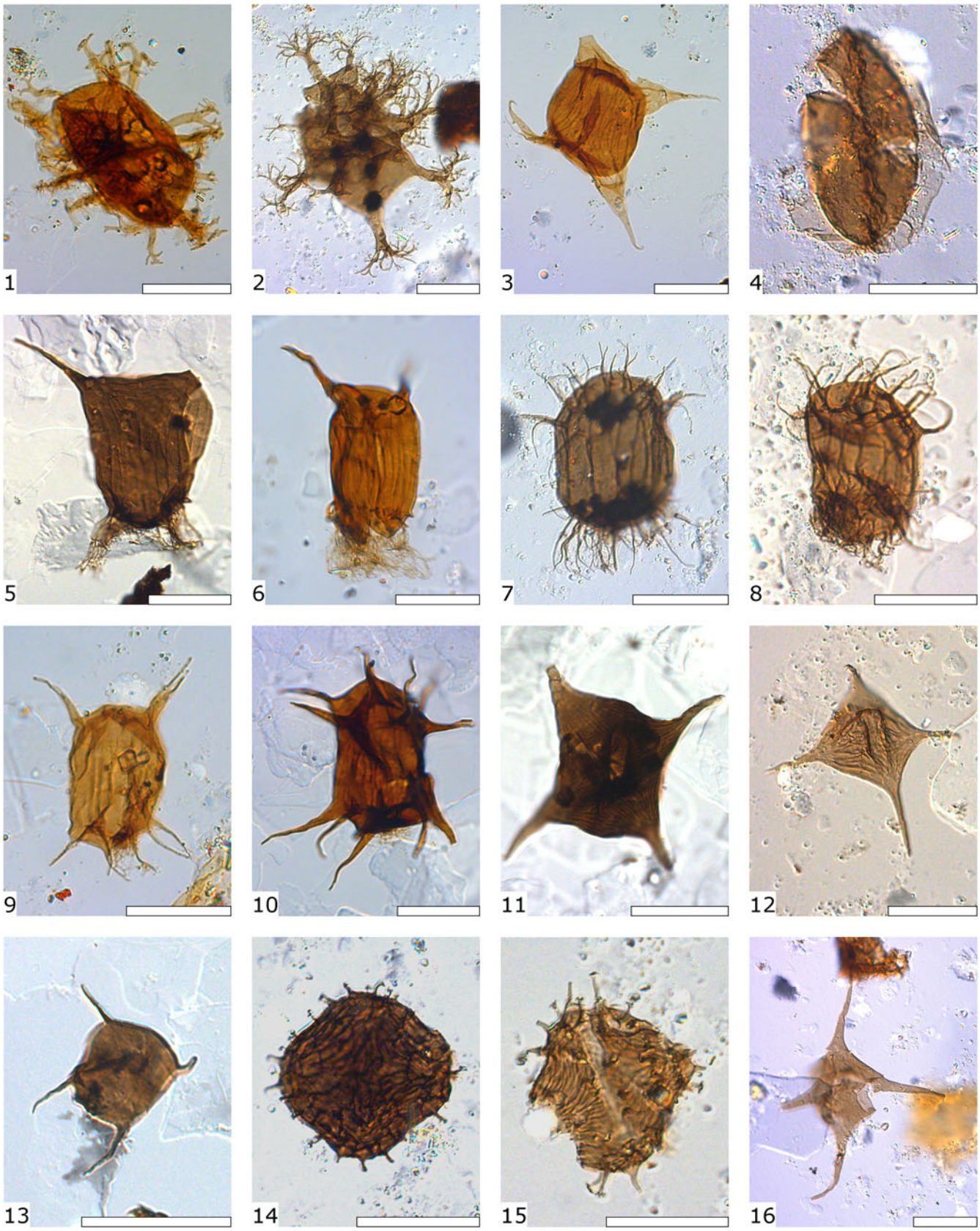

Plate 1. Specimens of selected taxa from the Ordovician of the Paisa-1 well, Llanos Orientales Basin, Colombia. 1. *Adorfia* cf. *hoffmanensis*, Paisa-1 5030–5040′ IIES-PAL-0679, England Finder (EF): D10/2. 2. *Vogtlandia multiradialis*, Paisa-1 5030–5040′ IIES-PAL-0679; EF: U49. 3. *Eisenackidium orientalis*, 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 μm.

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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 Fl1 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 (Fl2) (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 Fl2 (Servais et al. 2018).

The absence of taxa that are characteristic of younger intervals, such as *Frankea*, *Arkonia*, *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 (Fl2) 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, caving 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 Chribiquete (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 tuberata*), 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

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Leiosphaeridia, with records of *Arbusculidium filamentosum*, *Striatotheca*, *Vavrdovella*, *Dactylofusa velifera*, and *Acanthodiacrodium* 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. Similarily, 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*,

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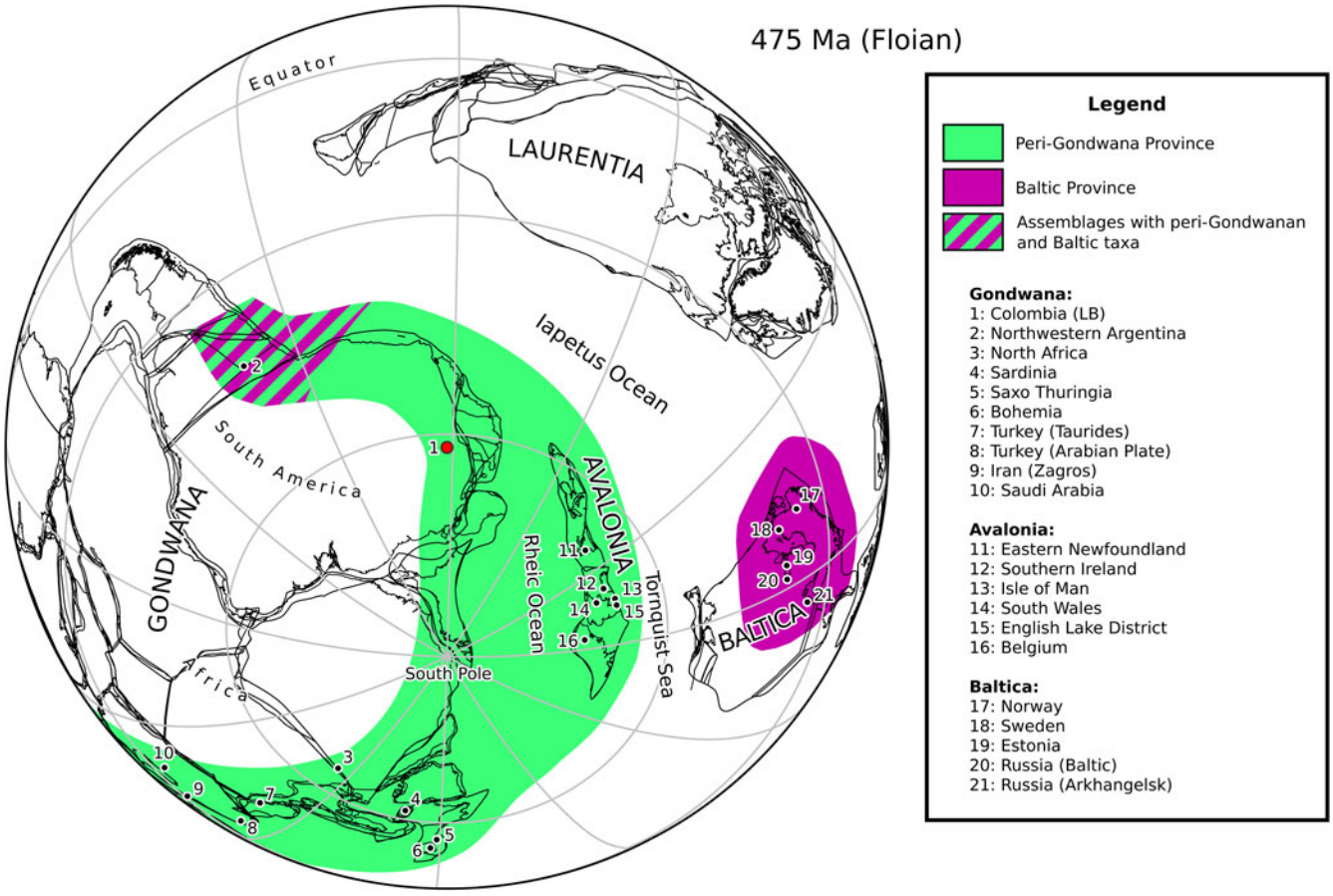

Figure 5. Lower Ordovician (Floian, 475 Ma) palaeogeographical reconstruction (orthographic projection) showing the distribution of the Lower Ordovician phytoplankton palaeobioprovinces in accordance with the plotted study locality (in red) and selected acritarch localities (from Molyneux et al. 2013). 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 'peteinosphaerid-*Dicommopalla* class' is characteristic of a shoal environment, and the 'baltisphaerid-veryhachid-*Polygonium*-micrhystridid 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

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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 locatities 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, Ningiang, 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 *Peteinosphaeridum* 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*, *Arkonia* 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.

