

# Emergence, biodiversification and extinction of the chitinozoan group

YNGVE GRAHN\* & FLORENTIN PARIS†

\*Universidade do Estado do Rio de Janeiro, Faculdade de Geologia, Bloco A – Sala 4001, Rua São Francisco Xavier 524, 20550-013 Rio de Janeiro, R.J., Brazil

†Université de Rennes 1, Géosciences Rennes, UMR 6118 du CNRS, 35042 Rennes-cedex, France

(Received 11 December 2009; accepted 27 May 2010; first published online 7 July 2010)

**Abstract** – Chitinozoans are considered as reproductive bodies of marine invertebrates, called chitinozoophorans. These chitinozoophorans were most likely to have been small, pelagic or necto-pelagic, soft-bodied, probably wormlike animals, and judging from the size of chitinozoans, they probably measured from a few millimetres to a few centimetres in length. The chitinozoophorans most likely survived by grazing on phytoplankton. There is no evidence of a large colonization of the pelagic niche in the Cambrian, but from the Early Ordovician onward, this niche was exploited chiefly by graptolites and chitinozoophorans. Both groups inhabited nearshore and offshore habitats, but in contrast to the graptolites, the chitinozoans displayed their highest diversity at high latitude, in less distal (that is, upper and lower offshore) environments. The chitinozoan group evolved rapidly during the Ordovician and reached its maximum Ordovician diversity in the late Darriwilian. From the first occurrence of chitinozoans in early Tremadocian times, to the biodiversity crisis in latest Ordovician times, nearly 80 % of the morphological innovations took place. Until their extinction in the latest Devonian, chitinozoans survived through several biodiversity crises: in the early Late Ordovician, late Hirnantian, late Wenlock, earliest Emsian, and in the latest Frasnian (Kellwasser event). During the melting of the Hirnantian ice sheet, most Ordovician genera and species became extinct, but some genera extended beyond the boundary (e.g. *Spinachitina*, *Belonechitina*, *Cyathochitina*, *Ancyrochitina*). The Hirnantian glaciation was not directly responsible for the dramatic extinction of organic-walled microfossils, but it certainly accelerated the extinction of lineages that had already been weakened since the early to mid-Katian. The late Wenlock and earliest Emsian graptolite crises affected the chitinozoophorans to a lesser degree, and the latest Frasnian Kellwasser event did not greatly affect chitinozoophorans. The disappearance of the chitinozoan group at the end of the Famennian resulted from a combination of factors, for example, the chitinozoophorans probably no longer had the genetic potential for successful adaptations to successive drastic environmental changes (only one species is known from the latest Famennian), their usual niche was invaded by more efficient groups, and their usual food supply disappeared or was no longer sufficient. The latter factor is supported by the contemporaneous decline in phytoplankton.

Keywords: Chitinozoa, palaeobiodiversity, extinction events, Early Palaeozoic.

## 1. Introduction

The various shapes of chitinozoan vesicles (e.g. discoidal, spherical, tubular, conical, etc.) are commonly represented in numerous unrelated fossil and extant unicellular organisms or reproductive cycles of metazoans. Thus, chitinozoan affinities based on shape have led to numerous radically different biological assignments (for a discussion, see Paris *et al.* 1999). The inferred chitinous composition of the chitinozoan vesicle wall was used by Eisenack (1931, 1968), Collinson & Schwab (1955) and Jenkins (1970) to support particular inferred biological affinities. However, Voss-Foucart & Jeuniaux (1972) and Jacob *et al.* (2007) were unable to establish the presence of chitin in the organic vesicle wall. This presents two possibilities: (1) that the molecular structure of chitin is not preserved through geological time or (2) the wall of

chitinozoan vesicles contained no chitin. The available data do not allow us to establish which is correct (Jacob *et al.* 2007).

Kozłowski (1963) was the first to use the mode of chitinozoan aggradation in biological affinity arguments. Specimens of the genus *Desmochitina* Eisenack 1931, which were contained within an organic-walled cocoon, were considered by Kozłowski to be similar to polychaete eggs enclosed in a similar structure. However, the various types of attachments to form chains or other types of vesicle aggregation cannot be evaluated for their biological affinity significance, since many invertebrates display a similar mode of egg laying.

Grahn (1981) named the supposed marine metazoan parent organisms ‘chitinozoophorans’, and considered chitinozoans to be the reproductive bodies of a marine invertebrate. Paris (1981) discussed the possibility of small, pelagic or nectic, soft-bodied, wormlike (judging from the elongate coiled chains) animals as the parent

\* Author for correspondence: yngvegrahn@gmail.com

organism, and based on the size of the chitinozoans, deduced that these would range from a few millimetres to a few centimetres in length. The distribution and biodiversification pattern of the chitinozoans may not exactly reflect those of the chitinozoophorans. A pelagic or necto-pelagic animal may use different strategies (see Paris & Nölvak, 1999) in laying its eggs: (1) the eggs were freely spread in the water, or (2) they were attached to floating objects (e.g. seaweed) or the chitinozoophorans attached their eggs to any object that offered protection (e.g. Grahn, 1984b). It is likely that two modes of occurrence could be expected for such eggs in a fossil state: (1) evidence of eggs before laying, that is, the 'intra-oviduct stage' (e.g. frequently coiled chains persisted after the decay of the females; see Paris & Nölvak, 1999; fig. 3), and (2) evidence of eggs after laying (cocoon, organized clusters, isolated vesicles). The chitinozoan vesicles were probably surrounded by a mucous or gelatinous layer (e.g. Paris & Nölvak, 1999; fig. 4). This is corroborated by the occurrence of a chain of *Lagenochitina esthonica* Eisenack, 1955, found in Tremadocian beds from England (Y. G., unpub. data), which was surrounded by framboidal pyrite where a mucous or gelatinous layer could be expected. Soft tissues, even of a gelatinous nature, are known to be frequently preserved through alteration of organic sulphur compounds to pyrite (Stanley & Sturmer, 1983). An important condition for such preservation is a quick burial, preferably in organic-rich sediments (Brett & Baird, 1986). These clusters should not be confused with secondary stacking (e.g. faecal pellets, stuck vesicles, etc.).

Chitinozoans evolved rapidly during Ordovician times. From their first occurrence in the early Tremadocian to the biodiversity crisis in the latest Ordovician, nearly 80 % of morphological innovations took place (Paris & Nölvak, 1999; Paris *et al.* 1999). Chitinozoans had already reached their maximum Ordovician diversity by the late Darriwilian (Fig. 1). Until their extinction in latest Devonian times, the chitinozoan group survived several biodiversity crises: in the early Late Ordovician (Paris *et al.* 2004), late Hirnantian, late Wenlock, earliest Emsian, and in the latest Frasnian (Kellwasser event). The general trend through time is shown in Figure 1.

The occurrence of chitinozoans in all types of sedimentary rocks (except for reefs and coarse, well-sorted sandstones), including black shales and cherts devoid of any bioturbation or evidence of benthic fauna, suggests that the chitinozoophorans were, most likely, part of the zooplankton (Vandenbroucke *et al.* 2010). It is probable that chitinozoophorans grazed on phytoplankton. This pelagic niche appeared in the Cambrian (Servais *et al.* 2008), but was only exploited from the Early Ordovician onward. It was also occupied by graptolites, which appeared a little earlier in the fossil record than chitinozoophorans (Cooper, 1999). However, the specific diversities of these two groups are inverted with relation to climatic belts: intertropical zones were dominated by highly diversified graptolite

faunas and higher latitudes by chitinozoophorans. This is demonstrated for the early Sandbian by Vandenbroucke *et al.* (2010). These authors also concluded that graptolites and chitinozoophorans did not share exactly the same ecosystem.

The fluctuation of the diversity of the chitinozoans through time, from the origination of the group in the early Tremadocian, to its final extinction in the latest Famennian, was evaluated using the 'CHITINOVOSP' database initiated by Paris & Bernard (1994) and updated by one of us (F. P.). All chitinozoan species described since Eisenack's first species description in 1931 are recorded in this database (1214 species). Besides the various taxonomic form fields, the database also includes palaeogeographic and stratigraphic information. The latter entries contain the total range of the recorded species at System, Series and Stage levels. The database has been periodically updated and the last international subdivisions adopted by IUGS are used (that is, the most recent Ordovician global stages).

The number of species per stage can be found by querying the database. These numbers should be regarded as approximate values, as the total range of each species is often a matter of estimation, related to the accuracy of the available stratigraphic information. In addition, ill-defined species included in the database add some further bias. Nevertheless, as the same treatment has been applied throughout the Palaeozoic record of chitinozoan species, the resulting general trends seem to reflect fairly well the actual biodiversification pattern of the group (Fig. 1), as supported by detailed sections providing a well-documented diversity trend for some short time intervals.

