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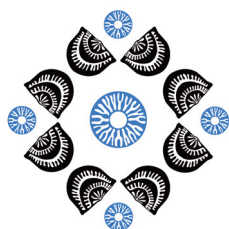
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Corresponding author:

Yan Liang
liangyan@nigpas.ac.cn

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On future directions of Ordovician chitinozoan research

Yan Liang^a, Olle Hints^b, Jaak Nõlvak^b and Peng Tang^a

^a State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

^b Department of Geology, Tallinn University of Technology, Ehitajate 5, 19086 Tallinn, Estonia

ABSTRACT

Chitinozoans have been known to science for nearly a century. Due to their biostratigraphic utility, chitinozoans were intensively studied from the 1960s to the 1980s, and they have an important place in Ordovician stratigraphy nowadays, alongside graptolites and conodonts. However, identifying chitinozoans is often complicated due to poorly illustrated and documented type specimens. During the last decades, descriptions of new species have decreased significantly, whereas open nomenclature has been adopted widely. The affinity of chitinozoans has been discussed in several recent papers, but further exceptional specimens and the application of up-to-date study techniques are needed to understand their biological functioning. The Ordovician chitinozoan biozonal schemes were mostly established in the 1990s. With much more data subsequently reported, many biozones currently need revision, and possibly new useful zones could be established. Herein we discuss how to tackle the problems in chitinozoan research by building an open-access database and restudying the poorly documented type materials using advanced techniques. This would foster progress and facilitate studies in systematics, evolution, biostratigraphy, palaeogeography and the biological affinity of chitinozoans.

Introduction

Ninety-two years have passed since the first report of chitinozoans by Eisenack (1931). In the history of chitinozoan research, three episodes can be recognised: (1) mainly systematic studies from the 1930s to the 1950s, (2) a rapid development period from the 1960s to the 1980s, mainly due to the demand from the oil industry, and (3) an era of applied biostratigraphy since then. The questions on biological affinity, biodiversity, and biogeography have been discussed in different periods, however, with a limited number of publications compared to biostratigraphic studies. Servais et al. (2013) reviewed the first eighty years of chitinozoan studies, and a more detailed history with supporting references could be found there.

The Ordovician was a crucial period for chitinozoans. The oldest taxa are widely reported from the middle Tremadocian without regard to the debating report from the Cambrian (Shen et al. 2013). The group flourished in the late Darriwilian to the Sandbian and had a significant diversity decrease during the end-Ordovician extinction (Achab and Paris 2007). Ordovician chitinozoan biozonations in Baltica, North America and North Gondwana were established around the 1990s (Achab 1989; Paris 1990; Nõlvak and Grahn 1993) and proved useful in regional and global correlations, especially where graptolites and conodonts were rare or missing. The key materials supporting different arguments for the chitinozoan biological affinity are mostly from the Ordovician, including the clusters supporting the metazoan egg hypothesis (Paris and Nõlvak 1999) and the reproductive specimens suggesting protist biology (Liang et al. 2020).

Modern palaeontology has set higher goals for high-resolution biostratigraphy and comprehensive pursuits based on big data to decode major biological events and the motivation behind them. However, the contribution from chitinozoans has remained somewhat limited. In terms of past work experience on chitinozoans, we review some problems in contemporary chitinozoan research and put forward ideas on what could be done to further advance chitinozoan research.

Current trends and problems in chitinozoan research

Taxonomy. In total, 563 publications (excluding abstracts) related to chitinozoans have been analysed, and 1131 species from 57 genera have been erected (Fig. 1) according to Paris et al. (1999). About two-thirds of all species were erected from the 1960s to

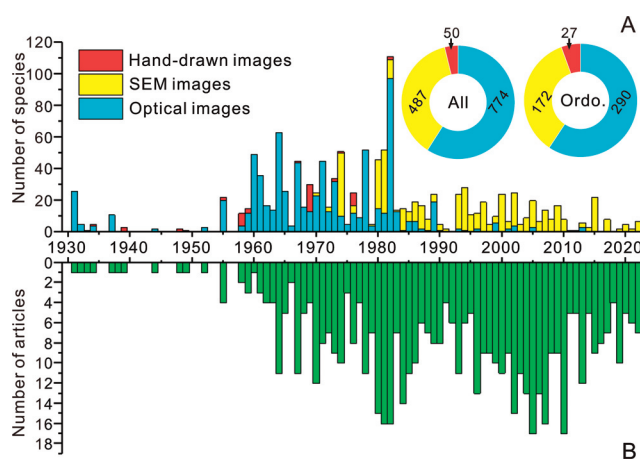


Fig. 1. Erected chitinozoan species (A) and publications (B) over the past 92 years. The data are based on the CHITINOVOSP database of Florentin Paris from 2014, publications listed in the ChitDB (Hints et al. 2018) online database, and supplementary data we have assembled.