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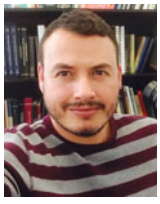

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Appendix 1

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
Arkonia 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 Vanguestaine 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

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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 & Willière 1962
Veryhachium valiente Cramer 1964
Vogtlandia multiradialis Burmann 1970
Vulcanisphaera tuberata (Downie 1958) Eisenack et al. 1973

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Article VI

Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton

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Main Manuscript for

Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton

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the dataset; A.P. conducted paleoclimate simulations; G.B. performed species distribution simulations; A.Z, C.M., T.S., A.P. and G.B. wrote the paper.

This PDF file includes:

Main Text

Figures 1 and 2

Tables 1 and 2

Abstract

The decline in species richness from the equator to the poles, known as the latitudinal diversity gradient (LDG), is probably the most commonly observed macroecological pattern nowadays, but the timing of its establishment, its ubiquity in the geological past and controlling factors remain uncertain. Here we analyze the latitudinal distribution of diversity of the earliest representatives of marine phytoplankton in the fossil record, i.e. the acritarchs, for the early Paleozoic (Cambrian─Ordovician interval, ca. 541 to 444 Ma) at the global scale. We show that acritarchs exhibited a LDG since the early Cambrian, and that this unimodal gradient was centered on the mid-latitudes of the Southern Hemisphere instead of the equator, as classically observed for most modern taxa. This atypical pattern stems from the fact that this LDG actually corresponds to a truncated bimodal gradient (i.e. having its northern peak of diversity missing) that probably results from an uneven preservation of sediment/acritarchs, a smaller sampling effort, and/or a lower initial diversity in the Northern Hemisphere due to the limited amount of suitable ecospace. Our findings suggest that variation in the shape of the acritarch LDG through time resulted primarily from the long-term climate cooling that characterized the early Paleozoic, as shown by both empirical and modeled data; and that the latitudinal distribution of acritarch diversity was influenced by both mean annual and seasonal fluctuations in sea-surface temperature, and to a lesser extent salinity and the extent of continental shelves.

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Significance statement

The latitudinal diversity gradient (LDG) – the decrease in species number from the equator to the poles – is considered as the most pervasive large-scale biological pattern on Earth, but the timing of its establishment, its ubiquity in the geological past and explanatory mechanisms remain uncertain. Here, we show that acritarchs – the first representatives of marine phytoplankton in the fossil record – exhibited a LDG as early as the beginning of the Cambrian, when most major marine phyla appeared. However, this LDG was atypical, showing a single peak of diversity in the Southern and not in the Northern Hemisphere. Our findings suggest that variation of this LDG through time resulted from both annual sea-surface temperature and long-term climate fluctuations.

\body

Main Text

Introduction

The latitudinal diversity gradient (LDG), i.e. the increase in taxonomic diversity from the poles to the equator, is probably the most striking and pervasive biogeographical pattern on Earth (1–3). Despite being a ubiquitous phenomenon documented for a large variety of functional and taxonomic groups, its origin, frequency among fossil groups, as well as its explanatory mechanisms remain widely debated. Proposed explanations for this pattern can be grouped into six categories: geographic area (4), geometric constraints (5), energy availability (6), habitat heterogeneity (7), evolutionary mechanisms (8), and niche theory (9, 10). While some of these explanations can be tested through neontological approaches, the effect of long-term phenomena such as climate changes and biological evolutionary events are inextricable using only extant taxa (11–13). The fossil record thus offers a unique and complementary perspective for studying the LDG as it can provide insights on its appearance, stability through time and long-term control mechanisms. Studies of the LDG on fossil data have shown that it extends back to the Paleozoic (ca. 541─252.9 Ma; 13–16), but that the strength of the gradient has varied through time (17), and the pattern

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even disappeared during intervals of mass extinctions (8). For the early Paleozoic (i.e. Cambrian─Ordovician, ca. 541─444 Ma), the presence of a LDG has been documented for three marine groups − brachiopods (13, 18), bryozoans (18) and chitinozoans (19) – as well as for the whole marine diversity of the Paleobiology Database (20; https://paleobiodb.org). Their LDGs consist of unimodal gradients (i.e. one diversity peak) centered on low to mid-latitudes of the Southern Hemisphere (i.e. between 0 and 45°S), whereas for most extant organisms, the LDG is either unimodal with a peak of diversity centered at the equator, or bimodal with two peaks of diversity centered on the mid-latitudes of each hemisphere (21–25). In the present study, we expand our perspective on the LDG to the main representatives of phytoplankton in the early Paleozoic, i.e. the acritarchs. Defined as organic-walled microfossils of uncertain biological affinity (26), most of them are now considered to be cysts of marine, generally phytoplanktonic unicellular algae (27), and some may have a close biological affinity with dinoflagellates, as suggested by biomarkers and morphological similarities (28). So far, acritarchs have been mainly used as tools for biostratigraphical, paleogeographical and paleoenvironmental reconstructions (29–31), but only few researchers considered them for what they are, i.e. the main source of information on phytoplankton in the early Paleozoic, and studied them as such through macroevolutionary and macroecological approaches (32, 33). Yet, acritarchs have the most densely and continuously sampled fossil record of any phytoplanktonic group at the global scale over the early Paleozoic (34), and therefore constitute a unique material to study macroecological dynamics during this crucial period of the history of Life. Our approach was to (*i*) determine the potential timing of establishment of a LDG for early Paleozoic acritarchs and its evolution through time according to long-term climate changes, (*ii*) analyze the relationship between the latitudinal distribution of acritarch diversity and abiotic factors whose values were reconstructed using paleoclimate simulations, and (*iii*) compare the shape of acritarch LDGs to modeled LDGs based on the same paleoclimatic and paleogeographic context.

We conducted our analyses over 11 time bins covering the Cambrian–Ordovician interval with a new database of more than 9k occurrences of acritarch genera from localities with known paleogeographic

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coordinates (*SI Appendix*, Table S1). Latitudinal paleobiodiversity curves were reconstructed by means of range-through indices (see Material & Methods). The relationships between acritarch diversity and abiotic factors (i.e. continental shelf area, sea-surface temperature and salinity) were tested for three key stages, i.e. the Cambrian stage 4, the Darriwilian and the Hirnantian, by means of (*i*) the non-parametric Kendall's rank correlation coefficient applied between the LDG and each abiotic factor separately, and (*ii*) a generalized linear model (GLM, see *SI Appendix*) with a response variable (i.e. diversity) following a Poisson distribution. Finally, we modeled species diversity for the Cambrian stage 4, the Darriwilian and the Hirnantian using a model based on the MacroEcological Theory on the Arrangement of Life (METAL; see *SI Appendix* and 10, 35, 36) forced with the sea surface temperature (SST) values simulated using the climate model (see *SI Appendix*) on available paleogeographical reconstructions (37).

