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Quantitative evaluation of microplankton palaeobiogeography in the Ordovician–Early Silurian of the northern Trans European Suture Zone: implications for the timing of the Avalonia–Baltica collision

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Abstract

Quantitative analysis of assemblage similarity among chitinozoan and acritarch associations recovered from various sedimentary sequences across the Trans European Suture Zone (TESZ; southern Baltic Sea and northern Germany region), permits evaluation of changes in microplankton palaeobiogeography during the Ordovician in the study area. The present data confirm strong palaeobiogeographic differences between the lower Ordovician of the Rügen area, and the coeval domains of the East European Platform (EEP), corroborating the idea that the subsurface of Rügen should be considered palaeogeographically as the eastern extension of Avalonia.

Cluster analysis of chitinozoan assemblages from numerous wells in the Rügen area, and one well from the southern margin of the EEP indicates that chitinozoan bioprovincialism reached its maximum during the Llanvirn; during this period, the Rügen microplankton communities were clearly Gondwanan in character. Calculations using the coefficient of similarity support the conclusion of a high similarity between Llanvirn acritarch assemblages from the Rügen subsurface and from coeval Perigondwana localities (e.g. Tunisia). Since the early Caradoc, this Gondwanan affinity of the Rügen microfossils starts to lessen, and becomes negligible during the late Caradoc. During latest Caradoc–early Ashgill through Llandovery times the chitinozoan assemblages from either side of the TESZ are undistinguishable. If palaeobiogeographical differentiation is primarily related to palaeolatitudinal distance, then the present data support closure of the Tornquist Ocean during late Caradoc–Ashgill times. The presence of reworked Llanvirn acritarchs of Perigondwanan affinity in middle Ashgill sedimentary sequences at the southern margin of the EEP, clearly shows that by this time erosion of an uplifted area was taking place. Accordingly, the closure of the Tornquist Ocean, and consequent Avalonia–Baltica collision must have taken place during the time interval between the middle Caradoc and the early middle Ashgill (Rawtheyan).

New chitinozoan data from boreholes H 2 and K 5, offshore of Rügen Island, northern Germany, allow for precise biostratigraphic dating. In the pre-Devonian part of H 2, *Siphonochitina formosa* indicates an Abereiddian (Early Llanvirn) age, facilitating correlation with boreholes Binz 1/73 and Lohme 2/70 of Rügen. In borehole K 5, the occurrence of *Belonechitina robusta* and *Tanuchitina bergstroemi* permits attribution of the investigated pre-Carboniferous sequence to the middle-late Caradoc, and, possibly, early Ashgill. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: acritarchs; Avalonia; Baltica; chitinozoans; Ordovician; palaeobiogeography; Rügen; Trans European Suture Zone

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1. Introduction

The existence of a major ocean separating the palaeocontinents Gondwana and Baltica during the early to middle Ordovician (termed Tornquist Sea or Tornquist Ocean) was first proposed by Cocks and Fortey (1982) on the basis of palaeobiogeographical data (Fig. 1). Numerous additional lines of evidence from palaeomagnetism (Scotese and McKerrow, 1990, 1991; Torsvik et al., 1992; Torsvik et al., 1993), structural analysis (Anderton, 1982), geochronological studies of detrital zircons (von Hoegen et al., 1990; Haverkamp et al., 1992), and sediment petrography (Giese et al., 1994), have, directly or indirectly, substantiated the Cocks and Fortey (1982) hypothesis.

In late Cambrian to early Ordovician times, the northern margin of Gondwana was affected by extensive rifting events resulting in a series of northwards-drifting continental terranes (e.g. Avalonia, Armorican Terrane Assemblage; Ziegler, 1986; Berthelsen, 1992; Torsvik et al., 1992; Meissner et al., 1994). It is generally accepted that during the northward drift of the microcontinent Avalonia (sensu Cocks and Fortey, 1982), the Tornquist Ocean basin was being consumed (Fig. 1). Although the detailed geodynamic process related to the oceanic subduction is still largely speculative, formation of the so-called Danish–North German–Polish Caledonides is certainly associated with the Avalonia–Baltica collision, and thus to the closure of the Tornquist Ocean (e.g. Berthelsen, 1992; Tanner and Meissner, 1996 and references therein). This orogenic event is usually referred to as ‘Caledonian’.

Analyses of macrofossil distribution (brachiopods, trilobites, and to some extent ostracods) from Avalonia and Baltica localities shows that faunal interchange between the two palaeocontinents began during the Caradoc–Ashgill, and by the Early Silurian, Avalonia, Baltica, and Laurentia shared essentially similar trilobite and brachiopod communities (Cocks et al., 1997). Generic similarity of ostracod faunas in Britain (Avalonia) and Baltoscandia was high in the Caradoc and increased in the Ashgill (Vannier et al., 1989). Avalonia and Baltica ostracod faunas remained

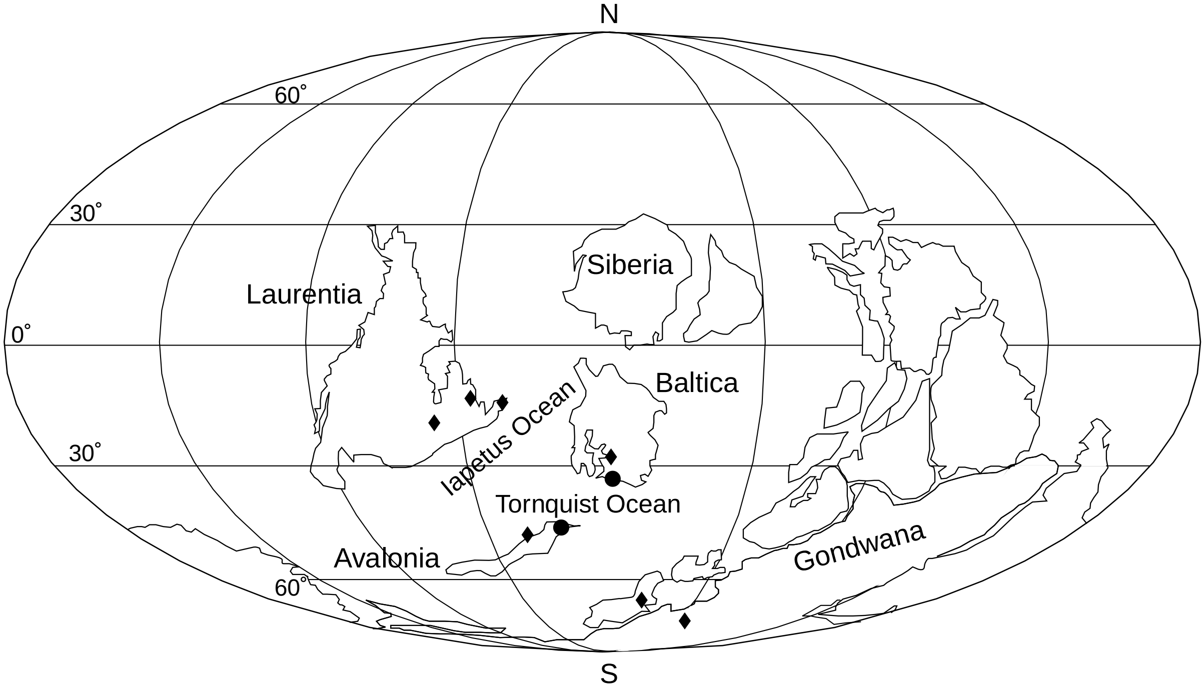


Fig. 1. Plate tectonic configuration for the middle Ordovician (modified from Scotese and McKerrow, 1991; Wicander et al., 1999). (●)-Location of study sections. (◆)-Locations of assemblages used for comparison and quantitative analysis.

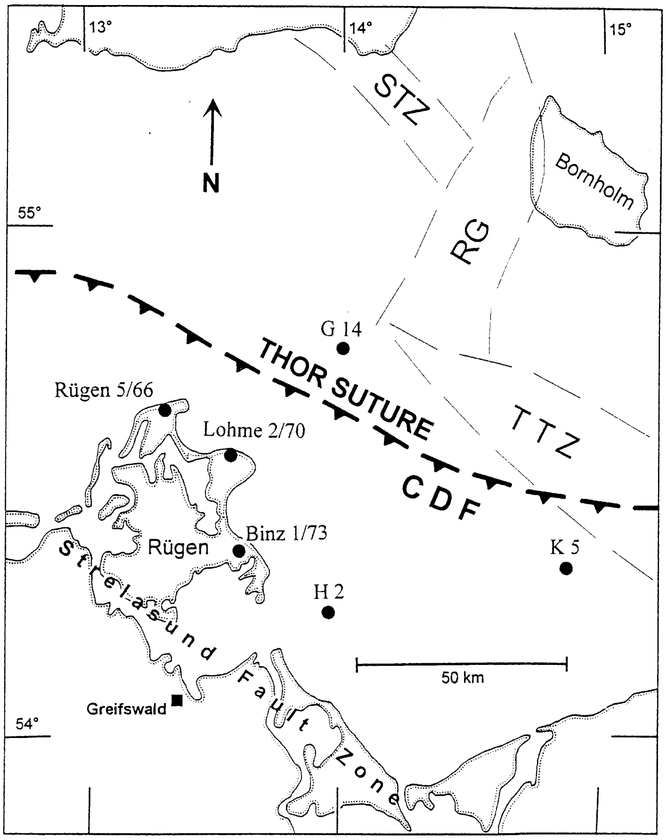


Fig. 2. Map of Rügen and adjacent areas showing the location of the study boreholes. Abbreviations: STZ = Sorgenfrei-Tornquist Zone; RG = Rønne Graben; TTZ = Teisseyre-Tornquist Zone; CDF = Caledonian Deformation Front. Modified from Beier and Katzung (1999).

distinct from those in Laurentia up to latest Silurian times (Berdan, 1990; Cocks et al., 1997). On the basis of this palaeobiogeographic data, closure of the Tornquist Ocean is generally thought to have taken place in late Ordovician to earliest Silurian times (e.g. Dean, 1985; Fortey and Cocks, 1988). However, a more precise estimate of the time of this event is not possible on the basis of comparisons of fossil affinity alone, because faunal and floral interchange between the shelf communities of two continents approaching each other is likely to start much earlier in time than the actual continental collision (Fortey and Cocks, 1988).

