Review of Palaeobotany and Palynology 198 (2013) 2–13

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Review papers

Reprint of 'Eighty years of chitinozoan research: From Alfred Eisenack to Florentin Paris'☆

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ARTICLE INFO

Article history:
Received 4 June 2012
Received in revised form 21 March 2013
Accepted 6 May 2013
Available online 13 August 2013

Keywords:
Chitinozoa
zooplankton
palynomorphs
Lower Palaeozoic

ABSTRACT

In the early 1930s Alfred Eisenack first reported unknown, bottle-shaped, organic-walled microfossils that he had discovered in erratic boulders from the south-eastern shores of the Baltic Sea. Eisenack erected the new group Chitinozoa to classify these strange microfossils of unknown biological affinity. From the 1930s to the 1950s, a few publications appeared reporting new findings and providing descriptions of these fossil organisms. It was only since the 1960s, with the development of the oil industry and the intensive biostratigraphical use of organic-walled microfossils, that publications dealing with chitinozoans became more numerous and that the description of new genera and species rapidly increased. The peak of description of new species was reached in the 1960s, but the number of publications remained high into the late 1990s. Since the 1990s the research activities on chitinozoans are conducted by a much smaller number of scientists. One of the major driving forces of chitinozoan research in the last forty years was Florentin Paris at the University of Rennes (Brittany, France). He first established a high-resolution chitinozoan biostratigraphy of the Ordovician of southern Europe and played an active role in bringing all scientists together for the development of global biostratigraphical schemes and palaeobiogeographical scenarios of the Ordovician, Silurian and Devonian. It was also Florentin Paris, together with his Estonian colleague Jaak Nõlvak, who suggested the now widely accepted biological interpretation that Chitinozoa are most probably egg cases of a planktonic organism unknown from the fossil record. F. Paris was also the first to collaborate w ith experts to use biogeochemical analyses and the C isotope signal of the chitinozoans to better understand their biological affinity and detect biogeochemical changes in Palaeozoic oceans.

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☆ "This article is a reprint of a previously published article. A publishers' error resulted in this article appearing in the wrong issue. The article is reprinted here for the reader's convenience and for the continuity of the special issue. For citation purposes, please use the original publication details; T. Servais et al./Review of Palaeobotany and Palynology 197 (2013) 143–151".
DOI of original article: http://dx.doi.org/10.1016/j.revpalbo.2013.05.008.

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0034-6667/$ – see front matter.
http://dx.doi.org/10.1016/j.revpalbo.2013.08.001

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1. Introduction

Alongside the acritarchs (generally related to phytoplanktonic organisms), the spores and pollen grains (related to land-plants) and the scolecodonts (elements of the jaws of polychaetes), the chitinozoans are considered today as one of the major groups of the Palaeozoic organic-walled microfossils (palynomorphs). The group was first discovered and described some 80 years ago by Eisenack (1930), who proposed the name Chitinozoa for these bottle- or urn-shaped organic microfossils. Since the 1960s the chitinozoans have become very important in biostratigraphy, and today they are widely considered as one of the major groups providing solid biostratigraphical correlations at local, regional and global scales, with a similar or, in some intervals, even more precise resolution than that of the graptolites and conodonts, considered as the two 'classical' biostratigraphic fossil groups of the Ordovician, Silurian and Devonian. In addition, chitinozoans have the advantage that they can be easily found in both limestones and mudstones, unlike graptolites and conodonts, respectively.

During the last 40 years, Florentin Paris, 'Directeur de Recherches' at the *Centre National de la Recherche Scientifique* (CNRS) at the University of Rennes (Brittany, France), was the driving force behind chitinozoan research. He contributed to all aspects of chitinozoan investigations: taxonomy, biostratigraphy, palaeobiogeography, palaeoecology, palaeobiodiversity and biogeochemistry. The stratigraphical information provided by his work proved to be crucial for the understanding of regional geology and palaeobiogeography, first of all of Brittany, but later of the entire Armorican Terrane Assemblage, southern Europe and most areas of the 'northern Gondwana domain'.

This paper attempts to outline the main trends in chitinozoan research of the last 80 years, i.e. since the pioneering work by Alfred Eisenack in the early 1930s to the standards reached at the beginning of the 21st century. We do not attempt to provide an exhaustive list of all the chitinozoan papers that have been published since 1930; readers are invited to consult the listed bibliography to find the references not cited herein. Because Florentin Paris was one of the major actors in chitinozoan research during the last 40 years, this review will inevitably highlight his contribution during that period. This review paper is the first of a set of papers of a special issue on Palaeozoic marine palynomorphs respectfully dedicated to Florentin Paris.