the 1980s. The number of new species described in the 1990s and the 2000s decreased significantly, while the number of publications slightly increased. In the 2010s, only 51 species were formally established. However, identifications using open nomenclature have become more common. The main reasons for the decrease in new taxonomy might be: (1) the biostratigraphic significance motivated most of the chitinozoan study, and once the main biostratigraphic indicators were described, other species mattered less since conducting systematics is very time-consuming; (2) chitinozoan taxonomic data were preserved in a scattered way, therefore not being readily available, hampering comparison and identification; (3) perhaps most importantly, due to the lack of standard criteria and with limited imaging techniques adopted in early chitinozoan research, poor images and insufficient descriptions of type specimens left confusion in the taxonomy of some early established chitinozoans. Also, many species have been erected based on a very small collection or even a single specimen (e.g., Taugourdeau and de Jekhowsky 1960; Combaz and Peniguel 1972; Obut 1973). Only about a third of holotypes have a scanning electron microscopy (SEM) image available, while the rest were photographed under an optical microscope or were hand-drawn (Fig. 1A). These imaging methods usually fail to provide detailed morphological information. This, in turn, has a negative impact on the systematics of chitinozoans.

Revision of such poorly documented type specimens is not easy. The holotypes are kept in many different institutions worldwide and some holotypes have been lost or broken due to various reasons and circumstances. Recently, a case study of a revision of the widely distributed and well-known *Lagenochitina esthonica* has been carried out (Liang et al. 2022), providing an example of how to solve such issues. The most important part of the work is that the materials are from the same area and stratigraphic level as the lost holotype. At the same time, a sufficient number of specimens and high-quality SEM images are statistically analysed to present the variation in shape and size, which further distinguishes the two species within the group. The stratigraphic ranges sum-

marised based on all the reported occurrence data provide a solid support for such revisions.

Biostratigraphy and biogeography. Ordovician chitinozoan biostratigraphic schemes in the main palaeocontinents were established around the 1990s, and only relatively minor updates have been made since then. However, abundant new occurrence data has been accumulated since the 1990s, and some biozones need revision to better meet the high-resolution biostratigraphic standards. For example, the *Euconochitina symmetrica* Biozone was put forward to be coincident with the base of the Floian in North America and North Gondwana (Webby et al. 2004; Cooper and Sadler 2012). However, Tremadocian occurrences were reported from South China (Zhang and Chen 2009; Wang et al. 2013; Liang et al. 2017), Avalonia (Amberg et al. 2017), and also North Gondwana (Nowak et al. 2016). A recent revision of graptolites and chitinozoans from the type horizon of *E. symmetrica* suggests that *E. symmetrica* characterises the upper Tremadocian *Sagenograptus murrayi* Graptolite Zone and could reach the Floian (Achab and Maletz 2021). *E. symmetrica* is not the only case. Zonal species such as *Lagenochitina esthonica*, *Conochitina raymondii*, *Eremochitina baculata* and *Eremochitina brevis*, to name but a few, all have new occurrence data below or above the initially proposed range of the zone. Therefore, an updated composite global range chart considering all the occurrence data of these biozonal species has to be prepared to better serve stratigraphic correlations.

Chitinozoans are generally considered to represent geographically widespread plankton, with limited implications for palaeogeography. However, in the Ordovician, it seems that at least three major chitinozoan palaeobiogeographic provinces could be recognised with specific biozonations, i.e., Baltica, North America and North Gondwana palaeobiogeographical provinces, almost corresponding to part of the three palaeocontinents. The concept of chitinozoan provinces has been discussed in several studies (e.g., Paris 1990, 1993, 1996), but the formal definition of provinces still requires a compilation of global occurrence data and statistical analysis. How much do the chitinozoan assemblages vary between different palaeocontinents and between different environments within palaeocontinents? How do chitinozoan assemblages change over time? These aspects need to be much better understood using direct evidence and occurrence data. Then, chitinozoans could play a more important and reliable role in biostratigraphy.