Interpreting the isotopic age patterns of detrital micas from Cambro-Ordovician clastic successions across the Trans European Suture Zone (TESZ), Dallmeyer et al. (1999) found evidence of a 'Caledonian' (450–425 Ma; late Ashgill) thermal overprint thought to be associated with the closure of the Tornquist Ocean and subsequent deformation and metamorphism.

In this study, palynological (chitinozoans and acritarchs) data from five subsurface sections (G 14, southern Baltic Sea; H 2, K 5, Binz 1/73, Rügen 5/66, and Lohme 2/70, Rügen Island area, northern Germany; Figs. 1, 2) are used, in combination with selected *bona fide* published data from Perigondwana and Baltica localities, as the basis for a quantitative analysis of the evolution of planktic faunal and floral affinities between Avalonia and Baltica throughout the Ordovician. This data, together with information derived from reworked and in situ palynomorphs from the upper Ordovician of the G 14 borehole, permit us to constrain the time of closure of the Tornquist

Ocean within a time interval ranging from the early Burrellian (early middle Caradoc) to the Rawtheyan (late middle Ashgill).

2. Lower Palaeozoic microplankton biogeography

In recent times, there has been considerable improvement in the knowledge of the Lower Palaeozoic biogeographical distribution of palynomorphs, especially acritarchs and chitinozoans. Detailed accounts on the palaeobiogeography of Ordovician microplankton, either based on critical review of previous works or on new studies, are found in Playford et al. (1995); Servais and Fatka (1997), and Tongiorgi and Di Milia (1999) for acritarchs, and in Achab (1988, 1991), Achab et al. (1992), and Paris (1981, 1993), for chitinozoans. We briefly summarise herein those aspects of acritarch and chitinozoan Ordovician palaeobiogeography that are most relevant to this study.

2.1. Acritarchs

Recent studies of Ordovician acritarch assemblages from selected localities with reliable macrofossil biostratigraphic control and known palaeogeographic setting (e.g. Playford et al., 1995, Tongiorgi and Di Milia, 1999; Vecoli, 1996, 1999; Vecoli et al., 1999a), and re-evaluation of published works, show that acritarch bioprovincialism started during early–middle Arenig time (Tongiorgi and Di Milia, 1999), and reached its maximum during the entire Llanvirn, when at least two distinct microphytoplankton communities developed. The initial community (or ‘microflora’) was mainly, but not exclusively, distributed in high-latitude, cold-water areas, of the northern margin of Gondwana (from western Argentina in the west, to South China in the east; i.e. the Mediterranean Province of Vavrdová, 1974). Characteristic acritarch genera of this microflora are *Arbusculidium* Deunff, 1968, *Arkonia* Burmann, 1970, *Coryphidium* Vavrdová, 1972, *Dicrodiacrodium* Burmann, 1968, *Frankea* Burmann, 1970 emend. Servais, 1993, and *Striatotheca* Burmann, 1970 (Li, 1987; Tongiorgi and Di Milia, 1999). A second microflora (termed ‘Baltic’) was primarily diffused in relatively low-latitude, warm-water regions (e.g. the East European Platform (EEP); i.e. the Baltic Province of Vavrdová, 1974). The concept of acritarch bioprovincialism was first introduced by Vavrdová (1974) with the definition of the ‘Mediterranean’ and ‘Baltic’ Provinces. Vavrdová’s (1974) concept was accepted in its fundamental principles by numerous subsequent authors (e.g. Martin, 1982; Li, 1987; Albani, 1989). However, Tongiorgi and Di Milia (1999) noted that the definition of the Baltic Province of Vavrdová (1974) based on the “prevalence of acanthomorphids” and “absence of diacrodians” is not adequate because acanthomorphic acritarchs are abundantly represented also in most middle Ordovician assemblages from the Mediterranean Province, and diacrodians may occur also in Arenig–Llanvirn strata of the East European Platform (Ribecai and Tongiorgi, 1995; Tongiorgi and Di Milia, 1999). A rigorous re-definition of the Baltic Province has been recently proposed by Tongiorgi and Di Milia (1999), based on the presence of some characteristic *Peteinosphaeridium* species (Playford et al., 1995), such as *P. bergstroemii* Staplin, Jansonius and Pocock, 1965, *P. velatum* Kjellström, 1971, *P. hymenoferum* (Eisenack, 1931) Fensome et al., 1990, and *P. dissimile* Górka, 1969, together with the distinctive *Pachysphaeridium* and *macropylum* informal taxonomic groups (Ribecai and Tongiorgi, 1999).

Acritarch palaeobiogeographical data from other regions (e.g. North America, Australia, North China, Siberia) are much less detailed, and presently do not allow for precise definition of further early Ordovician bioprovinces. Moreover, in post-Llanvirn times, acritarch provincialism appears to gradually break down, and late Ordovician microphytoplankton assemblages show conspicuous similarity at the generic and specific level throughout the world (Le Hérissé, in Molyneux et al., 1996).

2.2. Chitinozoans

The distribution of chitinozoans in the sedimentary record suggests a planktic mode of life for these microfossils (or their parent organisms; e.g. Laufeld, 1974; Grahn, 1982). Detailed studies on chitinozoan biogeography show that the oceanic dispersion of these palynomorphs was mainly controlled by climatic factors, i.e. indirectly by palaeolatitude and/or palaeocurrents (e.g. Achab, 1988, 1991; Achab et al., 1992; Paris, 1981, 1993). These latter studies also indicate that chitinozoan biogeographic provincialism was at its maximum in the middle Ordovician, probably as a consequence of the marked continental fragmentation at that time with resulting creation of distinct ecological realms.

The addition of new high-quality chitinozoan data from all over the world will ultimately lead to a unified global view of the temporal and lateral distribution of chitinozoans during the Ordovician (Paris et al., 1999a). However, because of the marked chitinozoan bioprovinciality during this period, three main regional chitinozoan biozonations are presently in use: one for Baltoscandia (Nõlvak and Grahn, 1993, updated by Nõlvak, 1999), one for North Gondwana (Paris, 1990), and one for Laurentia (Achab, 1989).

Paris (1993) showed that chitinozoan palaeobiogeographical data can be successfully used for testing the respective positions of northern Africa and different European regions during the early Palaeozoic, by calculating and evaluating the coefficient of similarity of Clark and Harteberg (1983) on accurately described and well-preserved chitinozoan assemblages. By simple species comparison, Samuelsson and Verniers (2000) found that chitinozoan assemblages recovered from successions deposited on Avalonia in the Brabant Massif, Belgium, were comparable to North Gondwana faunas up to and including the middle Caradoc.

From the above discussion, it follows that during late Arenig–Llanvirn times, acritarchs and chitinozoans can be effectively used as palaeogeographic indicators, and are potentially applicable for recognition and mapping of exotic terranes in north-central Europe.

3. Geological setting and stratigraphy

The study area (Fig. 2) encompasses the transition between the East European Platform, characterised by essentially undeformed Cambrian through Silurian successions, and the so-called 'Caledonian' fold belts of Central Europe, distinguished by deformed Lower Palaeozoic clastic sequences. At a deeper crustal level, this transition corresponds to the boundary between the old Archean-Proterozoic lithosphere of the East European Craton (EEC), and the younger lithosphere beneath the latest Neoproterozoic-Palaeozoic central European mobile belts, the so-called TESZ. These different crustal types were juxtaposed during the Caledonian and Variscan orogenic episodes (Berthelsen, 1992; Pharaoh et al., 1997; Pharaoh, 1999). The most prominent tectonic lineament of the study area is the Thor Suture (Berthelsen, 1998), formerly the 'Caledonian Deformation Front (CDF)', which coincides with the northernmost boundary of deformed lower Palaeozoic sedimentary successions and represents the suture between the palaeocontinents Avalonia and Baltica (cf. Pharaoh, 1999). The position of the Thor Suture is known with some degree of precision offshore of Rügen Island, northern Germany (Giese et al., 1994; Dallmeyer et al., 1999), but less accurately in Denmark and Poland, where borehole control is insufficient or not conclusive, and the deformation front can only be identified on the basis of geophysical evidence (Pharaoh, 1999, and references therein).

