



Research paper

The diversity of the Permian phytoplankton

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ARTICLE INFO

Article history:

Received 11 February 2012

Received in revised form 3 August 2012

Accepted 12 March 2013

Available online 29 March 2013

Keywords:

Permian
phytoplankton
acritarch
diversity

ABSTRACT

The Paleozoic fossil record of organic-walled microphytoplankton is represented by the acritarchs, organic-walled microfossils (OWMs) considered mostly as the resting cysts of phytoplanktonic organisms, although the biological affinities of the acritarchs are, by definition, unknown. Acritarchs appear in the Precambrian and reach their highest diversity in the Lower and Middle Paleozoic (Cambrian to Devonian). After a drastic diversity drop in the Devonian, they are considered to be of very low diversity in the Upper Paleozoic (Carboniferous to Permian), where some authors claim the presence of a 'phytoplankton blackout' due to nutrient depletion in the oceans. Here we present a synthesis of the Permian fossil record of acritarchs. The revision shows that Permian acritarch descriptions have largely been neglected, compared to other palynomorph groups, such as spores and pollen grains. While larger organic-walled cysts, as known from the Lower and Middle Paleozoic, are usually absent, many smaller acritarchs are commonly found in Permian palynological assemblages. In addition, several OWMs interpreted as fungal spores have been described, but also possible green algae, including chlorophycean, prasinophycean or zygnematophycean algae. During most of the Permian stages, OWMs show genus richness of about 20 to 30 genera. Some genera, such as *Michrhystridium* and *Veryhachium*, have been reported in over 40 publications. Nevertheless, many Permian acritarchs still need to be documented in detail, and additional systematical studies, in particular of the very small taxa, are needed to fully understand the diversity and significance of Permian phytoplankton.

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1. Introduction

The modern marine phytoplankton is dominated by three algal groups: calcareous coccolithophorids, siliceous diatoms and organic-walled dinoflagellates. While the calcareous and siliceous phytoplankton only diversified in the Mesozoic, the presence of organic-walled microphytoplankton in the fossil record dates back to the Precambrian (e.g., Katz et al., 2004). Organic-walled microphytoplankton have largely been recorded from the Paleozoic, whereas siliceous microplankton seems absent and calcareous phytoplanktonic organisms only possibly exist since the early Paleozoic, probably due to preservation problems (Munnecke and Servais, 2008). The highest diversities of organic-walled phytoplankton are recorded in the Lower and Middle Paleozoic, with a possible maximum of diversity being reached during the Ordovician and Early Devonian (e.g., Molyneux et al., 1996; Strother, 1996; Servais et al., 2004). During the Ordovician, sea levels were very high, and the epicontinental shelves had their greatest extension, triggering the 'Great Ordovician Biodiversification Event' with abundant

phytoplankton playing an important role at the base of newly established trophic webs (Servais et al., 2008, 2010). The abundant and diverse phytoplankton present in the Devonian oceans (Le Hérisse et al., 2000) was also involved in the 'Devonian nekton revolution' (Klug et al. 2010). It was only during the Late Devonian and towards the Devonian–Carboniferous boundary that acritarch diversity dramatically dropped (e.g., Mullins and Servais, 2008).

Acritarchs were considered to become almost absent in the Carboniferous and Permian, because larger cysts are no longer observed in the fossil record. This drop of diversity of resting cysts in the fossil record has been related to different paleoenvironmental conditions, such as nutrient changes in the oceans, or changes in $p\text{CO}_2$ (see recent discussions in Riegel, 2008; Strother, 2008; Strother et al., 2010). Riegel (1996, 2008) named this Late Paleozoic interval with a virtual absence of organic-walled phytoplankton the 'Phytoplankton Blackout', because (after the Late Devonian acritarch 'extinction' and a 130 million year period of absence of large phytoplanktonic cysts in the fossil record) organic-walled dinoflagellate cysts are only recorded since the Triassic and did not strongly diversify before the Late Triassic and Jurassic. Servais et al. (2006) questioned the existence of a 'phytoplankton blackout', because the absence of resting cysts in the fossil record does not necessarily imply the absence of the phytoplankton in the Late Paleozoic oceans. In modern oceans, only a minor part of the dinoflagellates produce resting cysts that are fossilizable (e.g., Head, 1996).