The durations of the Wenlock and Ludlow stages as calculated by Sadler, Cooper & Melchin (2009) are much shorter than the duration of the Ordovician and Devonian stages. Consequently, in order to have a time slice roughly in the same range, the chitinozoan specific diversity is expressed at series level for Wenlock and Ludlow on Figure 1. However, a more detailed graph is provided for the Silurian (Fig. 2) with specific diversity also evaluated at stage level for the Wenlock and the Ludlow. This different time slicing points out a drop in diversity in the Homeric roughly contemporaneous with the late Wenlock graptolite crisis (see the *lundgreni* event in Section 5). The two graphs also illustrate the great influence of the time slicing on the diversity curves.

Some discrepancies are noted when calibrating chronostratigraphic subdivisions with the most recent numerical scales. The mean chitinozoan diversity per million years shows higher values for the Darriwilian, the Aeronian and the Pridoli, when using the numerical calibration of Ogg, Ogg & Gradstein (2008), with regard to those proposed by Sadler, Cooper & Melchin (2009). However, these different calibrations do not introduce significant bias, as the general trends of the resulting graphs are similar (Fig. 1). As demonstrated by a more detailed evaluation of the diversity of

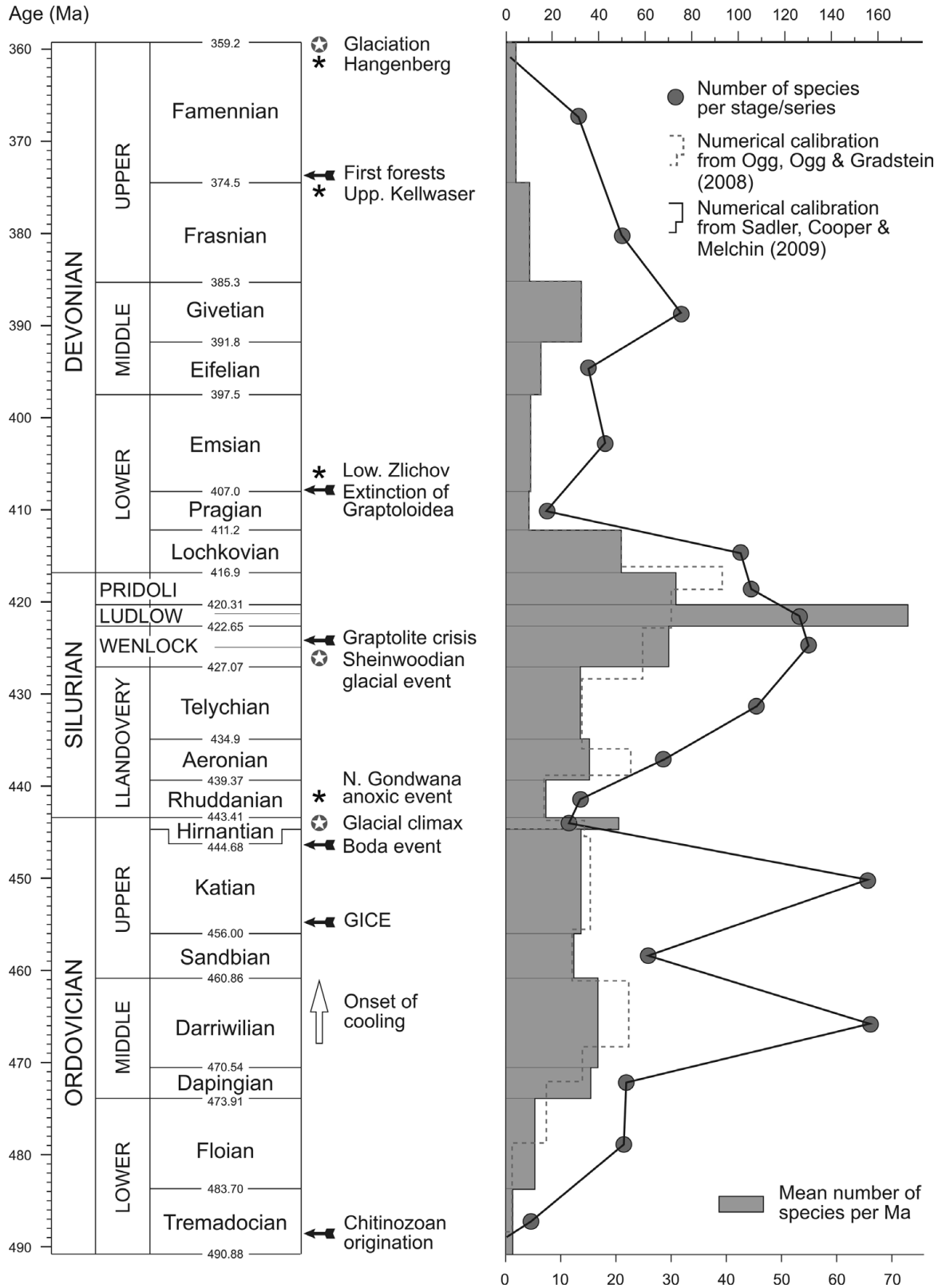


Figure 1. Global evaluation of the chitinozoan biodiversification from the origin of the group in the early Tremadocian to its extinction in the latest Devonian. The solid circles indicate the number of species per stage (Ordovician and Devonian) or per series (Silurian). The graph represents the mean diversity of the chitinozoans per million years for the stages or series (durations based on Sadler, Cooper & Melchin, 2009). An alternative graph (dashed line) is based on the time calibration by Ogg, Ogg & Gradstein (2008). The most significant events are indicated along the time scale. Open arrow: Darriwilian cooling (Trotter *et al.* 2008; Ainsaar *et al.* 2010); black arrow: biological and oceanological events (Jaeger, 1978, 1991; Meyer-Berthaud, Scheckler & Wendt, 1999; House, 2002; Joachimski *et al.* 2002; Kaljo *et al.* 2008; Servais *et al.* 2008; Bergström *et al.* 2009a; Hints *et al.* 2010); black star: main anoxic events (Chlupáč & Kukul, 1988; House, 2002); circled star: main glacial events (Streeel *et al.* 2000; Lehnert *et al.* 2010). The values of the biodiversity of the chitinozoan at species level are from the database ‘CHITINOVOSP’ of F. Paris.

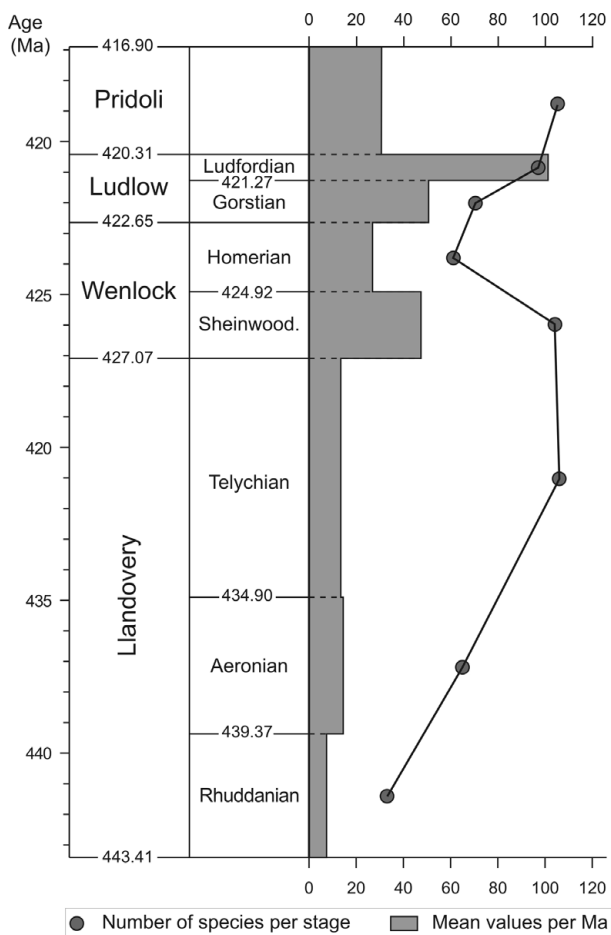


Figure 2. Global biodiversity of the Silurian chitinozoans species per stage (solid circles) and mean value of their specific diversity per million years for each stage. (Numerical calibration from Sadler, Cooper & Melchin, 2009.)

Ordovician chitinozoans (Paris *et al.* 2004), one of the critical points when elaborating such curves is the unbalanced quality of the available data; for instance, some time slices and some areas have been more extensively investigated than others (e.g. the diversity curve tends to mirror the number of available samples; see Paris *et al.* 2004, fig. 28.2–3) and this must be kept in mind when discussing diversity fluctuations.