Results and Discussion

We find a unimodal latitudinal gradient of acritarch genus diversity for each time bin (i.e. four Cambrian series and seven Ordovician stages; Fig. 1 & *SI Appendix*, Fig. S1). The small amplitude gradient observed at the beginning of the Cambrian (i.e. Terreneuvian, ca. 531 Ma) may be explained by a poor sampling effort or preservation bias (*SI Appendix*, Fig. S2). Contrary to the classical unimodal LDG observed for many modern taxa (e.g. neritic and terrestrial taxa, 25, 38), the acritarch LDG does not exhibit a diversity maximum at the equator or near the tropics, but rather over mid-latitudes of the Southern Hemisphere (i.e. 35−40°S) during the Cambrian series 2 (ca. 515 Ma; Fig. 1, *SI Appendix*, Fig. S1). The diversity peak then slowly drifts southwards, reaching 45°S during the Furongian (ca. 491.2 Ma) and its highest latitudinal position (i.e. 50−60°S) during the Tremadocian−Dapingian interval (ca. 485.4−467.3 Ma), before splitting in two peaks corresponding to the drift of areas of high diversity (i.e. Baltica and the Armorican Terrane Assemblage; *SI Appendix*, Fig. S4) during the Middle Ordovician (Fig. 1, *SI Appendix*, Fig. S1). Only the peak located at the lowest latitude and corresponding to Baltica persists

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until the end of the Ordovician (Fig. 1, *SI Appendix*, Fig. S1). Additionally to the position of peak diversity, the steepness of the LDG also changes through time. It drastically increases during the Floian in the Southern Hemisphere (ca. 473.85 Ma), paralleling an augmentation in diversity in the equatorial and low latitudes of the Northern Hemisphere (Fig. 1, *SI Appendix*, Fig. S1). A similar tropical diversification is apparent for marine organisms considered as a whole, and it does not reflect changes in the relative abundance of depositional environments, in environmental and lithological heterogeneity, or in paleogeography (20). This transition from a poor Cambrian to a highly diversified Ordovician intertropical zone is probably related to a global climate change (19, 39, 40). While the Cambrian corresponded to a greenhouse climate with equatorial SST probably too high to sustain highly diverse communities (*SI Appendix*, Fig. S3; 41), a steady cooling trend occurred through the Early Ordovician to reach the range of modern equatorial SST by the Middle Ordovician (*SI Appendix*, Fig. S3; 39), allowing all major marine groups to colonize low latitudes (42), before ending in a glaciation associated to a massive extinction during the Hirnantian (43). Temporal variations in the position of the LDG diversity peak of early Paleozoic acritarchs and the general shape of this LDG thus appear to have been related to the climatic regimes of the Cambrian−Ordovician interval, and to a lesser extent to the position of continental masses. Brayard et al. (23) have shown through a modeling approach that the position of peak diversity and steepness of LDGs in marine environments depend on the shape and magnitude of the latitudinal SST gradient: sigmoid-like SST gradients generate a bimodal LDG with peaks of diversity located at mid-latitudes, while a reduced steepness of the SST gradient leads to a weakened unimodal LDG with a plateau of equal diversity between the tropics. This implies that bimodal LDGs with diversity peaks at intermediate latitudes are a characteristic feature of icehouse periods, whereas unimodal LDGs with an equatorial peak or a plateau of equal diversity are characteristic of greenhouse periods (see 12 and references therein). Alternatively, Beaugrand et al. (36, fig. 4) have shown that in case of a global cooling, the LDG steepness increases because of the movement of species towards the equator, leading to a unimodal gradient centered at the equator, whereas in case of global warming, it is attenuated because of the poleward shift of species, leading to a bimodal gradient with peaks of diversity at intermediate

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latitudes. The LDG of early Paleozoic acritarchs is steeper and its peak of diversity closer to the equator during the colder Middle-Late Ordovician than during the Cambrian, and no equatorial peak or plateau of equal diversity is observed under the Cambrian greenhouse climatic conditions (*SI Appendix*, Fig. S1). This more corresponds to the model of Beaugrand et al. (36) and its deviation from Brayard et al.'s (23) model might be explained by a threshold temperature effect: peak diversity could not occur at the equator during the Cambrian because equatorial temperatures were too high to allow most organisms to survive; and this peak slowly shifted towards more equatorial latitudes during the Ordovician cooling, with a rapid first step of diversification at equatorial latitudes during the Early Ordovician (i.e. Floian, *SI Appendix*, Fig. S1). As such, it seems that – as for the majority of marine groups of organisms – long-term climate trends had an important influence on the distribution of diversity of early Paleozoic phytoplankton.

The results of our analyses of correlation between SST and acritarch diversity support this hypothesis. For the Cambrian stage 4, seasonal variation in SST (SST_{diff}, i.e. the difference between summer and winter SST) appears as a positive predictor of acritarch diversity in the three best GLMs ($169.95 < AICc < 171.28$, $R^2=0.58$; Table 1). For the Darriwilian, which corresponds to the major diversity peak of the GOBE and during which global climate was cooler than during the Cambrian (*SI Appendix*, Fig. S3; 42), SST_{diff} is also significantly correlated to diversity as revealed by Kendall's test ($\tau = 0.53$, $p < 0.01$; Table 2), and mean annual SST (SST_{an}) is a negative predictor of diversity (AICc=186.59, $R^2=0.61$; Table 1). Eventually, during the colder Hirnantian stage (*SI Appendix*, Fig. S3), the best GLM shows that SST_{an} and SST_{diff} negatively and positively predict the latitudinal distribution of acritarch diversity, respectively (AICc = 133.83, $R^2=0.88$; Table 1); and Kendall's test shows significant 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 together, these results – which are complementary as the Kendall's coefficient and GLMs do not test the same relationship between the variable of interest and its potential predictors − clearly show the existence of a relationship between SST, and especially its seasonal variations, and the spatial distribution of acritarch diversity throughout the early Paleozoic. Temperature has often been cited as one of the main explanatory factors for large-scale distribution patterns of organisms (10, 24, 44). Many studies, in both

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marine and terrestrial environments, have shown that present-day temperature, along with some other environmental factors such as precipitation on land and productivity in the sea, are powerful first-order predictors of LDG patterns (44 and references therein). In the marine realm, Tittensor et al. (45) have shown that SST was the only environmental predictor highly correlated with diversity across 13 taxonomic groups, a finding confirmed for phytoplankton in particular (46). Our results show that acritarchs are no exception to this rule, and that as far back as the early Paleozoic, the spatial distribution of phytoplankton diversity was controlled, at least in part, by this abiotic variable.

Salinity is known to affect the distribution patterns of marine organisms at local (e.g. 47) and sometimes at regional scales (48), but its influence on global distribution patterns of diversity seems to be weak (45, 49). Regarding early Paleozoic acritarchs, Kendall's tests reveal a positive correlation between diversity and both mean annual sea-surface salinity (SSS_{an}) and squared SSS_{an} (SSS^2) during the Cambrian stage 4 ($\tau = 0.44$, $p < 0.01$; Table 2), and SSS^2 also appears as a predictor of diversity with the GLM ($169.95 < AICc < 171.28$, $R^2=0.58$; Table 1). For the Darriwilian, SSS_{an} and SSS^2 appear, respectively, as positive and negative predictors of diversity using a GLM ($AICc=186.59$, $R^2=0.61$; Table 1). For the Hirnantian, only the GLM shows that SSS^2 positively predicts the latitudinal distribution of acritarch diversity ($AICc=133.83$, $R^2=0.88$; Table 1). A relationship thus seems to exist between the early Paleozoic acritarch diversity and salinity. However, given that SSS values remain quite stable in the inter-tropical zone from the Cambrian stage 4 to the Hirnantian (*SI Appendix*, Fig. S3d) while a major shift of diversity is recorded in this area during the Early Ordovician, we argue that temperature was a more limiting factor of acritarch diversity, because the colonization of the inter-tropical zone by acritarchs during the Floian is not associated with a change in SSS, but much more likely with a diminution in SST (42).

The third abiotic factor investigated here, i.e. continental shelf area (CSA), has often been found to be related to marine diversity (50), but it should not be considered *a priori* as a bias. Indeed, during transgression events, flooded continental areas increase, offering more niche space and opportunities for diversification, and impacting the production of sediments, which provides a general explanation for the covariation between fossil marine biodiversity and the amount of marine sedimentary rocks (51).