The region immediately north of the Thor Suture in the Denmark–North Germany area thus represents the southwestern margin of the EEP, which constituted the foreland of the Central European Caledonian orogen (Berthelsen, 1992; Beier et al., 1997; Maletz et al., 1997, 1998).

The G 14 borehole is located offshore of Rügen Island, northern Germany, a few kilometres north of the Thor Suture (Fig. 2). Isotopic investigations by Tschernoster et al. (1997), clearly show that the crystalline basement of the G 14 well, with its undeformed, flat-lying sedimentary cover, belongs to the southern part of the Baltic Shield. The Lower Palaeozoic part of the sedimentary succession is almost identical to the well known Lower Palaeozoic strata exposed on the island of Bornholm (Franke et al., 1994; Samuelsson et al., 2001; personal core inspection, February 1999): above the crystalline basement, a rather thick (ca. 315 m) Lower to Middle Cambrian fluviatile to shallow marine-subtidal clastic sequence occurs, followed by thinner shallow marine/black shale sequences of Late Cambrian to Arenig age (upper Alum Shale Formation). Then, an approximately 20 m thick fine, carbonate-rich sandstone–siltstone succession of Caradoc–Ashgill age follows. The Ordovician is overlain by some 350 m of Silurian marine shale/fine-clastic strata.

The Rügen boreholes (Rügen 5/66, Lohme 2/70, Binz 1/73, H 2, and K 5) are all located south of the Thor Suture (Fig. 2). In these boreholes, the Lower Palaeozoic is mainly represented by thick Ordovician clastic sediments characterised by gently to steeply inclined stratal dips, and by frequent occurrence of medium- to coarse-grained graywackes (Giese et al., 1994; Katzung et al., 1993). Numerous publications deal in detail with the lithology, sedimentology, and chronostratigraphy of the Rügen successions (e.g. Jaeger, 1967; Giese et al., 1994; Piske et al. 1994; Zagora, 1997; Servais and Molyneux, 1997; Maletz, 1998; Samuelsson et al., 2000; Samuelsson and Servais, 2001). The palaeogeographic position of the lower Palaeozoic of Rügen has been a matter of debate (e.g. Erdmann, 1991; Franke, 1990a, b; Servais and Katzung, 1993; Cocks et al., 1997), because of the lithological, geometrical, and compositional differences between the Cambro-Ordovician of Rügen and the coeval sedimentary cover of the EEP. According to Oliver et al. (1993), the Palaeozoic of Rügen could be considered to be derived from the (poorly defined) northern margin of Perigondwana, either as part of Avalonia, or as a different, independent terrane. The recent palynological studies of Servais and Katzung (1993) and Servais (1994) emphasised the high-latitude 'Perigondwanan' affinity of the Ordovician acritarch floras from Rügen, and the similarity between these latter and coeval assemblages from western Germany, Belgium, England and Wales. The provenance analysis of the Ordovician greywackes of Rügen by Giese et al. (1994) indicate a heterogeneous active continental margin as the most likely detrital source for the sediments, and they support the inclusion of the Rügen successions in the eastern extension of Avalonia. Dallmeyer et al. (1999) suggested that the Rügen Palaeozoic represents an allochthonous Perigondwanan nappe complex, thrust onto the Baltic shield.

4. Material and methods

The material studied consists of 19 core samples from borehole G 14 (southern Baltic Sea; Samuelsson et al., 2001), and five and eight samples from boreholes H 2 and K 5, respectively (offshore of Rügen Island, northern Germany). Additionally, biostratigraphic information from previous investigation of boreholes Rügen 5/66, Binz 1/73 (Samuelsson et al., 2000), and Lohme 2/70 (Samuelsson and Servais, 2001) was used for the quantitative analysis of assemblage similarity. Samples which are referred to in the text are indicated with the borehole name followed by the sampling depth in metres (Figs. 3 and 4). Part of the study samples were collected in 1999 by the authors at the core stores in Sternberg, northern Germany, and part was provided by Dr. Thomas Servais (Villeneuve d'Ascq, France) and Dr. Jörg Maletz (Greifswald, Germany). Because a comprehensive study of the Ordovician acritarchs from the H 2 and K 5 boreholes is currently the object of a separate project, our analysis focuses primarily on chitinozoans; acritarchs were studied only from two levels of the H 2 section (3276.0 and 3278.0 m) which were regarded as particularly relevant for the present study.

Laboratory extraction and concentration of the palynomorphs was achieved by means of standard palynological processing (Wood et al., 1996). Chitinozans were hand-picked and mounted for optical and scanning electron microscopic (SEM) study; all the chitinozoan specimens in ca. 40 g of rock were examined and counted for semiquantitative abundance estimates (Figs. 3 and 4). Acritarchs were studied primarily in conventional smear-slides for transmitted-light optical microscopy; no quantitative estimates of species abundance were performed for the acritarch assemblages. SEM study and imaging of chitinozoans was performed at the Department of Geology and Pedology, Ghent University, with a JEOL Scanning Microscope 6400 at 10 kV. All illustrated specimens are deposited in the collection of the Research unit Palaeontology, Department of Geology and Pedology, Ghent University. Samples from the H 2 and K 5 boreholes studied for chitinozoans are housed in the collections of the Services Associés de Paléontologie, Université de Liège, Belgium.

4.1. Chitinozoans: cluster analysis

In order to analyse the palaeogeographical significance of the chitinozoan assemblages described in the present study, we used the multivariate statistical technique of cluster analysis. Cluster analysis mathematically evaluates the overall similarity between objects, which is then displayed in the form of a

H2	*Pistillachitina* cf. *elegans*	*?Lagenochitina* spp.	*Cyathochitina jenkinsi*	*Rhabdochitina* sp.	*Conochitina lepida*	*Cyathochitina campanulaeformis*	*?Siphonochitina* sp.	*Cyathochitina* spp.	*Conochitina* spp.	*Conochitina pachydaea*	*?Desmochitina* sp.	*Conochitina parviventer*	*Euconochitina* sp.	*Cyathochitina* cf. *varennensis*	*Lagenochitina* cf. *cybaea*	*Belonechitina* gr. *micracantha*	*Belonechitina* spp.	*Siphonochitina formosa*	**% undetermined Chitinozoa**	**number of Chitinozoa/g rock**	**number of Chitinozoa/sample**	**sample weight (g)**
3276.4	◎	◎	□	○	□	◎	◎	◎	◎	◎									●	2.5	119	47
3278.5	◎		○	○	●	□	◎	◎	◎		◎	◎							□	1.5	62	42
3280.5				◎	◎	□					◎		◎						■	2.8	110	40
3282.5			○	◎	□	◎		◎	◎	○	◎	□		◎	◎	◎	◎		●	2.4	99	41
3283.0			□	◎	□	○				◎		□				◎		◎	●	7.5	300	40

Fig. 3. Relative frequency of chitinozoan taxa recovered from the H 2 well. Key to symbols: (◆) = <1%; ◎ = 1–5%; (○) = 6–10%; (□) = 11–25%; (●) = 26–50%; (■) = 51–100%.

dendrogram. Comparison among objects is based on an agglomerative clustering algorithm which allows combining the most similar objects in clusters of successively higher ranks, until all objects are arranged in a single, hierarchical group (Hazel, 1970). We consider cluster analysis the most suitable multivariate method of quantitative palaeobiogeographical assessment because of its rather intuitive graphic output and ease of interpretation.

In our case, the objects to be compared were the chitinozoan assemblages recognised in the study boreholes. First, the chronostratigraphic significance of the assemblages was determined. For this, we integrated the biostratigraphic analysis of the chitinozoan assemblages with information from independent biostratigraphic data available for the sections (e.g. graptolite biozonation from Maletz, 1997, 1998) and cross correlation with co-occurring acritarch assemblages. The chitinozoan assemblages correspond to the following formal biozones established either in North Gondwana (Paris, 1990), Baltoscandia (Nõlvak and Grahn, 1993), or globally (for the Silurian; Verniers et al., 1995): *Lagenochitina destombesi* (late Tremadoc; Rügen 5/66 borehole), *Cyathochitina primitiva* (early–middle Arenig; G 14 borehole), *Siphonochitina formosa* (early Llanvirn; H 2, Lohme 2/70, Binz 1/73 boreholes), *Laufeldochitina striata* (late Llanvirn; G 14 and Rügen 5/66 boreholes), *Lagenochitina ponceti–Lagenochitina deunffi* (early Caradoc; Rügen 5/66 borehole), *Belonechitina robusta* (middle-late Caradoc; K 5 borehole), *Tanuchitina bergstroemi* (early Ashgill; K 5 borehole), *Ancyrochitina merga* (early-middle Ashgill; G 14 borehole), and *Spinachitina maennili* (early Llandovery; G 14 borehole).