## 2. The emergence of the chitinozoan group

The first chitinozoans appear during a transgression event with shaly facies above the Cambrian sandstones and after the negative TOCE (Top of Cambrian Excursion)  $\delta^{13}\text{C}$  curve (Zhu, Badcock & Peng, 2006). The chitinozoophorans colonized the niche as pelagic zooplankton together with dendroid graptolites (e.g. Dendrograptids, Anisograptids) and then with the first graptoloids. No undisputable chitinozoans have been recorded before the Ordovician, and the microfossils reported as chitinozoans from the Neoproterozoic Chuar Group by Bloeser *et al.* (1977) are most probably testate amoebas (Porter & Knoll, 2000; Porter, Meisterfeld & Knoll, 2003). Simple, smooth, quite

large chitinozoan forms (*Lagenochitina*, *Conochitina*) appear in the early Tremadocian. They are known from the middle part of the Fezouata Formation in Morocco (Elaouad-Debbaj, 1988), where the first known chitinozoans (*Lagenochitina destombesi*) occur below the *Adelograptus tenellus* graptolite Zone, and above early Tremadocian taxa (Destombes, Holland & Willefert, 1985; Paris, 1990). Early Tremadocian chitinozoans have also been reported from the Yangtze area in south China (Chen, Paris & Zhang, 2008). During the late Tremadocian, chitinozoans spread to areas outside north Gondwana, and the morphological diversification now also includes species with smaller vesicles (*Desmochitina*, *Euconochitina*), together with large specimens from the *Lagenochitina esthonica* group. Early late Tremadocian (*Adelograptus tenellus* graptolite Zone) chitinozoans have been reported from the upper El Gassi Formation in Algeria (Poumot, 1964, 1968; Combaz, 1967; Videt *et al.* 2010) and from the New Fields Farm borehole (908.15 m), 5 km west of Southam, Warwickshire, England (Y. G., unpub. data). De la Puente & Rubinstein (2009) described *Lagenochitina* from the *Aorograptus victoriae* graptolite Zone (Saladillo Formation), and chitinozoans from the lower Parsha Formation, Argentina. Chen, Paris & Zhang (2008) reported *Lagenochitina destombesi* from the late Tremadocian in the Yichang area (Fenxiang Formation), Hubei Province, China. The same species has been recovered from the Varangu regional stage of Estonia (Nölvak, 1999). During the latest Tremadocian, chitinozoophorans expanded to all the paleocontinents, for example, the upper Cienguillas and lower Obispo formations, east Codillera, Bolivia (Heuse, Grahn & Erdtmann, 1999), and the Montagne Noire/Aquitaine Basin, southwest France (Paris, 1984). Outside Gondwana they are known from a number of places such as the Björkåsholmen Formation in Skåne, south Sweden (Nölvak & Grahn, 1993; Grahn & Nölvak, 2010), Oslo Region, south Norway (Grahn & Nölvak, 2007a), and Isle of Rügen, NE Germany (Samuelsson, 1999); Leetse Formation, Estonia (Grahn, 1984a; Hints & Nölvak, 2006); Cow Head, Ledge Section, Newfoundland, Canada (Williams *et al.* 1999); and Altai, Siberia (Sennikov *et al.* 2008).

## 3. Chitinozoan maximum diversity in the late Darriwilian

The chitinozoophorans quickly expanded during Early and Middle Ordovician times (Fig. 1), and reached their maximum Ordovician diversity (only to be exceeded in the early Wenlock and Pridoli) in the late Darriwilian (Paris & Nölvak, 1999; Paris *et al.* 1999, 2004; Hints *et al.* 2010) after about 15 Ma. The genetic potential was probably high with a ‘plasticity’ of the genome of the chitinozoophorans favouring new combinations (Paris *et al.* 2004). The sea-levels were rising, but in the late Darriwilian a short lived regression (Dabard, Loi & Paris, 2007) occurred with the onset of a cooler climate (Trotter *et al.* 2008; Ainsaar *et al.* 2010). The regression



and the climate change affected chitinozoophorans, and chitinozoan diversity decreased until a recovery in the Katian (Fig. 1).

#### 4. The Hirnantian/Rhuddanian biodiversity crisis

The first major biodiversity crisis for chitinozoophorans on a global basis coincides with the Guttenberg  $\delta^{13}\text{C}$  excursion (GICE) in the early Late Ordovician (Paris & Nölvak, 1999; Paris *et al.* 2004; Achab & Paris, 2007; Bergström *et al.* 2009a,b). The decline in chitinozoan species diversity (Fig. 1) is in general connected with decreases in sea-level, most likely caused by the development of restricted intra-continental ice sheets (Hamoumi, 1999; Ainsaar, Meidla & Martna, 2004; Bourahrouh, Paris & Elaouad-Debbaj, 2004; Loi *et al.* 2010), or by increased tectonic activity. Subsequently, a change in sedimentation led to a positive change in  $\delta^{13}\text{C}$ , extinction, and a microfaunal crisis. Glaciation pulses leading to the Hirnantian glaciation (Bergström, Saltzman & Schmitz, 2006; Kaljo *et al.* 2008) started in the late mid-Katian (Bourahrouh, Paris & Elaouad-Debbaj, 2004; Loi *et al.* 2010). During the deglaciation of the Hirnantian ice sheet, most Ordovician genera and species became extinct. A few Ordovician genera (e.g. *Acanthochitina*, *Armoricochitina*) disappeared during the deglaciation of the Hirnantian ice sheet, when about 33% of the chitinozoan genera became extinct during the Late Ordovician. Almost all the species that originated in the Ordovician became extinct during the last part of the Hirnantian. The first chitinozoans with Silurian affinity (*Spinachitina oulebsiri*) occurred in the latest Hirnantian (upper *Normalograptus persculptus* Zone). Continuous sedimentation across the Ordovician/Silurian boundary is rare, but known from Skåne, south Sweden (Grahn, 1978, 1998; Nölvak & Grahn, 1993; Grahn & Nölvak, 2007b), possibly Anticosti Island, Canada (Achab, 1981; Soufiane & Achab, 2000; Bergström, Saltzman & Schmitz, 2006; Achab, Asselin & Desrochers, 2008; Melchin, 2008) and Dob's Linn, Scotland (Verniers & Vandenbroucke, 2006). In the former area, a barren zone occurs within the *Normalograptus persculptus* Zone, and before the appearance of Silurian chitinozoan lineages (e.g. *Belonechitina postrobusta*). At Dob's Linn the fossil record is not continuous. In Bohemia and southwestern France (A. Bourahrouh, unpub. Ph.D thesis, Univ. de Rennes, 2002), and Algeria (Paris, Bourahrouh & Le Hérisse, 2000; F. Paris, unpub. data), characteristic Ordovician species (e.g. *Desmochitina minor*, *Armoricochitina nigerica*, *Calpichitina lenticularis*, *Tanuchitina elongata*) thrived in open marine shelf environments after the end of the glaciation. They become extinct at the same level as in Skåne (that is, the uppermost *Normalograptus persculptus* Zone), but after the first occurrence of Silurian related taxa, such as *Spinachitina oulebsiri-fragilis* (Vandenbroucke *et al.* 2009b). The Hirnantian glaciation was therefore not directly responsible for the dramatic extinction of organic-walled microfossils. However, it certainly

accelerated the extinction of lineages that had already been weakened since the Katian, and favoured development of taxa better adapted to the habitats available high in the water column above the anoxic sea-bottom environments that persisted in some northern Gondwana areas for 10–15 Ma (Paris, Bourahrouh & Le Hérisse, 2000; Le Hérisse *et al.* 2003). Chitinozoans are abundant and highly diversified (Fig. 1) and recorded with other pelagic or epipelagic organisms such as graptolites, orthocones and leiospheres in the Silurian black shale. The poisoned anoxic sea-bottom was not suitable for any metazoan life (as indicated by lack of bioturbation, no benthic fossils, and no degradation of the organic matter). In western Gondwana the chitinozoophorans thrived during the early Silurian (Llandovery) deglaciations when the intracratonic basins had sea-way connections with the Rheic Ocean and subsequently shared the same fauna and phytoplankton (Grahn & Caputo, 1992; Grahn, 2005; Villeneuve *et al.* 1989; S. De la Puente, unpub. Ph.D. thesis, Univ. Nacional de Córdoba, 2009).