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However, this signal varies among groups of organisms, spatial scales and time intervals (52). Regarding acritarchs, CSA is significantly correlated with their diversity for the Cambrian stage 4 using Kendall's test (τ=0.47, $p < 0.01$; Table 2), and it appears as a positive predictor of diversity for the Darriwilian and the Hirnantian when analyzed through GLM (AICc = 186.59 and 133.83; R^2=0.61 and 0.88, respectively; Table 1, *SI Appendix*). This relationship is in fact almost inevitable for Paleozoic marine organisms. Indeed, because the Paleozoic oceanic crust has long been recycled in subduction zones, the vast majority of deposits accessible today were located on continental shelves at that time. Furthermore, the fact that modern dinoflagellates are most diverse in marine shelf areas compared to oceanic and lacustrine environments, and that organic-walled cyst production is most common in shelf areas (53), supports the genuine nature of this relationship for acritarchs.

Assuming that the diversity of early Paleozoic acritarchs is concentrated on continental shelves, we compared their empirical LDGs with the LDGs obtained by modeling species distribution on continental shelves only using the METAL model of Beaugrand et al. (10, 35, 36). Validated for modern plankton, fish and cetaceans (36), the METAL model shows that the primary cause of LDGs in the oceans lies in the interaction between species thermal tolerance and both seasonal and year-to-year fluctuations in temperature, together with the generation of a mid-domain effect in the ecological niche space. For the Cambrian stage 4 and the Darriwilian, modeled LDGs are bimodal with two peaks of diversity located 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). The northern peak of diversity is smaller than the southern one for both stages (Fig. 2). For the Hirnantian, the gradient is steeper and unimodal with a plateau of maximum diversity ranging from ~22.5°S to 27.5°N (Fig. 2). The three modeled LDGs end around 30°N for each stage because no continental shelf existed above this latitude during the early Paleozoic, the Northern Hemisphere being essentially covered by the Panthalassa Ocean. Modeled and empirical LDGs are significantly correlated for the Darriwilian (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 $\tau = 0.04$, $p = 0.83$, respectively). Although the Southern Hemisphere peaks of diversity of the modeled and empirical LDGs are located at close latitudes during the first two stages, some important differences can

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be observed: modeled LDGs are bimodal during the first two stages while empirical LDGs are unimodal, and the Hirnantian modeled LDG shows a plateau of equal diversity centered at the equator, while the empirical LDG shows a diversity peak located around 27.5°S. The change from a bimodal to a unimodal modeled LDG between the Darriwilian and the Hirnantian does not match our observations, but the fact that the peak of diversity moves towards lower latitudes during this interval in both cases (i.e. modeled and empirical; Fig. 1) shows the influence of the climate cooling on the latitudinal distribution of diversity, allowing taxa to colonize lower latitudes. Bimodal gradients are very common for extant marine organisms (21–25). They have been documented for marine taxa as varied as bivalves (54), brachiopods (55), bryozoans (56), foraminifers (10, 21), seaweeds (57) and copepods (10, 44). However, bimodal LDGs have never been observed for Paleozoic organisms (13, 18, 19). This marked difference may result either from the fact that modern LDGs are controlled by different factors than early Paleozoic LDGs, or that the early Paleozoic fossil record is biased and the LDGs one reconstructs are distorted images of the original ones. The fact that LDGs modeled here are bimodal, and that empirical unimodal LDGs centered on the mid latitudes of the Southern Hemisphere are characteristic of Paleozoic organisms, supports the second hypothesis. This seems all the more likely for acritarchs since the LDGs of extant pelagic organisms (16) and dinoflagellates in particular (58), as well as modeled LDGs of virtual planktic species (10, 23, 59), are also bimodal. Therefore, we argue that rather than being an atypical unimodal gradient centered on the mid-latitudes of the Southern Hemisphere, the early Paleozoic acritarch LDG probably corresponds to a truncated bimodal gradient whose Northern peak of diversity cannot be recovered or never existed. Either it cannot be recovered because of a reduced sediment and/or specimen preservation, and/or a smaller sampling effort in the Northern Hemisphere (e.g. absence of data from Siberia); or it never existed because some habitat-related factors essential for survival of acritarchs but not accounted for in the model were lacking in most of the Northern Hemisphere because of the small extent of landmasses.

This first quantitative analysis of the latitudinal distribution of early Paleozoic acritarch diversity shows that (*i*) the earliest representatives of marine phytoplankton were characterized by a LDG already since the Cambrian Explosion, (*ii*) this LDG corresponded to a truncated bimodal rather than a unimodal

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gradient, (*iii*) variation in the shape of this LDG through time can be attributed to both long-term climate cooling characterizing the early Paleozoic and plate tectonics, and (*iv*) the latitudinal distribution of acritarch diversity was influenced by SST and its seasonal fluctuations, but also to a lesser extent by salinity and the available area of continental shelf. These results strongly question the unimodal nature of other LDGs found for Paleozoic organisms, such as brachiopods and bryozoans (13, 18). We strongly support the combined use of empirical data and modelling approaches of both climate and diversity in the Past, as this could be the key to understanding still debated macroecological patterns.

Material and Methods

Fossil Occurrence Data. The dataset we used, initially created as part of the Phytopal project by Mullins et al. (unpublished), consists of 1503 species of acritarchs belonging to 287 genera and distributed among 328 fossil localities (*SI Appendix*, Table S1 & Fig. S4). Temporal resolution is at the series level for the Cambrian and at the stage level for the Ordovician. Geographic coordinates of fossil localities were recovered and their paleocoordinates were calculated by rotating their present-day coordinates with the software GPlates (60) version 2.0.0 using the rotation file supplied by Scotese (61) for each Cambrian series and Ordovician stage.

Latitudinal Diversity Gradient. We tested for the existence of a LDG by calculating the paleobiodiversity of acritarchs by 5° latitudinal bands at the genus level, because it is considered more robust than the species level for such analyses (see *SI Appendix*). We estimated the taxonomic richness by means of two 'range-through' indices (see review of Alroy, 62) including or excluding single-interval taxa: *RTinS* and *RTexS*, respectively. Range-through indices account for every taxon known to occur in a latitudinal band (i.e. real occurrence), as well as every taxon inferred to be present (i.e. recorded south and north of the considered latitudinal band). We conducted the diversity analyses at the series level for the Cambrian and at the stage level for the Ordovician.

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Correlation With Abiotic Factors. We tested the relationships between acritarch diversity and abiotic factors (continental shelf area, sea-surface temperature and salinity) for three key stages, i.e. the Cambrian stage 4, the Darriwilian and the Hirnantian. We simulated paleoenvironmental conditions using the Fast Ocean Atmosphere Model (FOAM) version 1.5 (see *SI Appendix*), with the continental reconstructions of Scotese and Wright (37). Continental shelf area was derived from the paleogeographical reconstructions, and values of sea-surface temperature and salinity were extracted from the climatic simulations. We tested the relationships between these abiotic factors and the latitudinal distribution of acritarch diversity (*RTexS*) using two approaches (see *SI Appendix* for details): (*i*) the non-parametric Kendall's rank correlation coefficient applied between the LDG and each abiotic factor separately, and (*ii*) a generalized linear model (GLM, see *SI Appendix*) with a response variable (i.e. diversity) following a Poisson distribution by means of a log link function, applied to all abiotic factors together, using the R packages 'MuMIn' (63) and 'MASS' (64).

Species Distribution Model. We modeled species diversity for the Cambrian stage 4, the Darriwilian and the Hirnantian using a model based on the MacroEcological Theory on the Arrangement of Life (METAL; see *SI Appendix* and 10, 35-36) forced with the SST values simulated using the climate model on the paleogeographical reconstructions of Scotese and Wright (37). We created pseudo-species having each a unique thermal niche with distinct degrees of eurythermy and thermophily (10, 35). We allowed pseudo-species to colonise any given region of the global ocean provided they could withstand the local monthly thermal regime. To estimate pseudo-species diversity, we randomly selected 10,000 among 101,397 possible pseudo-species and repeated the procedure 1,000 times. We integrated the number of pseudo-species for each 5° latitudinal bands and compared this modelled species diversity to the empirical genus acritarch diversity we observed.