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Mullins and Servais (2008) reviewed the diversity of the Carboniferous phytoplankton, and noted that phytoplankton diversity declined significantly from the Tournaisian to the Serpukhovian. Phytoplankton diversity in the Late Carboniferous was generally very low, with typically only 1–3 species being documented in each assemblage (Mullins and Servais, 2008).

Permian acritarch studies have generally been neglected. Most palynological investigations focus on spores and pollen grains that are usually abundant and diverse in Permian palynological assemblages. These plant-derived microfossils, which are much larger in size than phytoplankton in the same assemblages, are easier to observe and to describe (in particular with the light microscope). For these reasons pollen and spores became of great importance, not only for Permian palynostratigraphy, but also for paleogeographical and paleoenvironmental reconstructions.

Permian acritarchs recovered in palynological slides are generally very small in size, usually not reaching the diameter of 20 µm. They are therefore more difficult to study in detail with the light microscope. Permian acritarchs, similar to those from the Carboniferous, are generally considered to be of low diversity and low abundance, and they are not a significant component in biostratigraphic and paleobiogeographic studies.

In addition to acritarchs, organic-walled microorganisms related to the green algae (divisions Chlorophyta and Prasinophyta) have been documented in the Late Paleozoic (e.g., Colbath and Grenfell, 1995). These morphotypes probably include prasinophytes and various chlorophyte groups, including members of the Hydrodictiaceae and Botryococcaceae and members of the Zygnemataceae. In addition, fungal palynomorphs have been reported, in particular in the Late Permian, with an animated debate about a fungal spike in the late part of the Permian that might have been implicated in the Permian–Triassic extinction event (e.g. Eshet et al., 1995; Steiner et al., 2003).

A consistent summary of Permian phytoplankton has never been published and only two short reviews of Permian acritarchs have been presented (Li et al., 2004a; Traverse, 2007). Here we summarize the current knowledge on Permian organic-walled phytoplankton, with the aim to understand if significant diversity changes can be observed and if the geographical distribution of the assemblages allows any paleobiogeographical interpretation. We try to bring all literature data together, by reviewing all taxa listed by Fensome et al. (1990) and by compiling the more recent literature published after the compilation of the catalogue of Fensome et al. (1990). Like Mullins and Servais (2008), we review all OWMs of unknown affinities ('acritarchs'), including taxa such as the possibly non-marine genus *Mehlisphaeridium*, but also possible prasinophyte, chlorophyte, zygnematacean and hydrodictycean algae that are described in the literature. In addition, several taxa of OWMs from the Permian have been tentatively attributed to fungal spores (Eshet et al., 1995; Visscher et al., 1996; Sephton et al., 2009; Visscher et al., 2011).

It is beyond the scope of the present paper to discuss the possible biological affinities of all the different taxa described in the Permian. The genera *Leiosphaeridia* and *Polyedryxium*, regarded as prasinophytes by several authors, are here considered as acritarchs (i.e., organic-walled microfossils of unknown biological affinities). We do not propose any new attribution to biological groups and consider most taxa as 'acritarchs', i.e. organisms of unknown biological affinity. A few taxa are herein attributed to the green algae, following current consensus of their affinities in the literature (Colbath and Grenfell, 1995).

2. The Permian phytoplankton record

Although many papers mention acritarchs in palynological assemblages (particularly in works dedicated to Permian spores and

pollen grains), only about one hundred publications concern descriptions of acritarchs, prasinophytes, chlorophyte, zygnematacean and hydrodictycean algae from Permian strata. Fig. 1 summarizes the descriptions of marine organic-walled palynomorphs and probable phytoplankton in the individual papers on Permian palynology. For each individual article, the authors, the country from which the assemblages were described, and the biostratigraphical age that was provided in the study are indicated in Fig. 1. Following Fensome et al. (1990), we do not include miospores or other taxa (such as *Acanthotriletes*) that have been incorrectly assigned to the acritarchs.