#### 5. The late Wenlock crisis (*C. lundgreni* event) and earliest Emsian (pre-basal Zlichov event) graptoloid extinction

At the end of the Wenlock, a regression (Johnson, Kaljo & Rong, 1991; Johnson & McKerrow, 1991; Kaljo & Märss, 1991) severely affected the monograptids (*C. lundgreni* event) on a global basis (Koren & Urbanek, 1994; Štorch, 1995; Kozłowska-Dawidziuk, Lenz & Štorch, 2001). Only *Pristograptus dubius* survived from the monograptid line. Although the chitinozoophorans shared part of the same niche as graptolites, they were less affected, but nevertheless the diversity decreased considerably (Figs 1, 2) in the late Wenlock–early Ludlow (Paris & Nölvak, 1999; Paris *et al.* 1999). No glaciations or extraterrestrial (Jaeger, 1991) events (as indicated by the lack of unusually high presence of iridium) are known from the end of the Wenlock that can explain the graptolite crisis on a global basis. Quinby-Hunt & Berry (1991) discussed a hydrochemical explanation. A high global temperature during the Silurian, and a low oxygen concentration in the atmosphere, probably led to an extensive oceanic anoxia (Quinby-Hunt & Berry, 1991; Koren & Urbanek, 1994). A possible scenario is, therefore, a change in reduction conditions in the oceans leading to anoxic waters at low depths, far from the bottom, and expanding into the graptolite habitat, which would lead to only a thin layer of pelagic waters suitable for life (Quinby-Hunt & Berry, 1991; Koren & Urbanek, 1994). The appearance of dolomites with interbedded graptolitic shales in the latest Wenlock corroborates the presence of anoxia in the oceans. Deep-sea dolomites occur only under an increased reducing potential of sediments. A global oceanic disturbance, as yet unidentified, which severely affected graptolites, should consequently be reflected in carbon isotope ( $\delta^{13}\text{C}$ ) curves. These show depletion in some

sections in the late Wenlock–early Ludlow (Corfield & Siveter, 1992; Corfield *et al.* 1992; Kaljo, Kiipli & Martma, 1998). Chitinozoophorans were less affected (see Nestor, 2009) since they dominated in upper layers of the lower offshore to nearshore environments, while graptolites inhabited the pelagic (Vandenbroucke *et al.* 2009a) or alternatively the deeper parts of the ocean (Cooper, Fortey & Lindholm, 1991).

Graptoloid and chitinozoophoran diversity decreased dramatically during a regressive phase in the Pragian and earliest Emsian (Fig. 1), which resulted from the same oceanographic conditions as during the latest Wenlock (Jaeger, 1991). In the Prague Basin the last graptoloids became extinct in the uppermost Dvorce-Prokop Limestone (Jaeger, 1978), very close to base of the *bursa* chitinozoan biozone and to the former Pragian–Emsian transition (F. P., unpub. data). However, it must be stressed that this level is significantly younger than the controversial GSSP of the Emsian defined by the FAD of the *Polygnathus kitabicus* conodont index species (Yolkin *et al.* 2000). Only benthic dendroids survived the event (Chlupáč & Kukul, 1988). During a transgressive phase in the early Emsian (basal Zlichov event), the chitinozoans were still abundant but fairly poorly diversified (e.g. Paris, 1981). However, the disappearance of graptoloids had no major impact on the chitinozoan distribution, as new pelagic competitors occupied this more or less vacant pelagic niche after the disappearance of the graptoloids (e.g. ‘Thuringian ecotype’ ostracods; see Lethiers & Raymond, 1991).

### 6. Latest Frasnian anoxic crisis (Kellwasser event)

The latest Frasnian anoxic crisis (Kellwasser event) may be the consequence of a multiplicity of impacts (e.g. Alamo, Siljan, Flynn Creek). Moreover, these contributed to successive crises in the Frasnian (House, 2002), and finally resulted in the latest Frasnian mass extinction (McGhee, 2001). Kellwasser sediments are characterized by a general decrease of detrital input, and an increasing burial of organic matter. There was a decrease in oceanic CO<sub>2</sub> concentrations, that were very high during the Devonian, and an acceleration of terrestrial weathering (Elick, Driese & Mora, 1998). The increasing bioproductivity and eutrophication of the epi-iric seas (Joachimski *et al.* 2002; Filipiak, 2002; Racki *et al.* 2002) caused a decrease of oxygen levels and the development of anoxic seabottom conditions. Major tectonic movements (Racki, 1998) in the late Frasnian are reflected in a higher hydrothermal volcanic influence (Pujol, Berner & Stüben, 2006). A transgressive phase in the end of the Frasnian (Kellwasser event) occurred during a warm climate (Streel *et al.* 2000 and references therein). A regression in the beginning of the Famennian (Streel *et al.* 2000; House, 2002) was caused by a cooler global climate (possibly a short-lived glaciation in the earliest Famennian). The exceptional high concentration of chitinozoans in the basal Famennian

beds at La Serre, France, is probably not related to any physical mechanisms alone (Paris *et al.* 1996). The Kellwasser event affected benthic fauna and probably also chitinozoan predators, and the chitinozoophorans could therefore expand in the cooler earliest Famennian environment. Despite the very high abundance of chitinozoans in the lowermost Famennian bed at La Serre, the assemblage is monospecific (Paris *et al.* 1996). This drop of biodiversity was counterbalanced during the Famennian by a diversification of the group (Grahn & Melo, 2002) prior to the latest Famennian extinction. The peak in the <sup>87</sup>Sr/<sup>86</sup>Sr curve (Burke *et al.* 1982; Veizer *et al.* 1997) indicates an increase of silica in the oceans that might have been caused by the onset of the Eovariscan uplift and a mountain building-enhanced continental weathering (Averbuch *et al.* 2005).

### 7. Extinction of the chitinozoophoran group

Despite numerous palynological investigations of early Carboniferous marine strata, no chitinozoans have been recorded *in situ*. However, Middle and Late Devonian chitinozoans are frequently found reworked into Tournaisian strata. Tasch & Hutter (1978) reported finding chitinozoans from the Carboniferous. However, these are reworked from the Devonian and we interpreted some of them (blistered structures) as cyanobacteria colonies. The last records of chitinozoans *in situ* are from Brazil (Grahn & Melo, 2002; Grahn, Loboziak & Melo, 2003) in the late Famennian prior to the latest Famennian glaciation (lower VH Zone = upper VCo Zone) and from the *Retispora lepidophyta* biozones in the Illizi Basin, Algeria (Abdesselam-Rouighi & Coquel, 1997; Boumendjel *et al.* 1988). In both areas, *Fungochitina fenestrata* is generally followed by a monospecific *Fungochitina ultima* assemblage (Paris *et al.* 2000; Grahn & Melo, 2002; Grahn, Loboziak & Melo, 2003). The disappearance of the chitinozoans and therefore the extinction of the chitinozoophorans (Fig. 1) coincide with a regression and fall in sea-level (Hangenberg event) in connection with the glaciation in western Gondwana at the end of Famennian (*lepidophyta* biozones).

There are, however, several possible contributing factors to the extinction of the chitinozoophorans:

(1) The closing of oceans also disturbed the currents and thus the distribution of the food supply, as well as areas of upwelling. The assembly of Pangaea did not destroy the habitat of the chitinozoophorans as these planktic animals were in all Devonian oceans, including in the Panthalassa Ocean surrounding Pangaea. Moreover, suitable shallow marine environments were still available in the Early Carboniferous.

(2) The first forests developing in the early Famennian (Meyer-Berthaud, Scheckler & Wendt, 1999) drastically modified the terrigenous input in the ocean. The resulting chemical changes in the oceans and seas possibly affected the entire marine food chain, especially the phytoplankton.

(3) The development of these first significant forests led to an increase in the atmospheric oxygen level and possibly a decrease in the CO<sub>2</sub> pressure. The influence of the latter on chitinozoan diversity may be better evaluated when well-documented  $\delta^{13}\text{C}_{\text{org}}$  curves are available and can be calibrated with chitinozoan biodiversity curves.

(4) The proliferation of more efficient predators in the pelagic niche, such as ‘Thuringian ecotype’ ostracods (see Lethiers & Raymond, 1991, fig. 6), generated a drastic increase in competition with the chitinozoophorans for the use of the food supply. Moreover, some components of this microfauna were potential chitinozoan consumers and thus affected the number of vesicles reaching the sea-bottom. The arrival of new competitors happened earlier with the development of the ostracods of ‘Thuringian ecotype’ during the Frasnian (Lethiers, Baudin & Casier, 1998), and even earlier with the entomozoidea ostracods in the Silurian. Because no dramatic consequences are noted for the abundance and diversity of the pre-Famennian chitinozoans, the role of these predators in the extinction of the chitinozoans should not be overestimated.

(5) The drop in acritarch diversity and subsequently of the phytoplankton productivity during the Late Devonian has to be stressed (Riegel, 2008). This might represent an important factor in the survival of chitinozoophorans: that is, insufficient food supply and more efficient new competitors, such as pelagic ostracods.

(6) The latest Famennian glaciation generated a drop in the sea-level with drastic changes in marine environments: much shallower seas, uplift and even erosion of land, as demonstrated by the common reworking of Middle and Late Devonian palynomorphs into the Carboniferous. In western Gondwana the onset of the latest Famennian glaciation changed open marine conditions to brackish environments as indicated by the appearance of *Protosalvinia* (Niklas, Phillips & Carozzi, 1976; Loboziak *et al.* 1997) that occur somewhat later than the last chitinozoans (Grahn & Melo, 2002). This suggests that the chitinozoophorans were holomarine and could not adapt to brackish water conditions.