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452 **Figures and Tables**

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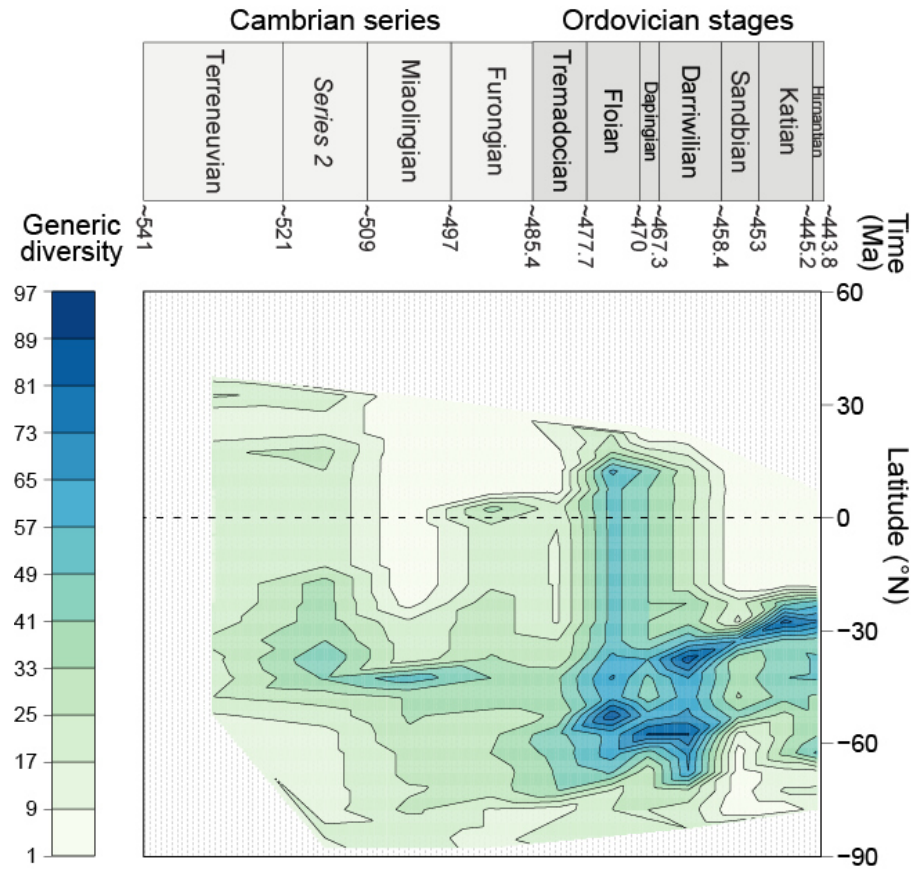

454

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.

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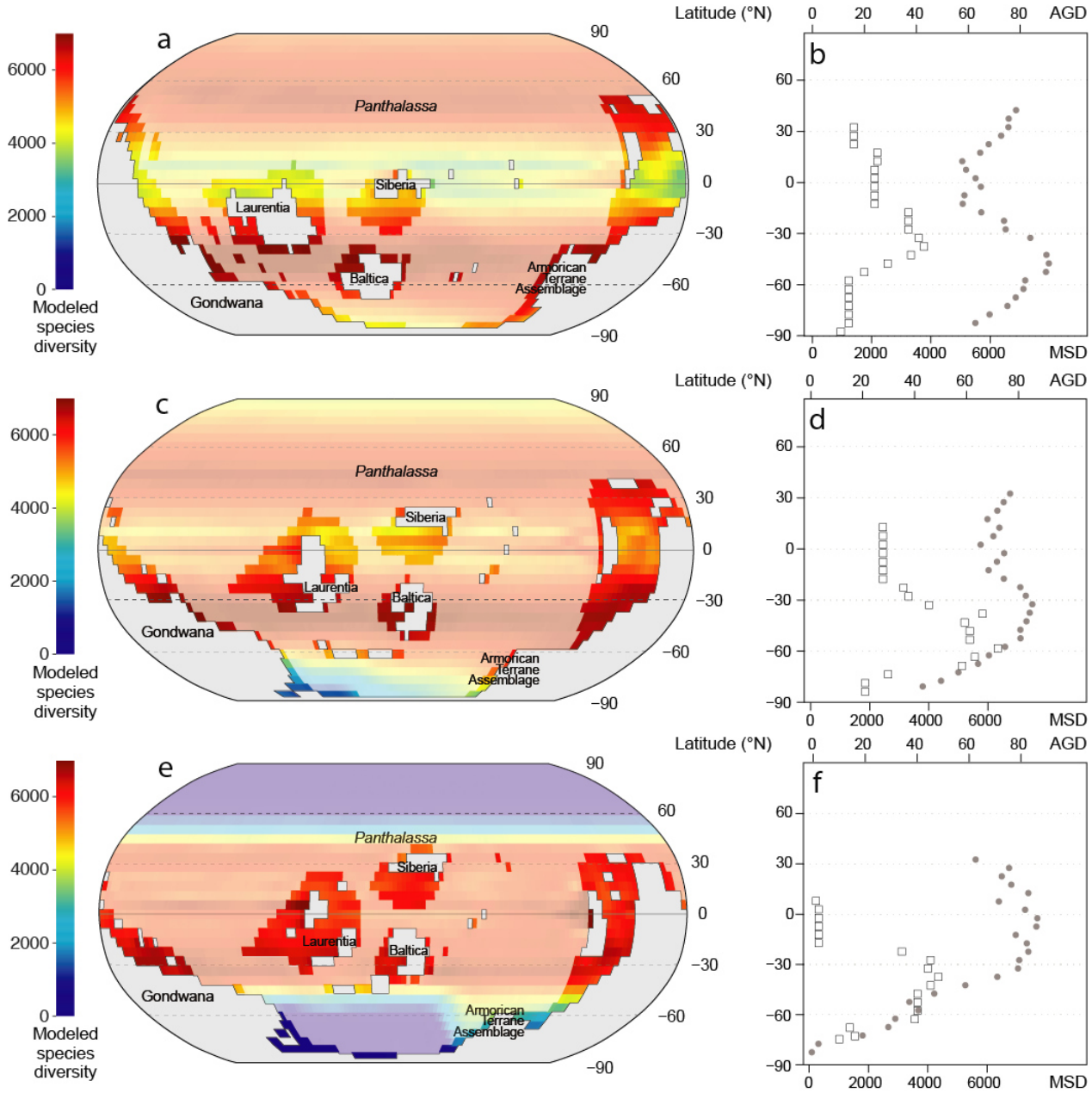

Figure 2. Comparison of latitudinal gradient of acritarch generic diversity and modeled species diversity for the Cambrian stage 4 (a-b; 510 Ma, 32 PAL, i.e. preindustrial atmospheric level of CO_2, 1 PAL = 280 ppm), the Darriwilian (c-d; 460 Ma, 12 PAL), and the Hirnantian (e-f; 445 Ma, 5 PAL). Modeled spatial distribution of species diversity corresponds to mean results of 1000 METAL simulations for continental shelves (< 200m, bright colors) and ocean surface (<200m, light colors), based on Scotese and Wright's (37) maps and SST simulated using the FOAM model, projected on a 5° x 5° spatial grid (a, c, e) and

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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.
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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^2	CSA	SST*an*	SST^2	SST*diff*	SSS*an*	SSS^2	SSS*diff*	AICc	Akaike weight
Cambrian stage 4	*P*	1.793	0.580				0.057		0.003		171.28	0.078
	Quasi P	1.793	0.580				0.057		0.003		Ø	Ø
	Neg. Bin.	1.119	0.577				0.053		0.003		169.95	Ø
Darriwilian	*P*	4.324	0.733	0.094	-0.118			19.647	-0.281		196.21	0.286
	Quasi P	4.324	0.733	0.094	-0.118			19.647	-0.281		Ø	Ø
	Neg. Bin.	1.887	0.611	0.118	-0.121			19.916	-0.286		186.59	Ø
Hirnantian	*P*	4.852	0.843	0.252	-0.258		0.259		0.018		158.91	0.331
	Quasi P	4.852	0.843	0.252	-0.258		0.259		0.018		Ø	Ø
	Neg. Bin.	1.887	0.884	0.295	-0.305		0.282		0.021		133.83	Ø

Abbreviations: *P*, Poisson; *Quasi P*, quasi-Poisson; *Neg. bin*.; negative binomial; CSA, contiental shelf area (10^6 km^2), SST*an*, mean annual sea-surface temperature; SST^2, squared SST; SST*diff*, difference between summer and winter SST; SSS*an*, mean annual sea-surface salinity; SSS^2, squared SSS; SSS*diff* difference between summer and winter SSS. Dispersion = residual deviance/degrees of freedom, overdispersion when > 1.