Notably, all biozones recognised in borehole G 14 correlate to Baltoscandian chitinozoan zonations (Nõlvak and Grahn, 1993; Nõlvak, 1999), while those identified in the Rügen sections are mostly comparable to North Gondwana-based zonations up to and including Caradoc times (Paris, 1990, 1996). On the basis of this simple observation alone, a certain degree of palaeogeographical affinity between Baltica and the G 14 succession, and northern Gondwana and the Lower Palaeozoic of Rügen can already be assumed. By means of cluster analysis, we expect to obtain a quantitative estimate of this degree of similarity between the various assemblages, and its change with time. This may also be considered a way to test the validity of chitinozoans as palaeogeographic indicators in light of the present new results.

Generally, local biochronostratigraphic subdivisions cannot be correlated directly. For example, the Baltoscandian Ordovician chitinozoan biozones define chronostratigraphic intervals which are in many cases much longer ranging than any of the average Gondwanan Ordovician chitinozoan biochronozones (see Paris, 1996, text-fig. 5). For this reason,

K5	*Cyathochitina* sp.	*?Eisenackitina ?lagenomorpha*	*Cyathochitina campanulaeformis*	*Cyathochitina jenkinsi*	*Belonechitina* spp.	*Belonechitina micracantha*	*Belonechitina* cf. *robusta*	*Conochitina ?chydaea*	*Belonechitina* cf. *wesenbergensis*	*Conochitina* spp.	*Eisenackitina* aff. *lagenomorpha*	*Rhabdochitina* spp.	*Tanuchitina* cf. *bergstroemi*	*Desmochitina minor*	*Desmochitina* sp.	**% undetermined Chitinozoa**	**number of Chitinozoa/g rock**	**number of Chitinozoa/sample**	**sample weight (g)**
4004.5	●	○	◎	○	○											●	0.8	30	39
4007.5	◎	□			◎	□	◎	◎	◎							■	2.5	94	38
4010.5		□			○					◎						■	0.5	21	39
4013.0	◎	●			●	◎		◎		◎	◎					●	1.5	60	40
4095.1	◎	□			○	□		◎			◎					■	3.7	146	40
4096.5		○			□	○	◎	◎	○	◎		○				●	1.1	45	40
4099.0						●										■	0.2	7	37
4112.0			◆		◎	◎				◎		◎	◎	◆	◆	■	7.5	307	41

Fig. 4. Relative frequency of chitinozoan taxa recovered from the K 5 well. Key to symbols: (◆) = <1%; ◎ = 1–5%; (○) = 6–10%; (□) = 11–25%; (●) = 26–50%; (■) = 51–100%.

we defined a series of time-intervals, which are large enough to allow comparison between chronostratigraphic equivalent chitinozoan assemblages. In other words, our subdivisions were scaled against the longest ranging among the assemblages to be compared.

The upper Tremadoc assemblage from the Rügen 5/66 borehole (dominated by the zone-index species *Lagenochitina destombesi* Elaouad-Debbaj, 1988) yielded too few species to permit any meaningful comparison with chitinozoan assemblages from elsewhere. Moreover, recent findings seem to demonstrate that *L. destombesi*, contrary to previous ideas, is a cosmopolitan species, occurring in Baltica as well as in Gondwana (Nõlvak, 1999). Hence, we did not attempt to view the late Tremadoc chitinozoan assemblages of this study in a palaeobiogeographical perspective.

On the basis of the biozonation discussed above, we defined the following subdivisions as a time frame for the cluster analysis (Fig. 5):

- early–middle Arenig, corresponding to the total-range zone *Cyathochitina primitiva* Biozone in Baltoscandia;
- early Llanvirn, corresponding to the *Siphonochitina formosa* Biozone in North Gondwana;
- late Llanvirn, corresponding to the *Laufeldochitina striata* Biozone in Baltoscandia;
- early–late Caradoc, approximately corresponding to the total stratigraphic range of the North Gondwana Biozones *Lagenochitina ponceti, Lagenochitina deunffi,* and *Belonechitina robusta*;
- early–middle Ashgill, roughly corresponding to the Baltoscandian *Tanuchitina bergstroemi* and the North Gondwana *Ancyrochitina merga* Biozones; and
- early Llandovery, approximately corresponding to the global *Spinachitina maennili* Biozone.

For each of the above intervals, we compared our assemblages with coeval assemblages previously described from localities of known Laurentia, Baltica, Avalonia, and North Gondwana palaeogeographic setting (see legend for Fig. 5).

Among the various types of agglomerative clustering methods, we have chosen the average linkage technique in which the distance between two given groups of objects is calculated as the mean of the distances between each pair of objects in the two clusters. In particular, because in our case the objects (chitinozoan assemblages) were of rather different size (i.e. significant differences in number of species), we used the Weighted Pair Group Median Average

(WPGMA) algorithm (Hazel, 1970) which assigns to each cluster equal weight. For measuring the similarity between assemblages, we used a binary coefficient based on a matrix of frequency of matches and mismatches of the presence or absence of a single variable (chitinozoan species in our case). The index used is the simple matching coefficient, calculated as follows:

$$\mathrm{SMc}_{ij} = (a + b)/(a + b + c + d)$$

the values of a, b, c, and d (either 1 or 0) are determined according to the following table (Table 1):

Table 1

		Sample *j*	
		Presence	Absence
Sample *i*	Presence	*a*	*b*
	Absence	*c*	*d*

All calculations and graphic elaboration were performed with the computer software MVSP of the Kovach Computing Services.

4.2. Acritarchs: similarity coefficient

Some problems exist for quantitative assessment of similarity between acritarch assemblages, especially if based only on a literature survey. Generally, acritarch assemblage diversity data from different workers are not comparable because of inconsistent taxonomic approaches. Although a very high number of acritarch species are described in the literature for the Ordovician alone (order of thousands, cf. Fensome et al., 1990), most of the authors still do not agree on fundamental questions like species concept and taxonomic treatment of morphological variability. Moreover, accurate descriptions of chronostratigraphically well-constrained acritarch assemblages exist from only a few regions. Therefore, for our analysis we have used either our own previous studies (e.g. Vecoli, 1999), or published data supported by good taxonomic descriptions and high-quality illustrations. In addition, the databases we used for calculations were constructed on the basis of shared species rather than genera, because of the higher palaeobiogeographical significance of the former. In this way, we obtained taxonomically consistent databases which could be compared with a high degree of accuracy.

The acritarch assemblage recovered from the H 2 borehole, was compared with coeval (middle Ordovician) assemblages from southern Tunisia (St-1 borehole; Vecoli, 1999), Baltica (Rapla borehole; Uutela and Tynni, 1991), and North America (Loeblich and Tappan, 1969; Loeblich, 1970a, b; Loeblich and Tappan, 1971, 1976, 1978). The comparison with middle Ordovician assemblages from North America is particularly problematic. Acritarchs from the middle Ordovician (Llandeilian Stage) Mountain Lake Member of the Bromide Formation, Oklahoma, USA, were described in a series of papers by Loeblich and Tappan (1969, 1971, 1976, 1978) and Loeblich (1970a, b). Unfortunately, these authors did not include the complete assemblages in their descriptions, but only the more representative and morphologically more interesting taxa. Moreover, the age of the Mountain Lake Member is indicated as late Llanvirn (Llandeilian), but possibly including part of the earliest Caradoc by Loeblich and Tappan (1978, text-fig. 2). Consequently, in interpreting the similarity between acritarch assemblages of our study area and from North America (as representative for Laurentia), we must consider the possible biasing effects of the above-mentioned difficulties.

We tested the similarity among the above acritarch assemblages by using the coefficient of similarity (CS) of Clark and Harteberg (1983), used successfully for bioprovincialism analysis of microfossil assemblages also by Bergström (1990); Paris (1993); Paris et al. (1995), and Le Hérissé et al. (1997):

$$\mathrm{CS} = 2v/a + b$$

where v is the number of species in common between the two compared assemblages; a and b are the total number of species in each assemblage, respectively. According to Clark and Harteberg (1983) values of $\mathrm{CS} < 0.2$ signify low similarity, $0.2 < \mathrm{CS} < 0.55$ values indicate moderate to high similarity, and $\mathrm{CS} > 0.55$ indicates very high similarity.

In interpreting the meaning of this particular measure of diversity among assemblages recovered from different localities, Clark and Harteberg (1983) and Bergström (1990) considered a correlation between CS values and geographic distance between the sample localities. Changes in CS values might, at least in part, reflect changes in plate tectonic configurations. This hypothesis is accepted herein, but we also take into consideration the possible effect of oceanic palaeocurrents which, although being determined by continent configuration, do not necessarily correlate to geographic distance.