The chitinozoophorans became extinct for multiple and in some cases related reasons:

(1) They possibly no longer had the genetic potential to develop innovations favouring successful adaptations to rapid environmental changes (intrinsic factors). The monospecific assemblage in the latest Famennian supports this possibility.

(2) Their predators became more and more efficient (extrinsic factors). There are examples of selective predation from the late Llandovery in Saudi Arabia, documented by faecal pellets with cracked vesicles of a large species of *Cyathochitina* (F. P., unpub. data). Based on the size of the pellets, the predators were not very large and would have been part of the zooplankton (e.g. entomozoidea ostracods, including the Devonian

‘finger-print’ ostracods) or of the necto-pelagos (small polychaetes or arthropods such as crustaceans or crustacean larvae, but the poor preservation potential has left no body fossils recorded).

(3) Their usual niche was invaded by a more efficient group, such as pelagic ostracods (extrinsic factor), but this can be envisaged only if the competitor group had a dramatic increase in abundance in the Famennian (e.g. the ‘Thuringian ecotype’ ostracods; see Lethiers & Raymond, 1991, fig. 6). Indeed, other pelagic ostracods (pelagic entomozoidea and myodocope ostracods) are reported from the Wenlock onwards (see Siveter, Vannier & Palmer, 1991); V. J. Perrier, unpub. Ph.D. thesis, Univ. Claude Bernard, Lyon, 2007; Perrier, Vannier & Siveter, 2007) and they had no lethal effects on the chitinozoophorans.

(4) Their usual food supply disappeared or was not sufficient to share with more efficient feeding groups. This is supported by the contemporaneous decline in phytoplankton.

As a hypothesis, the chitinozoan record may promulgate a false idea of the situation if the chitinozoophorans had drastically changed their mode of life (e.g. become parasites) or their usual environment. For instance, the chitinozoophorans may have moved onto land, with an insect-type behaviour and a subsequent dramatic change in their eggs (see Paris, 1981, p. 83). That is, there would no longer be any need to control osmotic pressure, but new membranes might have been necessary for the survival of the embryos. There are a number of similarities in ultrastructures between chitinozoans and modern insect eggs (Grahn & Afzelius, 1980; Paris, 1981). Arthropods are known to have colonized land in the Silurian when the chitinozoophorans were thriving, for example, chelicerates in the early Llandovery (F. P., unpub. data) including myriapods (Morrissey & Braddy, 2004) and arachnids (Jeram, Selden & Edwards, 1990) in the late Silurian. However, no significant diversification changes are noticed in the chitinozoan group at this time.

## 8. Concluding remarks

The chitinozoan group existed for about 130 Ma, from early Tremadocian to latest Famennian times. Chitinozoophorans (the chitinozoan animal) were pelagic zooplankton and shared part of this niche with graptolites and others. They were therefore less affected than other groups by the development of anoxic conditions in the deeper part of the water column (Rhuddanian black shales, Kellwasser event). Extinction of typical Ordovician taxa took place during the Hirnantian deglaciation, and while not directly responsible for the dramatic extinction of organic-walled microfossils, it certainly accelerated the extinction of lineages that had already been weakened since the Katian. This event also favoured the development of taxa better adapted to low oxygen levels in the anoxic oceanic environments prevalent during the Early Silurian (Rhuddanian). These Silurian lineages first appeared in the latest



Hirnantian (upper *Normalograptus persculptus* Zone). Extinction of the chitinozoan group occurred after a combination of events that restricted the environments for the chitinozoophorans and favoured new competitors. This, combined with the fact that lineages had been weakened since the Frasnian and were monospecific in the latest Famennian, meant that they no longer had the genetic potential to develop innovations to adapt to successive environmental changes. The contemporaneous decline in phytoplankton indicates that the food supply disappeared or was insufficient for the chitinozoophorans. Together with the pressure of more predators, these factors contributed to their extinction.

**Acknowledgements.** Yngve Grahn thanks the Faculty of Geology at Universidade do Estado do Rio de Janeiro (UERJ), and Dr C. S. Valladares, head of the post-graduate program at the Faculty of Geology for access to the facilities, and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, PQ 309751/2007-1) which made his work possible through grants. Oliver Chang Paris improved and updated the database (CHITINOVOSP) used by Florentin Paris for the evaluation of the chitinozoan biodiversity at species level. The authors are greatly indebted to Theresa Winchester-Seeto (Sydney, Australia) for scientific and linguistic improvements of the manuscript. We are indebted to Aicha Achab (Québec, Canada) for updated information on the range of the Late Ordovician chitinozoans in Laurentia. The reviewers, Thijs Vandenbroucke (Lille University, France) and Olle Hints (Tallinn Technical University, Estonia), are warmly acknowledged for helpful comments on the manuscript and for extensive discussions on the palaeoceanological distribution of the chitinozoans.

## References

- ABDESSELAM-ROUIGHI, F. F. & COQUEL, R. 1997. Palynologie du Dévonien terminal–Carbonifère inférieur dans le Sud-Est du bassin d'Illizi (Sahara algérien). Position des premières lycosporés dans la série stratigraphique. *Annales de la Société Géologique du Nord* **T.5** (2eme sér.), 47–57.
- ACHAB, A. 1981. Biostratigraphie par les Chitinozoaires de l'Ordovicien supérieur–Silurien inférieur de l'Île d'Anticosti. Résultats préliminaires. In *Subcommission on Silurian stratigraphy, Ordovician–Silurian Boundary Working Group* (ed. P. J. Lespérance), pp. 143–57. Field Meeting, Anticosti – Gaspé, Quebec, 1981. II. Stratigraphy and Paleontology.
- ACHAB, A., ASSELIN, E. & DESROCHERS, A. 2008. Revisiting the Upper Ordovician chitinozoan assemblages from Anticosti Island: implications for local, regional and global correlation. In *Paleozoic Climates* (eds B. Kröger & T. Servais), p. 11. Abstracts, International Congress – Congrès international, August 22–31, 2008, Lille, France.
- ACHAB, A. & PARIS, F. 2007. The Ordovician chitinozoan biodiversification and its leading factors. *Palaeogeography Palaeoclimatology Palaeoecology* **245**, 5–19.
- AINSAAR, L., KALJO, D., MARTMA, T., MEIDLA, T., MÄNNIK, P., NÖLVAK, J. & TINN, O. 2010. Middle and Upper Ordovician carbon isotope chemostratigraphy in Baltoscandia: a correlation standard and clues to environmental history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 13 pp. Doi:10.1016/j.palaeo.2010.01.003.
- AINSAAR, L., MEIDLA, T. & MARTMA, T. 2004. The Middle Caradoc facies and faunal turnover in the Late Ordovician Baltoscandian paleobasin. *Palaeogeography Palaeoclimatology Palaeoecology* **210**, 119–33.
- AVERBUCH, O., TRIBOVILLARD, N., DEVLEESCHOUWER, X., RIQUIER, L., MISTIAEN, B. & VAN VLIET-LANOE, B. 2005. Mountain building-enhanced continental weathering and organic carbon burial as major causes for climatic cooling at the Frasnian–Famennian boundary (c. 376 Ma)? *Terra Nova* **17**, 25–34.
- BERGSTRÖM, S. M., CHEN, X., GUTIÉRREZ-MARCO, J. C. & DRONOV, A. 2009a. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to  $\delta^{13}\text{C}$  chemostratigraphy. *Lethaia* **42**, 97–107.
- BERGSTRÖM, S. M., CHEN, X., SCHMITZ, B., YOUNG, S., RONG, J. Y. & SALTZMAN, M. R. 2009b. First documentation of the Ordovician Guttenberg  $\delta^{13}\text{C}$  excursion (GICE) in Asia: chemostratigraphy of the Pagoda and Yanwasha formations in southeastern China. *Geological Magazine* **146**, 657–78.
- BERGSTRÖM, S. M., SALTZMAN, M. M. & SCHMITZ, B. 2006. First record of the Hirnantian (Upper Ordovician)  $\delta^{13}\text{C}$  excursion in the North American Midcontinent and its regional implications. *Geological Magazine* **143**, 657–78.
- BLOESER, B., SCOPF, J. W., HORDYSTIR, R. J. & BREED, W. J. 1977. Chitinozoans from the Late Precambrian Chuar group of the Grand Canyon, Arizona. *Science* **195**, 676–9.
- BOUMENDJEL, K., LOBOZIAK, S., PARIS, F., STEEMANS, P. & STREEL, M. 1988. Biostratigraphy des miospores et des chitinozoaires du Silurien supérieur et du Dévonien dans le Bassin d'Illizi (S.E. du Sahara algérien). *Geobios* **21**, 329–57.
- BOURAHROUH, A., PARIS, F. & ELAOUAD-DEBBAJ, Z. 2004. Biostratigraphy, biodiversity and palaeoenvironments of the chitinozoans and associated palynomorphs from the Upper Ordovician of the Central Anti-Atlas, Morocco. *Review of Palaeobotany and Palynology* **130**, 17–40.
- BRETT, C. A. & BAIRD, G. C. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* **1**, 207–27.
- BURKE, W. H., DENISON, R. E., HETHERINGTON, E. A., KOEPLIN, R. B., NELSON, H. F. & OTTO, J. B. 1982. Variation of seawater  $^{87}\text{Sr}/^{86}\text{Sr}$  through Phanerozoic time. *Geology* **10**, 516–9.
- CHEN, X. H., PARIS, F. & ZHANG, M. 2008. Chitinozoans from the Fenxiang Formation (Early Ordovician) of Yichang, Hubei Province, China. *Acta Geologica Sinica* **82**, 287–94.
- CHLUPÁČ, I. & KUKAL, Z. 1988. Possible global events and the stratigraphy of the Palaeozoic of the Barrandian (Cambrian – Middle Devonian, Czechoslovakia). *Sbornik geologických věd Geologie* **43**, 83–146.
- COLLINSON, C. & SCHWALB, H. 1955. North American Paleozoic Chitinozoa. *Illinois State Geological Survey Report of Investigations* **186**, 33 pp.
- COMBAZ, A. 1967. Un microbios du Trémadocien dans un sondage d'Hassi-Messaoud. *Actes de la Société Linnéenne de Bordeaux* **104**, 1–26.
- COOPER, R. A. 1999. Ecostratigraphy, zonation and global correlation of earliest Ordovician planktic graptolites. *Lethaia* **32**, 1–16.