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479 **TABLE 2.** Results of Kendall's rank correlation tests between acritarch genus diversity per 5° latitudinal

480 band and SST, SSS and CSA.

Temporal interval	***n***	**CSA**	**SST*an***	**SST^2**	**SST*diff***	**SSS*an***	**SSS^2**	**SSS*diff***
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 (10^6 km^2); SST*an* , mean annual sea-surface temperature; SST^2 , squared SST; SST*diff* , difference between summer and winter SST; SSS*an* , mean annual sea-surface salinity; SSS^2, squared SSS; SSS*diff* , difference between summer and winter SSS. ***p < 0.001; **p < 0.01; *p < 0.05; no symbol = not significant.

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Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton

Supplementary Information

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Latitudinal diversity gradient (LDG). Analyses of the latitudinal distribution of diversity were conducted at the genus level because it is considered more robust than an analysis performed at the species level for three main reasons: (*i*) genera are easier to identify than species because they are defined by broader characteristics that remain identifiable when the species is unknown to the author or when preservation is incomplete (1), (*ii*) this level suffers less from inconsistent taxonomic treatment among different workers (2, 3), and (*iii*) for acritarchs in particular, many species are suspected to be ecophenotypes rather than different biological species (4), which inevitably leads to an overestimation of diversity at the species level. The fossil record of acritarchs is therefore assumed to be more preserved, and their stratigraphic and geographic ranges more accurate, at the genera than at the species level. We compared sampling effort for these temporal intervals using size-based rarefaction curves (5–7) computed using R (8) and the package 'vegan' (9). The rarefaction curves show that among the four Cambrian series

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and the seven Ordovician stages, the best sampled intervals are the Cambrian series 2, the Miaolingian (i.e. Cambrian series 3), the Floian, and the Darriwilian, and the least sampled ones are the Terreneuvian and the Sandbian (Fig. S2).

Paleoclimatic simulations. *The FOAM model*. Fields of sea-surface temperature and sea-surface salinity for the early Paleozoic were simulated using the Fast Ocean Atmosphere Model (FOAM) version 1.5 (10), a mixed-resolution general circulation model that has been routinely used to study climate in the deep time. The atmospheric component is a parallelized version of the National Center for Atmospheric Research's (NCAR) Community Climate Model 2 (CCM2) with radiative and hydrologic physics upgraded after CCM3 version 3.2 (11). It uses a R15 spectral resolution (4.5° × 7.5°) with 18 levels in the vertical dimension. The ocean model is the Ocean Model version 3 (OM3). It is a z-coordinate ocean general circulation model, run at a 1.4° × 2.8° resolution. Sea ice is simulated based on the thermodynamic component of the CSM 1.4 sea-ice model, which is based on the Semtner 3-layer thermodynamic snow/ice model (12). The coupled FOAM model is well designed for paleoclimate studies. It has no flux correction and its quick turnaround time allows for long millennium-scale integrations. FOAM has been widely used in paleoclimate studies (13–18).

Boundary conditions. In terms of boundary conditions, we used the continental configurations of Scotese and Wright (19) at 510 Ma for the Cambrian Stage 4, 460 Ma for the Darriwilian, and 445 Ma for the Hirnantian. Time-evolving solar luminosity values were calculated after the model of stellar physics of Gough (20). Orbital parameters were set to present-day values. We used previous modeling work and available geological constraints to select atmospheric CO_2 values (pCO_2) providing the most plausible climatic states for each time period under investigation. For 510 Ma, we used 32 PAL (preindustrial atmospheric level, 1 PAL = 280 ppm). Hearing et al. (21) demonstrated that the FOAM model simulates sea-surface temperatures on Avalonia (ca. 65° S) at 510 Ma that satisfactorily match the estimates derived from the geochemical analysis of fossil biogenic phosphate when simulations are run using this pCO_2 value. This pCO_2 level is also in line with the estimate derived from the GEOCARBSULF model (22). For

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460 Ma (Darriwilian), we used a pCO_2 of 12 PAL. Such radiative forcing was shown to trigger the growth of land ice over the South Pole (23), which is in agreement with recent studies suggesting that Ordovician ice sheets may have developed as early as the Mid Ordovician Darriwilian (24–26). The mean annual, topical sea-surface temperature simulated at 12 PAL (30.1 °C) corresponds well to the temperature estimate derived from geochemical analyses for the same period of time (27). For the Hirnantian, we selected a value of 5 PAL. This value is supported by the study of Pancost et al. (28), who analysed isotope fractionation between organic and inorganic carbon during photosynthesis (ε_p) and calculated a pCO_2 below ~8 PAL during the Katian. In addition, Pohl et al. (17) demonstrated a climatic instability in the Ordovician ocean-atmosphere system, which induces a strong global cooling when atmospheric CO_2 is lowered below 8 PAL in the FOAM model. They demonstrated that this strong cooling results from the sudden spread of sea ice to the mid-latitudes. The authors suggested that this instability may explain the strong cooling documented during the latest Ordovician based on geochemical data (27, 29). They also showed (23) that the extent of the ice sheet simulated under the cold climatic state matches well the geological record of glaciation (30), and that associated ocean temperatures are in good agreement with the climatic belts reconstructed for the Hirnantian by Vandenbroucke et al. (31) based on micropaleontological data. An analysis of the sea-ice fraction (not shown in the present study, but see ocean temperatures in Fig. S3 where –2 °C broadly represents the sea-ice extent) confirms that our model run conducted at 5 PAL using the continental reconstruction of Scotese and Wright (19) belongs to the cold climatic mode. The mean annual tropical sea-surface temperature in this model run (22.1 °C) is in agreement with the reconstruction of Trotter et al. (27). Concentrations of other greenhouse gases were kept to the present-day level. Non-vascular plants started colonizing the continents during the early Middle Ordovician (32). Vascular plants appeared later, during the Late Ordovician (33). The spatial coverage of these land plants remains debated (34–36). We therefore imposed a bare soil (rocky desert) at every land grid point (37, 38).

Initial conditions and model integration. Simulations were initialized using warm ocean temperatures to make sure that deep-ocean equilibrium was rapidly reached through oceanic convection. A uniform initial

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ocean salinity of 35 ‰ was imposed in every model run. Simulations were run until deep-ocean thermal equilibrium was reached (2000 years). The last 50 years were used to build the monthly climatology files used for the analyses.

Generalized Linear Model. To determine the predictor or combination of predictors of acritarch latitudinal diversity, the best GLM was identified for each stage by the second-order Akaike information criterion (AICc), which contains a correction for small sample sizes (39, 40). When the first best models had very close AICc values, we considered as predictors of diversity only the abiotic factors that occurred in the majority of models. When the best model (i.e. the one with the lowest AICc value) showed an overdispersion (i.e. residual deviance/degrees of freedom > 1), two alternative models were built by keeping only the predictors of this best model, and by using a negative binomial and a quasi-Poisson distribution instead.

Modeled diversity. The MacroEcological Theory on the Arrangement of Life (METAL; 41–43) states that biodiversity is strongly influenced by climate and environment, in a deterministic manner (44). This influence mainly occurs through the interactions between the species ecological niche and both climatic, and environmental changes. The theory uses the concept of ecological niche *sensu* Hutchinson (i.e. the range of a species tolerance when several factors are taken simultaneously) as an elementary emergent macroscopic process, to predict (*i*) local changes in abundance (45), species phenology, and biogeographic range shifts (46) at the species level, and (*ii*) the arrangement of biodiversity, including the latitudinal diversity gradient (47), and long-term community/ecosystem shifts, including regime shifts (48), at the community level. We assume here that the ecological niche integrates the sum of many physiological processes occurring at both the individual and population levels. This theory offers a way to make testable ecological and biogeographical predictions to understand how life is organized, and how it responds to global environmental changes (44–47). Pseudo-species and pseudo-communities (i.e. virtual species and communities) can be generated throughout the ocean provided that their ecological niche enables them to

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withstand local changes in the climatic and the environmental regime in time. Actual communities only represent a subset of the theoretical pseudo-communities because not all niches are occupied in a given location (48).