5. Results

5.1. Chitinozoan biostratigraphy

5.1.1. Borehole H 2

The chitinozoan assemblage recognised in the pre-Devonian H 2 section between 3283.0 and 3276.4 m is similar to those described from boreholes Binz 1/73 and Lohme 2/70, Rügen Island (Samuelsson et al., 2000; Samuelsson and Servais, 2001). Details of species occurrences and quantitative abundance values are given in Fig. 3.

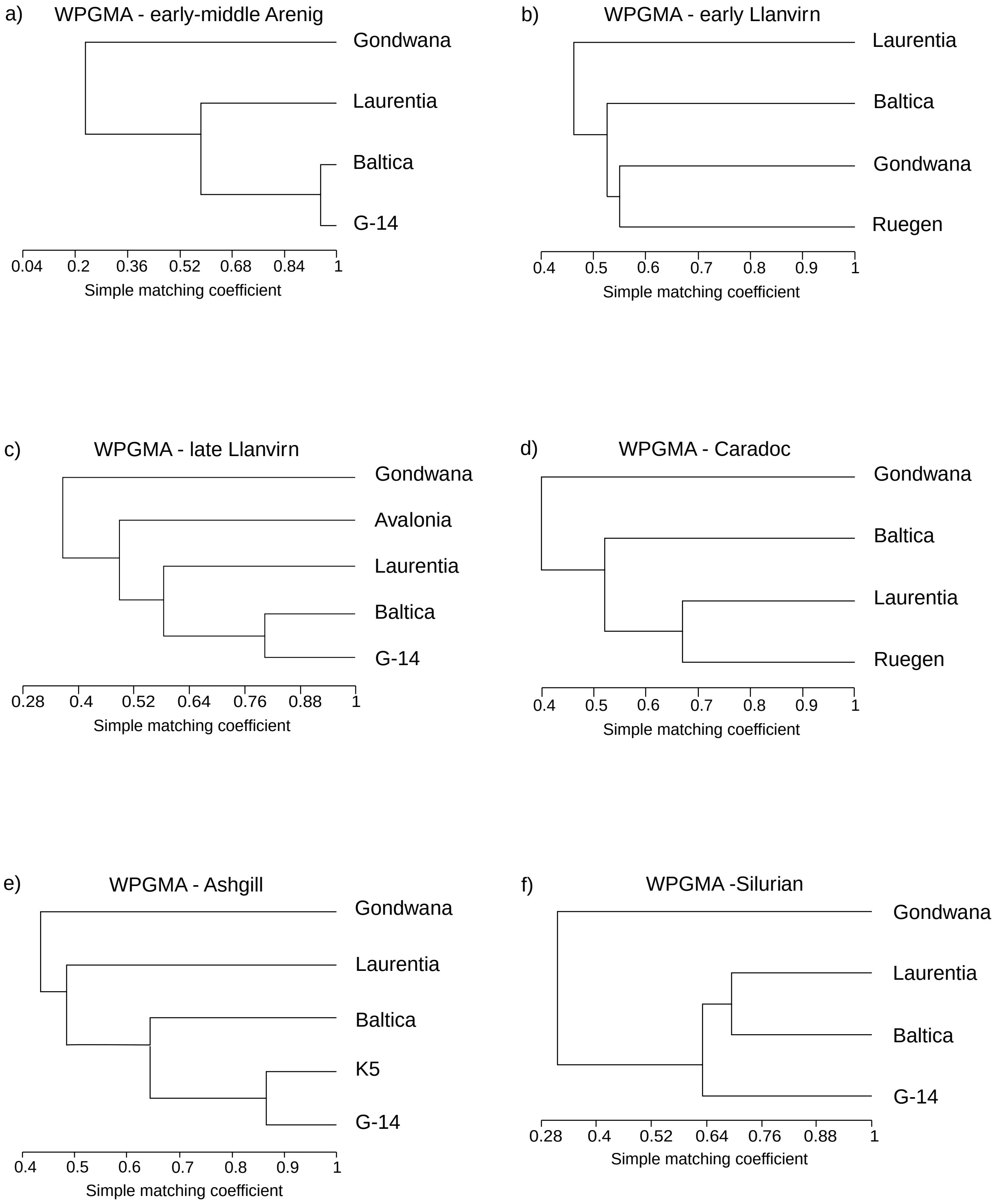
The most chronostratigraphically important species are *Conochitina parviventer* Jenkins, 1967 and *Siphonochitina formosa* Jenkins, 1967, occurring in at least one of the five investigated samples, and *Cyathochitina jenkinsi* Neville, 1974, present in all the samples except one (Fig. 3). The presence of *S. formosa* at 3283.0 m permits us to attribute the assemblage to the *S. formosa* North Gondwana chitinozoan Biozone, inferred to span the entire Abereiddian (Paris, 1990; Al-Hajri, 1995).

Maletz (1998) described the graptolite *Proclimacograptus angustatus* from an unspecified level between 3285.0 and 3275.0 m in the H 2 section, indicating an upper *artus* graptolite Zone (middle Abereiddian, early Llanvirn) to *teretiusculus* graptolite Zone (Llandeilan, late Llanvirn) relative age. Integrating our chitinozoan and acritarch data with the previous chronostratigraphic attributions, an upper *artus* to *murchisoni* graptolite Biozone (middle to late Abereiddian) age can thus be suggested for the studied interval. A straightforward correlation with sediments assigned to the *Siphonochitina formosa* Biozone also in Binz 1/73 (Samuelsson et al., 2000) and Lohme 2/70 (Samuelsson and Servais, 2001) is possible. Especially interesting is the correlation with the borehole Binz 1/73, as the presence of the graptolite *Pterograptus elegans* in the latter indicates a late middle Abereiddian age (Maletz, 1998), leaving the possibility open for a similar age also of the corresponding H 2 and Lohme 2/70 intervals.

5.1.2. Borehole K 5

The two separate intervals sampled from the pre-Carboniferous K 5 section (4112.0–4095.1 m, and 4013.0–4004.5 m) yielded similar chitinozoan assemblages (Fig. 4). The biostratigraphically most important species, *Belonechitina robusta* (Eisenack, 1959), occurs in both intervals, precisely at 4096.5 and 4007.5 m. According to Nõlvak and Grahn (1993), *B. robusta* ranges from the upper Idavere to the lower Nabala regional stages of Baltoscandia, equivalent to, respectively, the lower Burrellian (middle Caradoc) and upper Steffordian (upper Caradoc). The presence of damaged specimens very similar to *Tanuchitina bergstroemi* (Laufeld, 1967) in sample K 5-4112.0, possibly indicates a latest Caradoc–earliest Ashgill age (FAD of *T. bergstroemi* in Baltoscandia: Vormsi Stage, upper Streffordian; Nõlvak and Grahn, 1993). On the basis of these results, the two investigated intervals can possibly be assigned to the uppermost Caradoc–lowermost Ashgill. However, according to Nõlvak and Grahn (1993), *T. bergstroemi* and *B. robusta* cannot co-occur, because the LAD of the latter species (within the Nabala Stage of Baltoscandia, equivalent to the lower Steffordian)

Fig. 5. Dendrograms from the cluster analysis using the average linking technique and the Weighted Pair Group Median Average (WPGMA) algorithm as described in the text. For this analysis, we used our own chitinozoan data from the Rügen drillholes (Samuelsson et al., 2001; Samuelsson and Servais, 2001, Vecoli and Samuelsson, this work). For the other sections we used previously published data as follows: (a) Grahn, 1984 (Baltica); Benoît and Taugourdeau, 1961 and Paris, 1981 (Gondwana); Achab, 1980, 1982, 1986a (Laurentia). (b) Grahn, 1984 (Baltica); Paris, 1981 (Gondwana); Achab, 1983 and Neville, 1974 (Laurentia). (c) Grahn, 1981 (Baltica); Oulebsir, 1992; Oulebsir and Paris, 1995 (Gondwana); Jenkins, 1967 (Avalonia); Achab, 1986b (Laurentia). (d) Grahn, 1981, 1982 (Baltica); Rauscher, 1974 and Paris, 1979, 1981, (Gondwana); Achab, 1986a, 1987 and Jenkins, 1969 (Laurentia). (e) Grahn, 1982, Grahn et al., 1994, Nõlvak, pers. comm. for the *rugata* Zone and Eisenack, 1968 (Baltica); Paris, 1988, 1990 (Gondwana); Jenkins, 1970 (Laurentia). F. Nestor, 1994 (Baltica); Paris et al., 1995 (Gondwana); Grahn, 1985 (Laurentia).


a)
WPGMA - early-middle Arenig
Gondwana
Laurentia
Baltica
G-14
0.04 0.2 0.36 0.52 0.68 0.84 1
Simple matching coefficient
b)
WPGMA - early Llanvirn
Laurentia
Baltica
Gondwana
Ruegen
0.4 0.5 0.6 0.7 0.8 0.9 1
Simple matching coefficient
c)
WPGMA - late Llanvirn
Gondwana
Avalonia
Laurentia
Baltica
G-14
0.28 0.4 0.52 0.64 0.76 0.88 1
Simple matching coefficient
d)
WPGMA - Caradoc
Gondwana
Baltica
Laurentia
Ruegen
0.4 0.5 0.6 0.7 0.8 0.9 1
Simple matching coefficient
e)
WPGMA - Ashgill
Gondwana
Laurentia
Baltica
K5
G-14
0.4 0.5 0.6 0.7 0.8 0.9 1
Simple matching coefficient
f)
WPGMA -Silurian
Gondwana
Laurentia
Baltica
G-14
0.28 0.4 0.52 0.64 0.76 0.88 1
Simple matching coefficient

slightly precedes the first appearance of *T. bergstroemi*. If we assume that our badly preserved specimens attributed to *Tanuchitina* cf. *bergstroemi* are actually co-specific with *T. bergstroemi*, this could signify that either the age of the lower of the investigated intervals (4112.0–4095.1 m) is slightly younger than that of the overlying interval (4013.0–4004.5 m), or that the stratigraphic range of *T. bergstroemi* should be extended downward. Tectonic imbrications with repetition of series are indeed frequently observed in the Ordovician sequences of the subsurface of Rügen (e.g. Jaeger, 1967; Piske et al., 1994).