- COOPER, R. A., FORTEY, R. A. & LINDHOLM, K. 1991. Latitudinal and depth zonation of Early Ordovician graptolites. *Lethaia* **24**, 199–218.
- CORFIELD, R. M. & SIVETER, D. J. 1992. Carbon isotope change as indicator of biomass flux and an aid of correlation during *ludensis–nilssonii* (Silurian) time. *Proceedings of the Estonian Academy of Sciences Geology* **41**, 173–81.
- CORFIELD, R. M., SIVETER, D. J., CARLIDGE, J. E. & MCKERROW, S. 1992. Carbon isotope excursion near the Wenlock–Ludlow (Silurian) boundary in the Anglo-Welsh area. *Geology* **20**, 371–4.
- DABARD, M. P., LOI, A. & PARIS, F. 2007. Relationship between phosphogenesis and sequence architecture: sequence stratigraphy and biostratigraphy in the Middle Ordovician of the Armorican Massif (NW France). *Palaeogeography Palaeoclimatology Palaeoecology* **248**, 339–56.
- DE LA PUENTE, S. & RUBINSTEIN, C. 2009. Late Tremadocian chitinozoans and acritarchs from northwestern Argentina (Western Gondwana). *Review of Palaeobotany and Palynology* **154**, 65–78.
- DESTOMBES, J., HOLLAND, C. H. & WILLEFERT, S. 1985. Lower Palaeozoic rocks of Morocco. In *Lower Palaeozoic Rocks of the World. Vol. 4, Lower Palaeozoic Rocks of Northwest and West-Central Africa* (ed. C. H. Holland), pp. 91–336. Chichester: John Wiley and Sons.
- EISENACK, A. 1931. Neue Mikrofossilien des baltischen Silurs. I. *Paläontologische Zeitung* **13**, 74–118.
- EISENACK, A. 1955. Neue Chitinozoen aus dem Silur des Baltikums und dem Devon der Eifel. *Senckenbergiana Lethaea* **36**, 311–9.
- EISENACK, A. 1968. Über Chitinozoen des baltischen Gebietes. *Palaeontographica Abteilung A* **131**, 137–98.
- ELAOUAD-DEBBAJ, Z. 1988. Acritarches et Chitinozoaires du Tremadoc de l'Anti-Atlas central (Maroc). *Revue de Micropaléontologie* **31**, 85–128.
- ELICK, J. M., DRIESE, S. G. & MORA, C. I. 1998. Very large plant and root traces from the Early to Middle Devonian: implications for early terrestrial ecosystems and atmospheric p(CO<sub>2</sub>). *Geology* **26**, 143–6.
- FILIPIAK, P. 2002. Palynofacies around the Frasnian/Famennian boundary in the Holy Cross Mountains, southern Poland. *Palaeogeography Palaeoclimatology Palaeoecology* **181**, 313–24.
- GRAHN, Y. 1978. Chitinozoan stratigraphy and palaeoecology of the Ordovician–Silurian boundary in Skåne, southern Sweden. *Sveriges Geologiska Undersökning Serie C* **766**, 1–16.
- GRAHN, Y. 1981. Ordovician Chitinozoa from the Stora Åsbotorp boring in Västergötland, south-central Sweden. *Sveriges Geologiska Undersökning Serie C* **787**, 1–40.
- GRAHN, Y. 1984a. Ordovician Chitinozoa from Tallinn, northern Estonia. *Review of Palaeobotany and Palynology* **43**, 5–31.
- GRAHN, Y. 1984b. Early Caradoc Chitinozoa from Östergötland, south central Sweden. *Geologiska Föreningen i Stockholm Förhandlingar* **105**, 269–72.
- GRAHN, Y. 1998. Lower Silurian (Llandovery–middle Wenlock) Chitinozoa and biostratigraphy of the mainland of Sweden. *GFF* **120**, 273–83.
- GRAHN, Y. 2005. Silurian and Lower Devonian chitinozoan taxonomy and biostratigraphy of the Trombetas Group, Amazonas Basin, Northern Brazil. *Bulletin of Geosciences* **80**, 245–76.
- GRAHN, Y. & AFZELIUS, B. A. 1980. Ultrastructural studies of some chitinozoan vesicles. *Lethaia* **13**, 119–26.
- GRAHN, Y. & CAPUTO, M. V. 1992. Early Silurian glaciations in Brazil. *Palaeogeography Palaeoclimatology Palaeoecology* **99**, 9–15.
- GRAHN, Y., LOBOZIAK, S. & MELO, J. H. G. 2003. Integrated correlation of Late Silurian (Pridoli s.l.) – Devonian chitinozoans and miospores in the Solimões Basin, northern Brazil. *Acta Geologica Polonica* **53**, 283–300.
- GRAHN, Y. & MELO, J. H. G. 2002. Chitinozoan biostratigraphy of the Late Devonian formations in well Caima PH-2, Tapajós River area, Amazonas Basin, northern Brazil. *Review of Palaeobotany and Palynology* **118**, 116–40.
- GRAHN, Y. & NÖLVAK, J. 2007a. Remarks on older Ordovician Chitinozoa and biostratigraphy of the Oslo Region, southern Norway. *GFF* **129**, 101–6.
- GRAHN, Y. & NÖLVAK, J. 2007b. Ordovician Chitinozoa and biostratigraphy from Skåne and Bornholm, southernmost Scandinavia – an overview and update. *Bulletin of Geosciences* **82**, 11–26.
- GRAHN, Y. & NÖLVAK, J. 2010. Swedish Ordovician Chitinozoa and biostratigraphy: a review and new data. *Palaeontographica Abteilung B* **283**(1–3), 1–67.
- HAMOUMI, N. 1999. Upper Ordovician glaciation spreading and its sedimentary record in Moroccan North Gondwana margin. *Acta Universitatis Carolinae, Geologica* **43**, 111–14.
- HEUSE, T., GRAHN, Y. & ERDTMANN, B.-D. 1999. Early Ordovician chitinozoans from the east Precordillera of southern Bolivia. *Revue de Micropaléontologie* **42**, 43–55.
- HINTS, O., DELABROYE, A., NÖLVAK, J., SERVAIS, T., UUTELA, A. & WALLIN, Å. 2010. Biodiversity patterns of Ordovician marine phytoplankton from Baltica: comparison with other fossil groups and sea-level changes. *Palaeogeography Palaeoclimatology Palaeoecology*, 13 pp. Doi:10.1016/j.palaeo.2009.11.003.
- HINTS, O. & NÖLVAK, J. 2006. Early Ordovician scolecodonts and chitinozoans from Tallinn, north Estonia. *Review of Palaeobotany and Palynology* **139**, 189–209.
- HOUSE, M. R. 2002. Strength, timing and cause of mid-Palaeozoic extinctions. *Palaeogeography Palaeoclimatology Palaeoecology* **181**, 5–25.
- JACOB, J., PARIS, F., MONOD, O., MILLER, M. A., TANG, P., GEORGE, S. C. & BÉNY, J.-M. 2007. New insights into the chemical composition of the chitinozoans. *Organic Geochemistry* **38**, 1782–8.
- JAEGER, H. 1978. Late graptoloid faunas and the problem of graptoloid extinction. *Acta Palaeontologica Polonica* **23**, 497–521.
- JAEGER, H. 1991. Neue Standard-Graptolithenzonenfolge nach der ‘Grosen Krise’ an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **182**, 303–54.
- JENKINS, W. A. M. 1970. Chitinozoa. *Geoscience and Man* **1**, 21 pp.
- JERAM, A. J., SELDEN, P. A. & EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science* **250**, 658–61.
- JOACHIMSKI, M. M., PANCOST, R. D., FREEMAN, K. H., OSTERTAG-HENNING, C. & BUGGISCH, W. 2002. Carbon isotope geochemistry of the Frasnian–Famennian transition. *Palaeogeography Palaeoclimatology Palaeoecology* **181**, 91–109.
- JOHNSON, M. E., KALJO, D. L. & RONG, J. Y. 1991. Silurian eustasy. In *The Murchison Symposium: Proceedings of an International Conference on the Silurian System* (eds M. G. Bassett, P. D. Lane & D. Edwards), pp. 145–63. *Special Papers in Palaeontology* **44**.