Biological affinity. The biological affinity of chitinozoans has bothered palaeontologists since the 1930s. A thorough summary of the history of exploration of what chitinozoans are has been presented by Servais et al. (2013). Most commonly, chitinozoans have been considered to be eggs or cysts of unknown marine metazoans for the past three decades, after a series of publications (Taugourdeau 1981; Jaglin and Paris 1992; Paris and Nölvak 1999). However, two recent studies have challenged the ‘metazoan egg hypothesis’ based on the huge size variation of chitinozoan species and exceptionally preserved specimens possibly showing the reproduction moments (Liang et al. 2019, 2020). These new data have advocated most probably a protistan rather than a metazoan origin of chitinozoans. However, Vodička et al. (2022) have pre-

sented new evidence on monospecific chitinozoan clusters, interpreted as egg masses. Regardless of which hypothesis gains more support, the biological affinity of chitinozoans has re-attracted much attention after 20 years, which is undoubtedly a good trend to further improve our knowledge of this aspect. **Big data.** Digitalisation and visualisation of palaeontological data have become key areas in palaeontology, providing a completely new view of global palaeobiodiversity patterns, palaeobiological events, palaeoecology and palaeogeography (e.g., Alroy 2001; Kiessling 2005; Wagner et al. 2006; Alroy et al. 2008; Fan et al, 2020). At present, very limited chitinozoan data are available in the largest palaeontological database, the Paleobiology Database (PBDB, <https://paleobiodb.org>), and the Geobiodiversity Database (GBDB, <http://geobiodiversity.com>). Several specialised chitinozoan databases have also been developed, two of which are very helpful in chitinozoan studies. One of these is CHITINOVOSP, a chitinozoan type species database which stores information on the taxonomy, references, holotype images and the general stratigraphic range and palaeogeographic distribution. The other is ChitDB (<https://chitinozoa.net>; Hints et al. 2018), an online database that stores information on Ordovician–Silurian chitinozoans of the Baltic region. However, these two databases have their shortages: CHITINOVOSP is a static proprietary desktop application and is not easily available and accessible to researchers. The ChitDB is currently focused on Baltica, mostly only on the East Baltic region. Both databases have no or limited support to allow community-based assembly and editing of chitinozoan data. In addition, Achab et al. (2000) put forward the chitinozoan image and data acquisition system CHITINOS, which is intended for capturing chitinozoan data during palynological work or for assembly of data taken from the literature. However, the system is no longer in use. Verniers et al. (2002) also introduced the database CHITREF with published references and a list of all chitinozoan species. However, no further information has been updated since then.

Discussion and conclusions

To effectively facilitate chitinozoan studies, we suggest designing and constructing an open-access chitinozoan database for all documented chitinozoan species. The database could be built on the GBDB platform for two reasons: GBDB is one of the official databases of the International Commission on Stratigraphy and International Palaeontological Association; there is stable support and full-time technicians in charge of the database. The data structure will resemble the ChitDB and present combined information such as taxonomy, morphological features, high-resolution images, sample localities, specimen data, ages, and related references. All internet users can freely access and download the data, and registered users can participate in data entry, editing, and analysing. In short, the database would include all occurrence data globally and, once complete, will provide data services for studying chitinozoan macroevolution, biostratigraphy, palaeobiogeography and palaeoecology.

With all the information being freely accessible to everyone, it will substantially improve the study of chitinozoans.

It will save considerable time and energy in searching data and thus systematic identification becomes much easier. Moreover, further revisions on the poorly documented chitinozoans will be easier to carry out through global collaboration. Nowadays, chitinozoan experts are few, and the type collections are stored in different countries and institutions. With a platform presenting the wait-to-solve issues, palaeontologists who have access to those questionable holotypes or topotypic material could collaborate with interested chitinozoan specialists. Once the improved data on type specimens are accessible, the systematics will be greatly facilitated.

In updating the taxonomic issues and solving the palaeobiological queries, advanced imaging techniques, such as near-infrared microscopy, focused ion beam scanning electron microscopy, field emission scanning electron microscopy and X-ray computed micro-tomography could be applied and are essential for documenting interior structures and ultrastructures. In palaeobiological studies, detailed morphological examination of exceptionally preserved specimens and key structures, such as the prosome and operculum, will be of critical importance.

Furthermore, a revised taxonomy based on updated morphological and biological information, and global occurrence data will largely facilitate chitinozoan study in palaeobiogeography and palaeoecology, which, in turn, will lead to refined biostratigraphy.

As a small microfossil group with a relatively short geological history, we have to find a way for chitinozoan research not only because they could provide some valuable suggestions for biostratigraphy, but also because they existed in history with many unknown mysteries. The creation of a global community-driven chitinozoan database and revisions of poorly documented chitinozoan species with more high-resolution morphological features decoded by advanced techniques will be an inevitable stage. It will bring significant advances for chitinozoan studies. Once these tasks have been achieved, it might bring a new era for chitinozoan research and will be an important case study to show how far basic research can go with the support of big data and advanced techniques.

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