The other chitinozoan species recognised in the K 5 borehole (Fig. 4) are consistent with the suggested middle to late Caradoc and early Ashgill ages. The Llanvirn age suggested by Piske et al. (1994) on the basis of lithological correlation for the same deposits can be discounted by the present findings.

Correlation of the Ordovician K 5 intervals with other boreholes in the Rügen area south of the Thor Suture is at present not possible because of the lack of cored coeval strata. Before this study, the youngest fossil evidence recorded in the Rügen area was the presence of graptolites belonging to the *gracilis* Zone (Aurelucian, lowermost Caradoc) in the intervals 2610.7–2601.7 m and 1561.5–1556.8 m of the Rügen-5/66 borehole section (Maletz, 1998).

5.2. Cluster analysis

Dendrograms for each of the chronostratigraphic intervals defined above are shown in Fig. 5. In the diagrams, the similarity between the study assemblages, and the reference assemblages from literature data is indicated by the vertical lines. The degree of similarity and the branching hierarchy are the only important features of the diagrams, while the order of the objects on the vertical axis is not significant. In general, a relatively high level of similarity exists between the G 14 section and Baltica (i.e. in the early-middle Arenig, late Llanvirn, and in the Silurian). On the other hand, the Rügen assemblages tend to cluster together with Gondwana during the early Ordovician, and show an increasing similarity with Laurentia during Caradoc–Ashgill times.

5.3. Biostratigraphic and palaeobiogeographical evaluation of the acritarch assemblage from borehole H 2

The numerous and well-preserved acritarchs recovered from samples H 2-3276.0 and H 2-3278.0, constitute a homogeneous and diverse assemblage characterised, among others, by the presence of the stratigraphically important species *Arkonia tenuata* Burmann, 1970, *Arkonia virgata* Burmann, 1970, *Dicrodiacrodium ancoriforme* Burmann, 1968 emend. Servais, Brocke and Fatka, 1996, *Frankea breviuscula* Burmann, 1970, *Frankea sartbernardensis* (Martin) Colbath, 1986, *Stellechinatum celestum* (Martin) Turner, 1984, *Stelliferidium striatulum* (Vavrdová) Deunff, Górka and Rauscher, 1973, *Striatotheca quieta* (Martin) Rauscher, 1974, and *Striatotheca rarirrugulata* (Cramer et al.) Eisenack, Cramer and Díez, 1976. This assemblage can confidently be attributed to the Llanvirn; most of the above species have never been reported from pre-Llanvirn strata, except for *F. sartbernardensis*, which was observed in an horizon 'just below the Arenig–Llanvirn boundary' in the Skiddaw Group, Lake District, England (Rushton and Molyneux, 1989). Many of these species also occur in North Africa, in sediments dated as Llanvirn by graptolites of the *Didymograptus murchisoni* Zone (Vecoli, 1999). Similar assemblages, all considered of Llanvirn age were described from Jordan (Keegan et al., 1990), France (Rauscher, 1974), and Bohemia (Vavrdová, 1990a, b). Burmann (1970) and Servais and Katzung (1993) described similar Llanvirn assemblages from other boreholes in the island of Rügen. The rare post-Llanvirn occurrences of some of the above species in turbiditic sequences of Wales and eastern Ireland (e.g. Trythall et al., 1987; Molyneux, 1990), are probably due to sediment reworking.

The palaeobiogeographical significance of the acritarchs from the Rügen subsurface was addressed by Servais and Katzung (1993) and Servais (1994), who concluded that the lower Palaeozoic of this area could be attributed to Perigondwana. In the present study, we accept this interpretation, and test its validity by calculating the CS between the H 2 acritarchs and typical assemblages from North Africa (Tunisia; Vecoli, 1999), the Baltic region (Estonia; Uutela and Tynni, 1991), and North America (Indiana, Ohio,

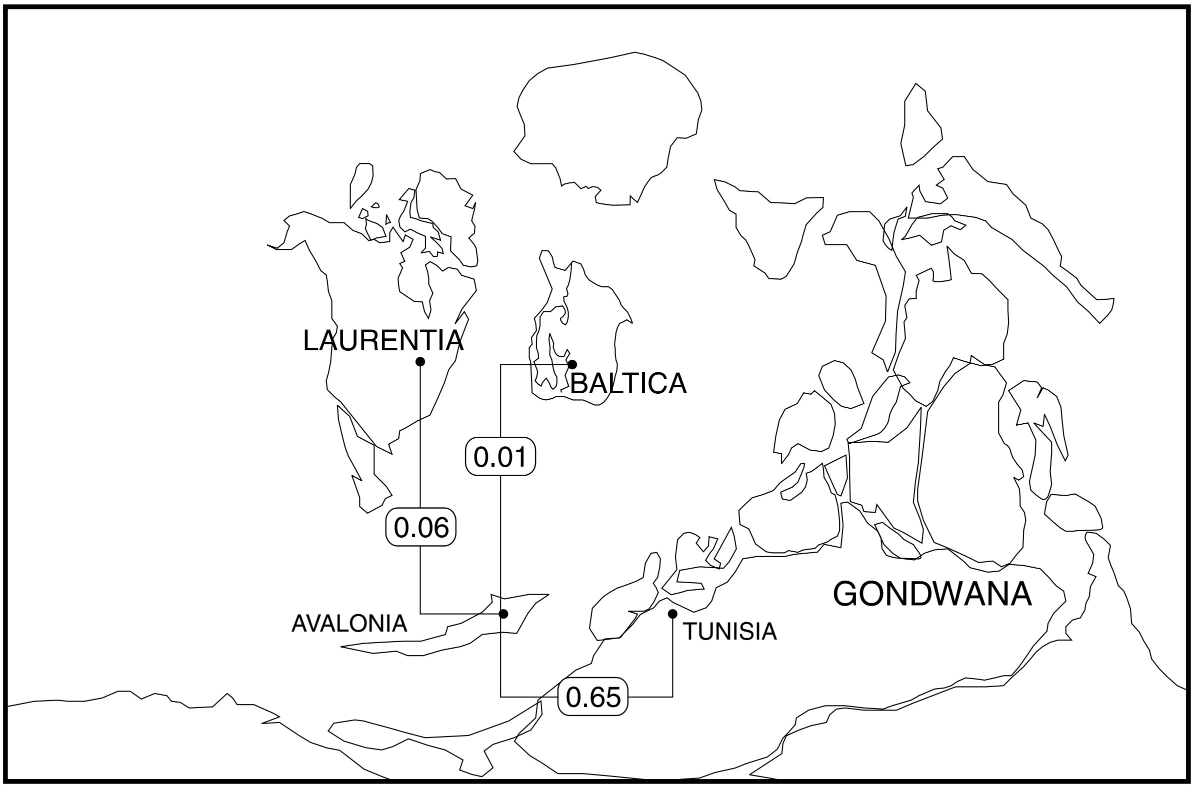


Fig. 6. Middle Ordovician palaeogeography (Llanvirn, 440 Ma; projection centred on 45° Lat. S) showing CS values between the study area and selected localities representative of major microphytoplankton palaeobioprovinces.

Kentucky, Oklahoma, USA; Loeblich, 1970a, b; Loeblich and Tappan, 1976, 1978). The results, shown in Fig. 6, clearly demonstrate the high similarity between the Llanvirn acritarch assemblages of Rügen and North Africa (Tunisia; CS = 0.65), in contrast to the very low correlation with Baltica (CS = 0.01) and Laurentia (CS = 0.06).

6. Discussion of results and conclusions

The collected chitinozoan and acritarch biostratigraphic data (present study; Samuelsson et al., 2000; Samuelsson and Servais, 2001; Samuelsson et al., 2001), integrated with previous information from graptolites (Maletz, 1997, 1998) permit a refined chronostratigraphic subdivision of the Ordovician clastic sequences of the Rügen area. This chronostratigraphic scheme can be utilised as a temporal framework for analysing the evolution of the palaeobiogeographic affinity of the studied microplankton assemblages throughout the Ordovician.