- JOHNSON, M. E. & MCKERROW, W. S. 1991. Sea level and faunal changes during the latest Llandovery and earliest Ludlow (Silurian). *Historical Biology* **5**, 153–69.
- KALJO, D. L., HINTS, L., MÄNNIK, P. & NÖLVAK, J. 2008. The succession of Hirnantian events based on data from Baltica: brachiopods, chitinozoans, conodonts, and carbon isotopes. *Estonian Journal of Earth Sciences* **57**, 197–218.
- KALJO, D. L., KIIPLI, T. & MARTMA, T. 1998. Correlation of carbon isotope events and environmental cyclicity in the East Baltic Silurian. In *Silurian Cycles – Linkages of Dynamic Stratigraphy with Atmospheric, Oceanic and Tectonic Changes* (eds E. Landing & M. Johnson), pp. 297–312. New York State Museum Bulletin no. 491.
- KALJO, D. L. & MÄRSS, T. 1991. Pattern of some Silurian bioevents. *Historical Biology* **5**, 145–52.
- KOREN, T. N. & URBANEK, A. 1994. Adaptive radiation of monograptids after the late Wenlock crisis. *Acta Geologica Polonica* **39**, 137–67.
- KOZŁOWSKA-DAWIDZIUK, A., LENZ, A. C. & ŠTORCH, P. 2001. Upper Wenlock and Lower Ludlow (Silurian) post-extinction graptolites, Všeradice Section, Barrandian area, Czech Republic. *Journal of Paleontology* **75**, 147–64.
- KOZŁOWSKI, R. 1963. Sur la nature des Chitinozoaires. *Acta Paleontologica Polonica* **8**, 425–49.
- LE HÉRISSE, A., BOURAHROUH, A., VECOLI, M. & PARIS, F. 2003. Palynological tracers of sea-ice cover extent during the latest Ordovician on the North African margin. *AAPG Hedberg conference. Paleozoic and Triassic petroleum systems in North Africa, February 18–20, Algiers, Algeria*, pp. 1–2.
- LEHNERT, O., MÄNNIK, P., JOACHIMSKI, M. M., CALNER, M. & FRYDA, J. 2010. Palaeoclimate perturbations before the Sheinwoodian glaciation: a trigger for extinctions during the “Ireviken Event”. *Palaeogeography Palaeoclimatology Palaeoecology*, 12 pp. Doi: 10.1016/j.palaeo.2010.01.009.
- LETHIERS, F., BAUDIN, F. & CASIER, J. G. 1998. Ostracodes de la limite Frasnien–Famennien en environnement anoxique (La Serre, Montagne Noire, France). *Revue de Micropaléontologie* **41**, 321–36.
- LETHIERS, F. & RAYMOND, D. 1991. Les crises du Dévonien supérieur par l'étude des faunes d'ostracodes dans leur cadre paléogéographique. *Palaeogeography Palaeoclimatology Palaeoecology* **88**, 133–46.
- LOBOZIAK, S., MELO, J. H. G., QUADROS, L. P. & STREEL, M. 1997. Palynological evaluation of the Famennian *Protosalvinia* (*Foerstia*) Zone in the Amazonas Basin, northern Brazil: a preliminary study. *Review of Palaeobotany and Palynology* **96**, 31–45.
- LOI, A., GHIENNE, J. F., DABARD, M. P., PARIS, F., BOTQUELEN, A., CHRIST, N., ELAOUAD-DEBBAJ, Z., GORINI, A., VIDAL, M. & VIDET, B. 2010. The Late Ordovician glacio-eustatic record from a high-latitude storm-dominated shelf succession: the Bou Ingarf section (Anti-Atlas, Southern Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 27 pp. Doi: 10.1016/j.palaeo.2010.01.018.
- MCGHEE, G. R. 2001. The “multiple impacts hypothesis” for mass extinction: a comparison of the Late Devonian and the late Eocene. *Palaeogeography Palaeoclimatology Palaeoecology* **176**, 47–58.
- MELCHIN, M. J. 2008. Restudy of some Ordovician–Silurian boundary graptolites from Anticosti Island, Canada, and their biostratigraphic significance. *Lethaia* **41**, 155–62.
- MEYER-BERTHAUD, B., SCHECKLER, S. E. & WENDT, J. 1999. Archaeopteris is the earliest known modern tree. *Nature* **398**, 700–1.
- MORRISSEY, L. B. & BRADY, S. J. 2004. Terrestrial trace fossils from the Lower Old Red Sandstone, southwest Wales. *Geological Journal* **39**, 315–36.
- NESTOR, V. 2009. Chitinozoan diversity in the East Baltic Silurian. *Estonian Journal of Earth Sciences* **58**, 311–6.
- NIKLAS, K. J., PHILLIPS, T. L. & CAROZZI, A. V. 1976. Morphology and paleoecology of *Protosalvinia* from the Upper Devonian (Famennian) of the Middle Amazon Basin of Brazil. *Palaeontographica Abteilung B* **155**, 1–30.
- NÖLVAK, J. 1999. Ordovician chitinozoan biozonation of Baltoscandia. *Acta Universitatis Carolinae, Geologica* **43**, 287–90.
- NÖLVAK, J. & GRAHN, Y. 1993. Ordovician chitinozoan zones from Baltoscandia. *Review of Palaeobotany and Palynology* **79**, 245–69.
- OGG, J. G., OGG, G. & GRADSTEIN, F. M. 2008. *Concise Geologic Time Scale*. Cambridge University Press, 177 pp.
- PARIS, F. 1981. Les Chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe (cadre géologique – étude systématique – biostratigraphie). *Mémoire de la Société géologique et minéralogique de Bretagne* **26**, 492 pp.
- PARIS, F. 1984. Bassins paléozoïques caches d'Aquitaine; biostratigraphie par les Chitinozoaires, Ostracodes, Tentaculites. *Documents de BRGM*, 13–17.
- PARIS, F. 1990. The Ordovician chitinozoan biozones of the Northern Gondwana Domain. *Review of Palaeobotany and Palynology* **66**, 181–209.
- PARIS, F., ACHAB, A., ASSELIN, E., CHEN, X.-H., GRAHN, Y., NÖLVAK, J., OBUT, O., SENNIKOV, N., VECOLI, M., VERNIERS, J., WANG, X.-F. & WINCHESTER-SEETO, T. 2004. Chapter 28: Chitinozoans. In *The Great Ordovician Biodiversification Event* (eds B. D. Webby, F. Paris, M. L. Droser & I. G. Percival), pp. 294–311. New York: Columbia University Press.
- PARIS, F. & BERNARD, D. 1994. “PHOTOCHITINO”, an image-incorporated electronic database for chitinozoan identification. In *CIMP Symposium on Palynology, Palaeoenvironments and Stratigraphy* (eds K. Dornig et al.), p. 32. Abstract. Sheffield, 7–10 September 1994.
- PARIS, F., BOURAHROUH, A. & LE HÉRISSE, A. 2000. The effects of the final stages of the Late Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well NI-2 (NE Algerian Sahara). *Review of Palaeobotany and Palynology* **113**, 87–104.
- PARIS, F., GIRARD, C., FEIST, C. & WINCHESTER-SEETO, T. 1996. Chitinozoan bio-event in the Frasnian/Famennian boundary beds at La Serre (Montagne Noire, Southern France). *Palaeogeography Palaeoclimatology Palaeoecology* **121**, 131–45.
- PARIS, F., GRAHN, Y., NESTOR, V. & LAKOVA, I. 1999. Proposal for a revised chitinozoan classification. *Journal of Paleontology* **73**, 549–70.
- PARIS, F. & NÖLVAK, J. 1999. Biological interpretation and paleobiodiversity of a cryptic fossil group: the “Chitinozoan animal”. *Geobios* **32**, 315–24.
- PARIS, F., WINCHESTER-SEETO, T., BOUMENDJEL, K. & GRAHN, Y. 2000. Toward a global biozonation of Devonian chitinozoans. *Courier Forschungsinstitut Senckenberg* **220**, 39–55.
- PERRIER, V. J., VANNIER, D. J. & SIVETER, D. J. 2007. The Silurian pelagic myodocope ostracode *Richteria migrans*. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **98**, 151–63.
- PORTER, S. M. & KNOLL, A. H. 2000. Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped

- microfossils in the Chuar group, Grand Canyon. *Paleobiology* **26**, 360–85.
- PORTER, S. M., MEISTERFELD, R. & KNOLL, A. H. 2003. Vase-shaped microfossils from the Neoproterozoic Chuar Group, Grand Canyon: a classification guided by modern testate amoebae. *Journal of Paleontology* **77**, 409–29.
- POUMOT, C. 1964. Trois nouveaux genres de Chitinozoaires de l'Ordovicien. *Documents internes CIMP(1965)*, 62–75.
- POUMOT, C. 1968. *Amphorachitina, Ollachitina, Velatachitina*, Trois nouveaux Genres de Chitinozoaires de l'Erg Oriental (Algérie-Tunisie). *Bulletin centre de recherches. Elf exploration production, Pau* **2**, 45–55.
- PUJOL, F., BERNER, Z. & STÜBEN, D. 2006. Palaeoenvironmental changes at the Frasnian/Famennian boundary in key European sections: chemostratigraphic constraints. *Palaeogeography Palaeoclimatology Palaeoecology* **240**, 120–45.
- QUINBY-HUNT, M. S. & BERRY, W. B. N. 1991. Late Wenlock (Middle Silurian) Global bioevent: possible chemical cause for mass graptolite mortalities. *Historical Biology* **5**, 171–81.
- RACKI, G. 1998. Frasnian–Famennian biotic crisis: undervalued tectonic control? *Palaeogeography Palaeoclimatology Palaeoecology* **141**, 177–98.
- RACKI, G., RACKA, M., MATYJA, H. & DEVLEESCHOUWER, X. 2002. The Frasnian/Famennian boundary interval in the South Polish–Moravian shelf basins: integrated event–stratigraphical approach. *Palaeogeography Palaeoclimatology Palaeoecology* **181**, 251–97.
- RIEGEL, W. 2008. The Late Palaeozoic phytoplankton blackout – artefact or evidence of global change? *Review of Palaeobotany and Palynology* **148**, 73–90.
- SADLER, P. M., COOPER, R. A. & MELCHIN, M. 2009. High-resolution, early Paleozoic (Ordovician–Silurian) time scales. *Geological Society of America Bulletin* **121**, 887–906.
- SAMUELSSON, J. 1999. Ordovician Chitinozoa from Rügen, North-East Germany. In *Quo Vadis Ordovician? 8th International Symposium on Ordovician System, Prague* (eds P. Kraft & O. Fatka), pp. 295–7. *Acta Universitatis Carolinae, Geologica* **43**.
- SENNIKOV, N. V., YOLKIN, E. A., PETRUNINA, Z. E., GLADKIKH, L. A., OBUT, O. T., IZOKH, N. G. & KIPRIYANOVA, T. P. 2008. Ordovician–Silurian biostratigraphy and paleogeography of the Gorny Altai. In *Trofimuk Institute of Petroleum Geology and Geophysics Sb Ras* (eds A. V. Sennikov & A. V. Kanygin), pp. 1–156. Novosibirsk; Publishing House Sb Ras.
- SERVAIS, T., LEHNERT, O., LI, J., MULLINS, G. L., MUNNECKE, A., NÜTZEL, A. & VECOLI, M. 2008. The Ordovician biodiversification: revolution in the oceanic trophic chain. *Lethaia* **41**, 99–109.
- SIVETER, D. J., VANNIER, D. J. & PALMER, M. C. 1991. Silurian myodocopes: pioneer pelagic ostracodes and the chronology of an ecological shift. *Journal of Micropalaeontology* **10**, 151–73.
- SOUFIANE, A. & ACHAB, A. 2000. Chitinozoan zonation of the Late Ordovician and the Early Silurian of the island of Anticosti, Québec, Canada. *Review of Palaeobotany and Palynology* **109**, 85–111.
- STANLEY, G. D. JR & STURMER, W. 1983. The first fossil ctenophore from the Lower Devonian of West Germany. *Nature* **303**, 518–20.
- ŠTORCH, P. 1995. Biotic crisis and post-crisis recoveries recorded by Silurian planktonic graptolite faunas of the Barrandian area (Czech Republic). *Geolines (Praha)* **3**, 59–70.
- STREEL, M., CAPUTO, M. V., LOBOZIAK, S. & MELO, J. H. G. 2000. Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth Science Reviews* **52**, 121–73.
- TASCH, P. & HUTTER, T. J. 1978. Pennsylvanian chitinozoans from Eastern Kansas. *Palinologia*, núm. extraord. **1**, 443–52.
- TROTTER, J. A., WILLIAMS, I. S., BARNES, C. R., LÉCUYER, C. & NICOLL, R. S. 2008. Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. *Science* **321**, 550–4.
- VANDENBROUCKE, T., ARMSTRONG, H. A., WILLIAMS, M., PARIS, F., SABBE, K., ZALASIEWICZ, J. A. & NÖLVAK, J. 2010. Epipelagic chitinozoan biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician seas: implications for a cooling Late Ordovician climate. *Palaeogeography Palaeoclimatology Palaeoecology*, 18 pp. Doi: 10.1016/j.palaeo.2009.11.026.
- VANDENBROUCKE, T., ARMSTRONG, H. A., WILLIAMS, M., ZALASIEWICZ, J. A. & SABBE, K. 2009a. Ground-truthing Late Ordovician climate models using the paleobiogeography of graptolites. *Paleoceanography* **24**, PA 4202.
- VANDENBROUCKE, T., GABBOTT, S. E., PARIS, F., ALDRIDGE, R. J. & THERON, J. N. 2009b. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. *Journal of Micropalaeontology* **28**, 53–66.
- VEIZER, J., BUHL, D., DIENER, A., EBENETH, S., PODLAHA, O. G., BRUCKSCHEN, P., JASPER, T., KORTE, C., SCHAAF, M., ALA, D. & AZMY, K. 1997. Strontium isotope stratigraphy: potential resolution and event correlation. *Palaeogeography Palaeoclimatology Palaeoecology* **132**, 65–77.
- VERNIERS, J. & VANDENBROUCKE, T. 2006. Chitinozoan biostratigraphy in the Dob's Linn Ordovician–Silurian GSSP, Southern Uplands, Scotland. *GFF* **128**, 195–202.
- VIDET, B., PARIS, F., RUBINO, J.-L., BOUMENDJEL, K., DABARD, M.-P., LOI, A. & GHIENNE, J.-F. 2010. Calibration of Ordovician sequences on the northern Gondwana platform. *Palaeogeography Palaeoclimatology Palaeoecology*, Doi: 10.1016/j.palaeo.2010.03.050, in press.
- VILLENEUVE, M., DIALLO, M. C., KELEBA, F., KOUROUMA, S., PARIS, F. & RACHEBOEUF, P. R. 1989. Données paléontologiques nouvelles sur le Paléozoïque du Bassin Bové (Guinée, Afrique de l'Ouest): conséquences stratigraphiques. *Comptes rendus de l'Académie des Sciences de Paris* **309**, 1583–90.
- VOSS-FOUCART, M. F. & JEUNIAUX, C. 1972. Lack of chitin in a sample of Ordovician Chitinozoa. *Journal of Paleontology* **46**, 769–70.
- WILLIAMS, S. H., NOWLAN, G. S., BARNES, C. R. & BATTEN, R. S. R. 1999. The Ledge section at Cow Head, western Newfoundland: new data and discussion of the graptolite, conodont and chitinozoan assemblages. *Acta Universitatis Carolinae, Geologica* **43**, 65–8.
- YOLKIN, E. A., KIM, A. I., WEDDIGE, K., TALENT, J. A. & HOUSE, M. R. 2000. The basal Emsian GSSP in Zinzil'ban Gorge, Uzbekistan. *Courier Forschungsinstitut Senckenberg* **225**, 17–25.
- ZHU, M.-Y., BADCOCK, L. E. & PENG, S.-C. 2006. Advances in Cambrian stratigraphy and paleontology: integrating correlation techniques, paleobiology, taphonomy and paleoenvironmental reconstruction. *Palaeoworld* **15**, 217–22.