Stratigraphy follows the Permian stratigraphical subdivisions of the International Commission on Stratigraphy (ICS), based on Gradstein et al. (2004). A stratigraphic scheme of the Permian is provided within Fig. 3. A comprehensive list of all Permian acritarch taxa (including author names) is provided in Appendix 1.

2.1. Early Permian (Cisuralian)

2.1.1. Gzhelian/Asselian

Only two papers have described organic-walled microplankton from Carboniferous–Permian boundary strata (Gzhelian/Asselian). In Argentina, Gutiérrez et al. (2005) identified *Botryococcus braunii*, *Leiosphaeridia* sp. and specimens attributed to *Brazilea* spp., from the Tupe Formation, located south of the Mina La Delfina locality, about 29 km northeast of San José de Jáchal. Gorter et al. (2008) reported the three genera *Botryococcus*, *Baltisphaeridium* and *Ulanisphaeridium* from the Treachery Formation, Lower Kulshill Group, Australia.

2.1.2. Asselian and Asselian/Sakmarian

Five studies mention phytoplankton from earliest Permian strata. In Antarctica, Kent et al. (1990) studied the palynology of the Beacon Supergroup sedimentary rocks exposed at Milorgfjella, Dronning Maud Land, and found a relatively rich and well preserved palynoflora, dominated by spores and pollen grains, but also including *Botryococcus* sp., *Dixalophasis* sp., and *Leiosphaeridia* sp., two prasinophytes (*Dictyotidium* sp., *Tasmanites* sp.), together with *Brazilea scissa*, *Tetraporina* sp. and *Quadrisporites horridus*.

Lindström (1995b) described several acritarchs from three localities in the northern Heimfrontfjella, Antarctica (namely A and C in Milorgfjella and Lidkvarvet in Sivorgfjella), including the taxa: Acritarch sp. A, *Botryococcus braunii*, *Leiosphaeridia* spp., *Lophosphaeridium* spp., *Dictyotidium* sp., *Tasmanites* sp. A, *Tetraporina gigantea*, *Tetraporina tetragona*, T. sp. A, *Brazilea scissa*, and *Quadrisporites horridus*.

Di Pasquo et al. (2010) studied three outcrops of the Libertad and Saucos Formations from the Los Saucos area in the Province La Rioja, western Argentina, and defined two assemblage zones, yielding the acritarch *Portalites gondwanensis*. They considered that the age of the assemblage 2 was of Asselian/Sakmarian.

Two studies described phytoplankton taxa from the Asselian to Artinskian in Uruguay. Beri et al. (2006) analyzed four samples of borehole DCLS24 from the San Gregorio Formation. Subsequently, Beri et al. (2010) analyzed 32 outcrop samples and thirty borehole samples from the Cerro Pelado Formation, including the acritarch genera *Deusilites*, *Leiosphaeridia*, *Micrhystridium*, *Pilasporites*, and *Portalites*, but also the genera *Brazilea* and *Tetraporina*, as well as *Quadrisporites* and *Botryococcus*.

2.1.3. Sakmarian and Sakmarian/Artinskian

About ten publications reported Sakmarian or Sakmarian/Artinskian phytoplankton taxa. Besems and Schuurman (1987) described two palynological assemblages from glacial deposits in the Al Khlata area of Oman. Both assemblages contain *Botryococcus braunii*. Stephenson et al. (2003) considered that the 'maximum flooding shale' in Oman is

Fig. 1. (a, b, c, d) Organic-walled microphytoplankton cited in Permian palynological papers. All taxa are here considered as acritarchs, i.e., of unknown biological affinities, except species marked as (*) representing possible fungi and as (**) representing possible green algae.

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