6.1. Chitinozoans

The results of the cluster analysis (Fig. 5) can be interpreted in terms of palaeogeographic reconstruction; in the present discussion, the similarity between assemblages is considered equivalent to palaeobiogeographic affinity.

6.1.1. Early–middle Arenig

The first dendrogram (Fig. 5a) clearly shows a high level of similarity between the G 14 assemblage and Baltica, which are grouped in a first-order cluster. A second-order cluster is formed by the joining of Laurentia to the Baltica–G 14 group, while Gondwana plots separately. This cluster configuration possibly emphasises the influence of palaeolatitudinal distance associated with oceanic circulatory effects on microplankton palaeobiogeographical differentiation. In fact, during Arenig time, Baltica was palaeolatitudinally closer to Laurentia than to the northern margin of Gondwana (Scotese and McKerrow, 1991). However, Arenig chitinozoans are poorly known from Baltoscandia; in Sweden, for example, Arenig sediments are mainly represented by reddish limestones containing badly preserved chitinozoans at best (Y. Grahn, pers. comm.). In contrast to the apparent strong difference between Baltica and Gondwana chitinozoan assemblages shown in this dendrogram, Grahn et al. (1996) demonstrated, for example, the presence of *Clavachitina poumoti* (Combaz and Peniguel, 1972) in Upper Arenig strata in the Granby crater, southern Sweden. This species is also known from Australia, Svalbard and eastern Canada (Grahn et al., 1996). Thus, the bioprovinciality of Arenig chitinozoan assemblages is probably not as straightforward as our results show. Instead, the dendrogram might reflect the scarcity of data. In any case, the very strong similarity of G 14 and the Suhrumägi (North Estonia) chitinozoan assemblages illustrated by the dendrogram should be emphasised.

6.1.2. Llanvirn

The two dendrograms for the Llanvirn (Fig. 5b, c) highlight the palaeobiogeographical affinity between the Rügen area and North Gondwana and confirm the similarity between the G 14 assemblages and the ones from Baltica. In the early Llanvirn diagram, Rügen and Gondwana form a first-order cluster which is then linked to Baltica. In the late Llanvirn dendrogram, Gondwana is evidently separated from a cluster formed by Laurentia, Baltica, and G 14. Avalonia plots separately, possibly showing a certain degree of palaeobiogeographical differentiation from North Gondwana. This suggests a significant increase in palaeolatitudinal distance between Baltica (and secondarily Laurentia) and Gondwana from early to late Llanvirn time, but also between Avalonia and northern Gondwana. From the present graphs, it is evident that chitinozoans clearly ‘see’ the Tornquist Ocean in the middle Ordovician, contrary to the opinions of Paris and Robardet (1990); Fortey and Mellish (1992); Fortey and Cocks (1992), and Paris (1993).

6.1.3. Early–late Caradoc

In the dendrogram for the Caradoc (Fig. 5d), the Rügen assemblages are primarily related to Laurentia, and secondarily to Baltica. The first-order linking between Laurentia and Rügen is not easily explained, and may be related to the relative low diversity of the Rügen assemblages in the Caradoc. Nonetheless, the diagram shows that a marked change in palaeobiogeographical affinity of the Rügen microplankton communities took place between the Llanvirn and the Caradoc, with increased loss of Gondwanan affinity. In fact, the most important feature of the diagram is the high level of dissimilarity between Rügen and Gondwana, indicating that during the Caradoc, the two areas had become widely differentiated from a palaeobiogeographical point of view. This strong palaeobiogeographic differentiation can possibly be explained by the widening of the Rheic Ocean between the northern margin of Gondwana and Avalonia. Evidently, during Caradoc time, the Rheic Ocean was wide enough to act as an effective barrier to microphytoplankton exchanges between Gondwana and Avalonia. This is also in general agreement with the Caradoc plate tectonic configuration proposed by Scotese and McKerrow (1991). Unfortunately, no Caradoc chitinozoans are present in the G 14 borehole for comparison.

6.1.4. Latest Caradoc–middle Ashgill

The dendrogram obtained for this interval (Fig. 5e) is essentially similar to the two previous ones, but a direct comparison between the chitinozoans from the G-14 borehole and the other Rügen section (K 5) is here possible, although the K 5 assemblage is rather undiversified and the age somewhat poorly constrained. The latest Caradoc–middle Ashgill Rügen and G 14 chitinozoans have a high level of similarity, and are grouped in a first-order cluster. Similarly to the previous case, the Rügen assemblages (now including G 14) appear more similar to Laurentian rather than Gondwanan assemblages, in accord with accepted palaeogeographic reconstructions (e.g. Torsvik et al., 1996).

6.1.5. Llandovery

The dendrogram for the Early Silurian (Fig. 5f) clearly demonstrates a major biogeographical separation between Gondwana and the cluster G 14–Baltica–Laurentia. This can be explained by an

Early Silurian closure of the Iapetus Ocean and by the southerly position of Gondwana with respect to Laurentia–Baltica during this period of geological time (e.g. Scotese and McKerrow, 1990; Berthelsen, 1992).

6.1.6. Palaeobiogeographical implications of the cluster analysis

The present results show that in the study area chitinozoan bioprovincialism reached its maximum during the Llanvirn, when it is not only possible to discriminate among Baltica, Laurentia, and Gondwana affinities, but also to differentiate between Gondwanan and possibly Avalonian chitinozoan bioprovinces. The chitinozoan assemblage reported by Jenkins (1967) from Shropshire, Welsh Borderland, was used as representative for Avalonia. This assemblage contains many newly described species which can be considered essentially of 'Gondwanan' affinity, with *Siphonochitina formosa* being the most important constituent. Other taxa, such as *Conochitina parviventer* and *Cyathochitina jenkinsi*, appear not to be typical components of Llanvirnian North Gondwanan chitinozoan assemblages (see Paris, 1990). However, some species frequently occurring in the Llanvirn of North Gondwanan, such as *Belonechitina robardeti* Paris, 1981, *Belonechitina punctata* Paris, 1981, and *Sagenachitina retifera* (Taugourdeau and de Jekhowsky, 1960) are absent in the contemporaneous Shropshire assemblage. It thus appears that during Llanvirn time, Avalonia is characterised by the species association *S. formosa–C. parviventer–C. jenkinsi*, which are also important constituents of Llanvirn strata in the Rügen area.

The marked Llanvirn biogeographical differentiation of chitinozoan fauna is a well established notion (e.g. Miller, 1996), and the present results certainly corroborates this view.

Although the chitinozoan bioprovinciality appears to slightly lessen since the early Caradoc, our study shows that during this time there are still some differences between Baltic and Gondwanan chitinozoan endemic associations. In particular, *Lagenochitina ponceti* Rauscher, 1973, *Lagenochitina deunffi* Paris in Henry et al., 1977, and *Linochitina mayensis* Rauscher, 1970 are only reported from North Gondwana in early Caradoc time. A weakening of chitinozoan provincialism due to communications between Baltica and parts of Gondwana during the Caradoc was hypothesised by Miller (1996, p. 319); but our results seem to show that Caradoc provincialism among chitinozoans might be higher than previously thought.

6.2. Acritarchs

Palaeobiogeographical data for acritarchs is by no means comprehensive, especially for post-Llanvirnian time, when apparently the acritarch floras from world-wide localities are of essentially similar composition (Le Hérissé, in Molyneux et al., 1996; Wicander et al., 1999). This might actually result from the fact that Caradoc acritarchs have been described from only a few localities (mainly from North America and parts of Baltica), and there are basically no reports of proved Caradoc acritarchs from North African localities.

The present results confirm the existence of a high degree of biogeographic differentiation during Llanvirn times (Fig. 6), when it is certainly possible to discriminate between Baltic-type and Gondwana-type assemblages, and to a lesser degree, between Gondwana-type and Laurentia-type assemblages. The striking affinity of the Rügen acritarch assemblages with typical Perigondwana microphytoplankton, as indicated by the high CS values, supports inclusion of the Lower Palaeozoic of Rügen within the Avalonia terrane as earlier suggested by Servais (1994). To attempt an explanation for such a marked acritarch (and chitinozoan) bioprovincialism in the Llanvirn is beyond the scope of the present paper, but the very low CS values between Avalonia–Gondwana, and Baltica–North America may imply that an oceanic circulatory effect was superimposed on the palaeolatitudinal control on microplankton dispersal (cf. Tongiorgi et al., 1995). In addition, one should still consider the possibility that the calculations of the CS are at least partially affected by biasing effects resulting from incomplete descriptions of acritarch assemblages, inconsistent taxonomic approaches, and unreliable stratigraphic data.

6.3. Implications for the geodynamic evolution of the north-east German Basin–Baltica borderland

The cluster analysis shows that chitinozoan assemblages from the south-western border of the Baltic Platform (i.e. G 14 borehole) and from Avalonia (K 5 borehole) are essentially similar in Ashgill time, indicating that any restrictive barrier to microplankton faunal exchanges between Avalonia and Baltica was removed by then. Although it is not possible to quantify the degree of oceanic separation on the basis of fossil affinity alone, we can assume the middle–late Caradoc as a lower age-limit for the time of the Avalonia–Baltica collision.