2. Chitinozoan research since its beginnings

2.1. The first discoveries: Alfred Eisenack

It was Alfred Eisenack, a German amateur collector, trained as a chemist and working as a school teacher, who first discovered and defined the Chitinozoa in the 1930s. He continued research after World War II as a scientific collaborator at the University of Tübingen. In the first half of the 20th century Eisenack studied the numerous fossils contained in the erratic boulders strewn by glaciers along the southeastern coast of the Baltic Sea near the town of Königsberg in Eastern Prussia, the present-day Kaliningrad, Russia. Many of the erratic Palaeozoic boulders yielded macrofossils (trilobites, graptolites, etc.) that allowed a precise age determination and an interpretation of their geographical origin. However, many boulders and erratic stones did not yield any macrofossils. Alfred Eisenack dissolved these apparently unfossiliferous samples in hydrochloric or hydrofluoric acids for the search of microfossils. From the residues he observed different organic-walled microfossils, not only acritarchs (named at that time 'hystrichospheres'), but also melanosclerites and new organic-walled microfossil groups that he described in a series of scientific publications (Eisenack, 1930, 1931, 1932, 1934, 1937, 1942, etc.). He named these new bottle- and urn-shaped microfossils, never described before, Chitinozoa, a name he created by linking the Greek terms 'chitin' (organic) and 'zoa' (animal). Eisenack discussed the possible biological affinities of the chitinozoans and concluded that they were the organic remains of animals, although it was later discovered that the chemical composition of the chitinozoan wall does not include any real 'chitin' (Dutta et al., 2007; Jacob et al., 2007; Voss-Foucart and Jeuniaux, 1972). The Chitinozoa still remain an enigmatic group in terms of their biological affinities, but their probable relationship to soft-bodied animals is now generally accepted.

2.2. The first 40 years: from 1930 to the early 1970s

In the first three decades (1930–1960), the chitinozoans were exclusively studied by using the light microscope. The investigations focused on the description (taxonomy) of new taxa and their stratigraphical distribution. The number of specimens investigated was generally rather small and many taxa have often been described on the basis of a few specimens only. The biometrical studies that are needed to understand the full morphological variability were usually absent in earlier publications, and only simple measurements were provided. Concepts of biostratigraphy and palaeobiogeography were in their infancy and the potential role of organic microfossils in palaeoenvironmental reconstruction not yet well perceived.

Following Eisenack's discovery, pioneering studies took place in France (Deflandre, 1944–1949) and in South America where Lange (1949, 1952, 1967a,b) documented chitinozoans from Brazil, while in North America Collinson and Schwalb (1955) and Collinson and Scott (1958) described chitinozoans from the Devonian and, slightly later, Wilson and Clarke (1960) reported the first Ordovician chitinozoans.

As documented by several authors (Jenkins, 1970a; Miller, 1996; Paris, 1996; Servais and Paris, 2000; Servais and Wellman, 2004; Taugourdeau, 1966; Taugourdeau et al., 1967) a revolution in chitinozoan studies took place in the late 1950s and the early 1960s in response to the significant demand for stratigraphical investigations by the oil industry. The *Commission Internationale de Microflore du Paléozoïque* (CIMP) was created in 1958 by Carboniferous spore and pollen workers to discuss taxonomic concepts. This new international society, that reached over 500 members in the 1970s to 1990s, erected sub-commissions for the different organic microfossil groups in the early 1960s, including the Chitinozoan Subcommission, that is still active today.

The 1960s and the early 1970s were a key period in chitinozoan research. Numerous positions in palynology were created both in the oil industry and in academia. Chitinozoans were extensively studied from various regions, such as the Saharan Platform (Taugourdeau, 1961; Taugourdeau and de Jekhowsky, 1960), Spain (Cramer, 1964, 1967; Cramer and Díez, 1978; Díez and Cramer, 1978), Canada (Jansonius, 1964; Legault, 1973), Sweden (Laufeld, 1967, 1974), the United Kingdom (Downie and Ford, 1966; Jenkins, 1967), Russia (Umnova, 1969), Belgium (Martin, 1969, 1973), the United States (Taugourdeau, 1965; Jenkins, 1967, 1970b; Urban and Kline, 1970; Urban, 1972; Urban and Newport, 1973; Wood, 1974; Wright, 1980; Wood and