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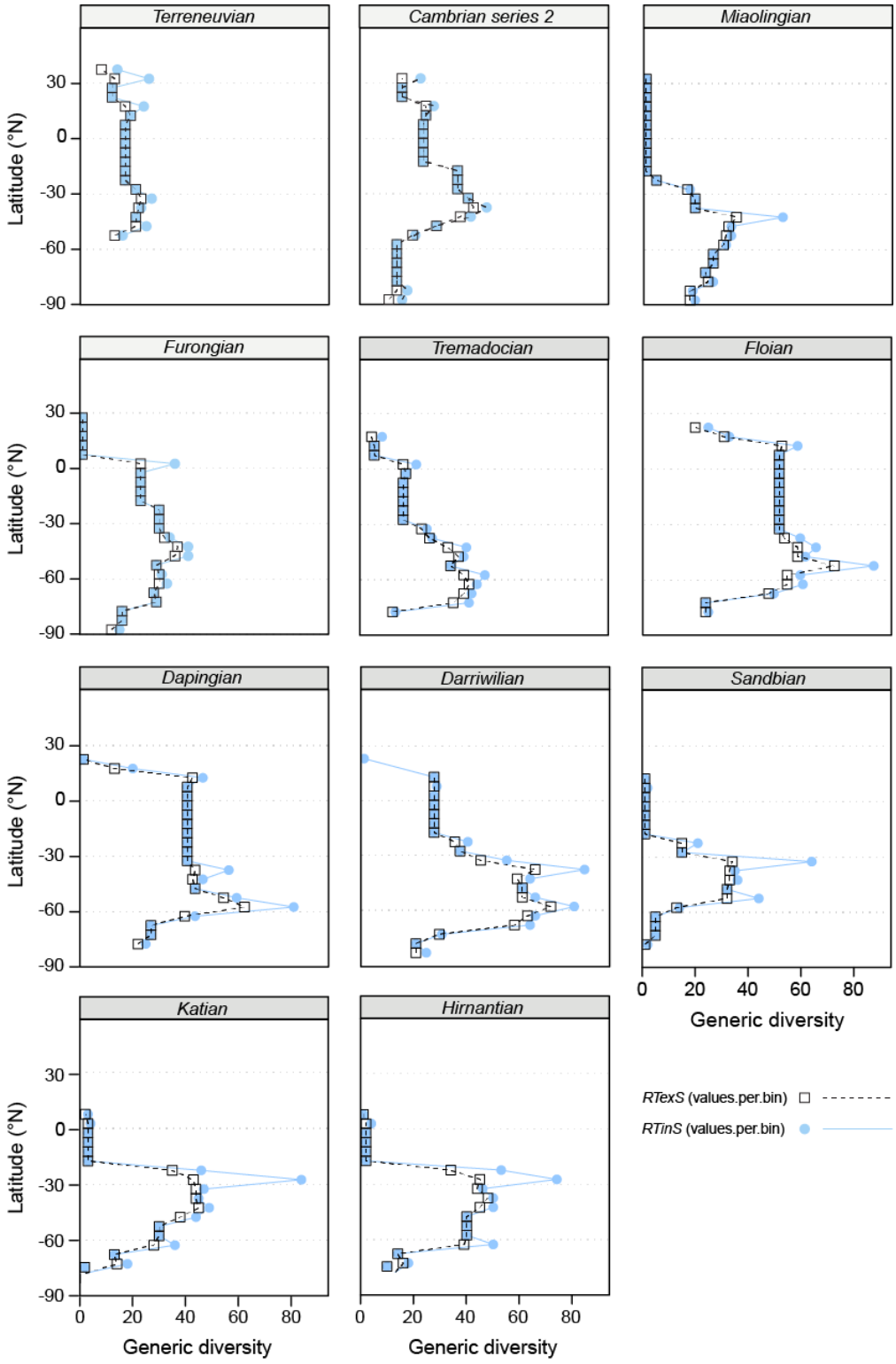

Figure S1. Acritarch genus diversity calculated per 5° latitudinal bands for each series of the Cambrian and each stage of the Ordovician. Diversity was calculated using the standard 'range-through' counting approach, with and without single-interval taxa (*RTinS* and *RTexS* and indices, respectively).

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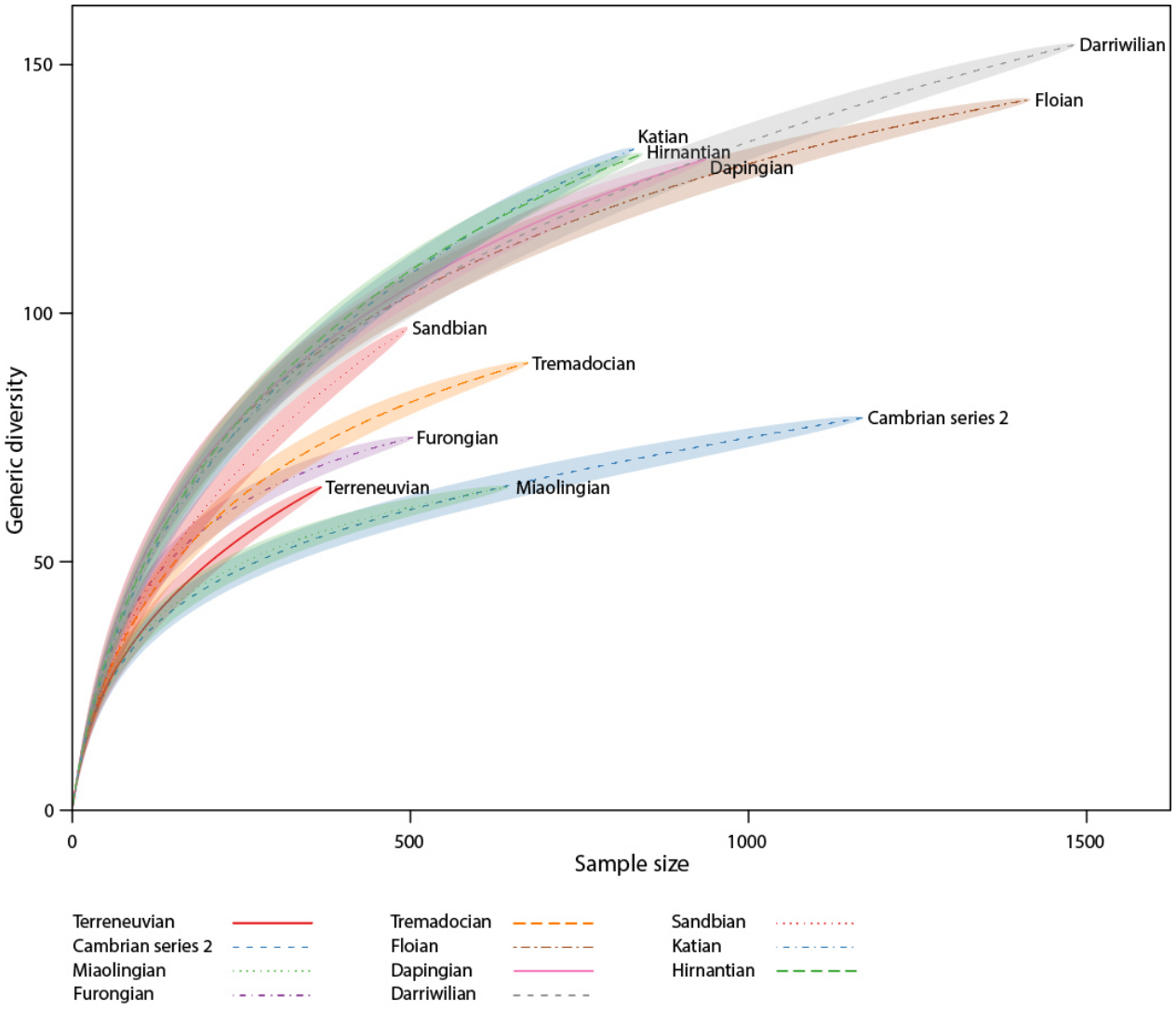

Figure S2. Size-based rarefaction curves and their associated standard deviation for early Paleozoic acritarch genera. Each curve corresponds to a Cambrian series or an Ordovician stage. The best sampled intervals are the Cambrian series 2, the Miaolingian (Cambrian series 3), the Floian, and the Darriwilian; and the least sampled are the Terreneuvian and the Sandbian.

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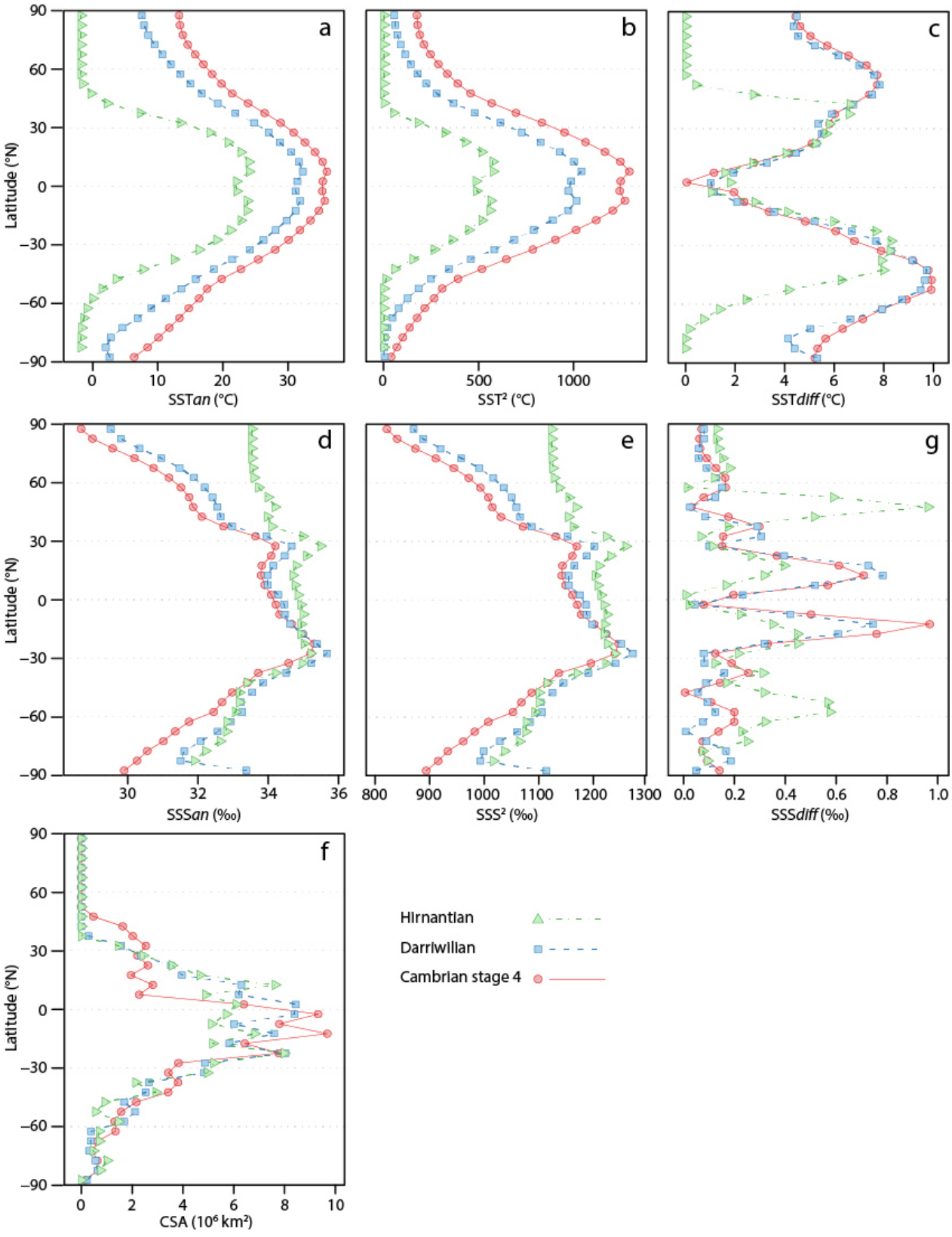

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714 **Figure S3.** Latitudinal distribution of modeled mean annual sea-surface temperature (SST), sea-surface
715 salinity (SSS) and continental shelf area (CSA, in millions of km^2) for the Cambrian stage 4 ($pCO2$=32
716 PAL), Darriwilian (12 PAL) and Hirnantian (5 PAL), per 5° latitudinal bands. a) mean annual SST
717 (SST*an*), b) squared mean annual SST (SST^2), c) seasonal variation in SST (SST*diff*, i.e. difference
718 between summer and winter SST), d) mean annual SSS (SSS*an*), e) squared mean annual SSS (SSS^2), f)
719 seasonal variation in SSS (SSS*diff*, i.e. difference between summer and winter SSS), g) CSA based on
720 Scotese and Wright's (19) maps.
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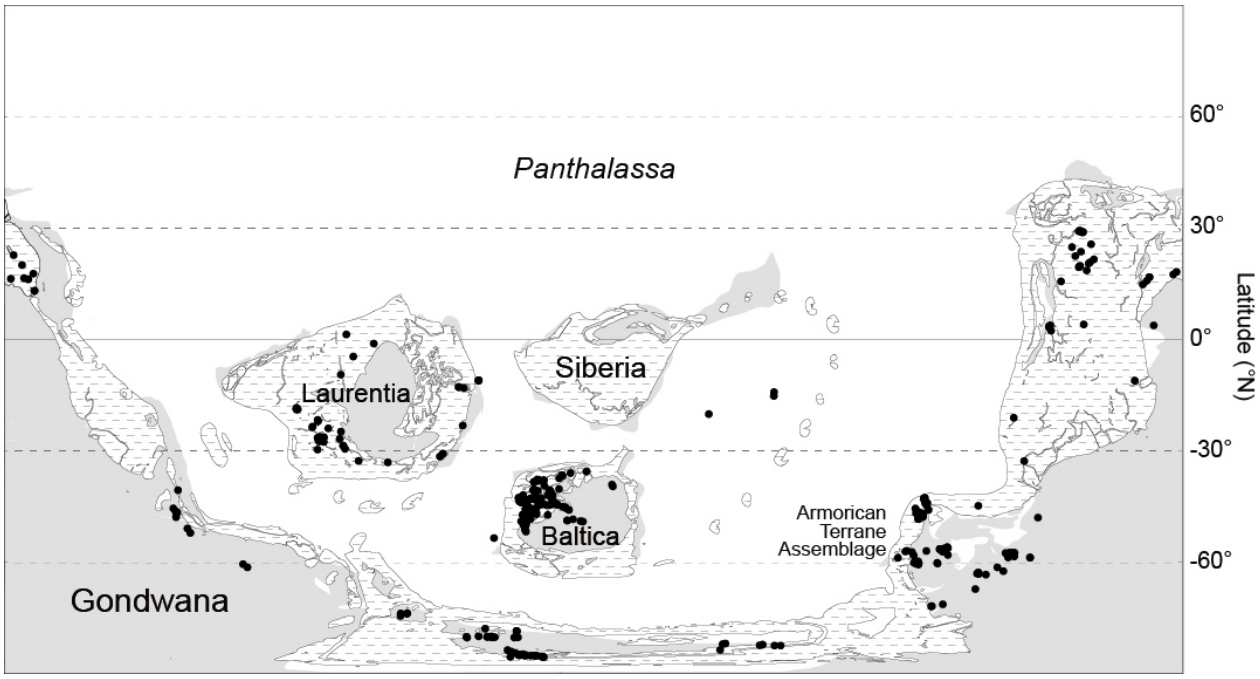

Figure S4. Paleogeographical context of the early Paleozoic. (a) Paleogeographical reconstruction for the mid-early Paleozoic (Jiangshanian, 491.75 Ma) computed with GPlates 2.0.0 (49) using the rotation file of Scotese (50), and paleolocation of the 328 fossil localities used in this study (black dots) for this time interval. Striped parts correspond to continental shelf areas after Scotese (50).

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