Sediments of middle or late Caradoc, and possibly early Ashgill age are recognised for the first time in the K 5 borehole, and no younger ages are known from the lower Palaeozoic of the Rügen area south of the Thor Suture. The presence of reworked acritarchs of Llanvirn age and Perigondwanan affinity in the Ashgill stratal sequences of the south-western border of the Baltic Platform (Samuelsson et al., 2001) proves that erosion of an uplifted area was taking place during latest Ordovician time (more precisely: Cautleyan to Rawtheyan, middle Ashgill; Samuelsson et al., 2001).

On the basis of sediment provenance studies (Vecoli et al., 1999b) the latter uplifted area could be identified as part of the so-called 'Danish–North German–Polish Caledonides' which formed on the northern edge of Avalonia (Berthelsen, 1992; Dallmeyer et al., 1999) as a response to the collision with Baltica. Accordingly, we can constrain the timing of closure of the Tornquist Ocean and consequent Avalonia–Baltica collision to have taken place in an interval within the middle Caradoc up to the Rawtheyan. This age interval (equivalent to approximately 10 Ma in terms of absolute time; chronological ages from Cooper, 1999), was sufficient for the development of the 'Danish–North German–Polish Caledonides' orogen and its partial erosion. During the same age-interval, a foreland basin formed in front of the orogen, on the south-western border of the Baltic Platform.

The above collisional scenario between a relatively small palaeocontinental mass (Avalonia) and a much bigger palaeocontinent such as Baltica, can be compared to present day situations such as those of Taiwan and New Zealand, where narrow mountain belts (50–200 km wide) are formed, and where residence time of material within the belt may be only 1 to 10 Ma (Harrison, 1994). Our results also support the previous McKerrow and Cocks (1986) hypothesis that the Tornquist Ocean closed in the Ashgill. New palaeomagnetic and ^{40}Ar/^{39}Ar data from southern Baltica also favour this interpretation (Eide and Torsvik, 2000).

7. Palaeontological notes

In this section, the biostratigraphically most important and/or the most common chitinozoan species occurring in the H 2 and K 5 boreholes are briefly discussed.

Morphological terminology and generic classification are in accordance with the recommendations in Paris et al. (1999). We have followed the recommendations for open nomenclature given by Bengtson (1988). For synonymy lists, we refer to Paris (1981) and Sutherland (1994). Summaries of species occurrences and quantitative abundance values are given in Figs. 3 and 4, respectively.

Group CHITINOZOA Eisenack, 1931 (*incertae sedis*)
Order Operculatifera Eisenack, 1931
Family Desmochitinidae Eisenack, 1931 emend. Paris, 1981
Subfamily Eisenackitininae Paris, 1981
Genus *Eisenackitina* Jansonius, 1964 restrict. Paris, 1981

Eisenackitina aff. *lagenomorpha* (Eisenack, 1931)
(Plate II, 2, 4, 8, 9, 10, 11)

Biometry: Average obtained from samples K5-4004.5, K5-4007.5, K5-4010.5, K5-4013.0, K5-4095.1 and K5-4096.5: $L = 103$ μm, range 73–145 μm, $N = 60$, SD = 15.0; $D_p = 75$ μm, range 56–98 μm, $N = 62$, SD = 9.7; $D_c = 49$ μm, range 35–69 μm, $N = 62$, SD = 8.0; $L_p = 68$ μm, range 47–100 μm, $N = 54$, SD = 11.9.

Remarks: The present specimens show a wide range of morphological variability. Their preservation is generally poor apart from a single well-preserved specimen (Plate II, 9). They all possess a wide flat base and a granular/spiny ornament irregularly distributed over the entire vesicle; part of them are relatively small, originally cylindro-conical to ovoid, with a more or less developed neck. The numerous specimens observed can be subdivided in two groups characterized, respectively, by a more or less elongated vesicle. An example of the more elongated form is the specimen illustrated in Plate II, 2. Both varieties are kept in open nomenclature because of their much earlier appearance in the fossil record than previously reported for *E. lagenomorpha*; the present population might thus represent a new species. Rare smooth varieties (Plate II, 8), showing shape and dimensions consistent with those of *E. lagenomorpha*, are considered cospecific with the present species. Sutherland (1994) attributed specimens similar to the shorter type to *E. lagenomorpha*?, and those of the more elongated type to *E. lagenomorpha*. The shorter among the present forms are also similar to specimens of *E. lagenomorpha* recovered by Laufeld (1974) from the Silurian of Gotland, Sweden.

Stratigraphic range: Sutherland (1994) reported a Ludlow to Pridoli (Silurian) age for *E. lagenomorpha*. The present specimens co-occur with *Belonechitina robusta*, and a middle to late Caradoc age is therefore plausible.

Order Prosomatifera Eisenack, 1972
Family Conochitinidae Eisenack, 1931 emend. Paris, 1981
Subfamily Conochitininae Paris, 1981
Genus *Conochitina* Eisenack, 1931 emend. Paris, Grahn, Nestor and Lakova, 1999

Conochitina parviventer Jenkins, 1967
(Plate I, 4, 5)

Biometry: Average obtained from samples H2-3282.5 and H2-3283.0: $L = 191$ μm, range 140–255 μm, $N = 4$, SD = 49.3; $D_{\mathrm{p}} = 65$ μm, range 13–50 μm, $N = 13$, SD = 12.0; $D_{\mathrm{c}} = 33$ μm, range 26–47 μm, $N = 8$, SD = 6.3; $L_{\mathrm{p}} = 84$ μm, range 50–125 μm, $N = 8$, SD = 25.6.

Remarks: In the Rügen material, as well as in the type-area (Jenkins, 1967), the present species invariably co-occurs with *Siphonochitina formosa* Jenkins. Although morphologically similar to *Conochitina pseudocarinata* Paris 1981, *C. parviventer* is potentially a good biostratigraphic marker for the *S. formosa* Biozone in the Rügen area.

Stratigraphic range: According to Jenkins (1967), the species is known from the Abereiddian (lower Llanvirn) to the Aurelucian (lower Caradoc). In the study area, *C. parviventer* is an important constituent of chitinozoan assemblages attributed to the *Siphonochitina formosa* Biozone (Samuelsson et al., 2000; Samuelsson and Servais, 2001).

Subfamily Eremochitininae Paris, 1981
Genus *Siphonochitina* Jenkins, 1967

Siphonochitina formosa Jenkins, 1967
(Plate I, 1–3)

Biometry: Average obtained from sample H2-3283.0: $L = 200$ μm, range 162–238 μm, $N = 2$, SD = 53.7; $D_{\mathrm{p}} = 46$ μm, range 40–60 μm, $N = 6$, SD = 7.2; $D_{\mathrm{c}} = 29$ μm, range 17–40 μm, $N = 5$, SD = 9.0; $L_{\mathrm{p}} = 83$ μm, range 63–125 μm, $N = 4$, SD = 28.5; $L_{\mathrm{siphon}} = 51$ μm, range 27–74 μm, $N = 3$, SD = 23.5.

Remarks: None of the present specimens show the elongated membranous bulb, which together with the drawn-out conical chamber, represents the primary characteristic of *Siphonochitina formosa* Jenkins. The recorded specimens appear instead morphologically closer to *Siphonochitina tenuicollis* Jenkins, 1967, which was considered a junior synonym of *S. formosa* by Paris (1981). We accept Paris' (1981) interpretation, and consider our badly preserved specimens conspecific with *S. formosa*. A single specimen (Plate I, 2) is very similar to *Laufeldochitina clavata* (Jenkins, 1967). According to the species description, the latter should have its maximum diameter close to the base; our specimen has its maximum diameter at approximately 1/3 of the chamber length from the base. We therefore also regard this specimen as a poorly preserved *S. formosa*.

Stratigraphic range: According to Paris (1990), *S. formosa* is an excellent marker for the lower Abereiddian (lower Llanvirn) *Didymograptus artus* graptolite Zone. However, similar forms, although untypical (Paris, pers. comm.), were reported from the lower Hanadir Member of the Qasim Formation, Saudi Arabia, in co-occurrence with the graptolite *Didymograptus murchisoni* (Al-Hajri, 1995). Accordingly, the stratigraphic range of *S. formosa* might extend to embrace the entire Abbereiddian. In the *S. formosa*-yielding strata of the Binz 1/73 drillcore, Maletz (1998) identified graptolites belonging to the

PLATE I
SEM photographs of selected chitinozoans from the H2 Oderinne well, east of Rügen Island, northern Germany.

1. *Siphonochitina formosa* Jenkins, 1967. Sample H2-3283.0 × 460.
2. *Siphonochitina formosa* Jenkins, 1967. Sample H2-3283.0 × 440.
3. *Siphonochitina formosa* Jenkins, 1967. Sample H2-3283.0 × 570.
4. *Conochitina parviventer* Jenkins, 1967. Sample H2-3282.5 × 340.
5. *Conochitina parviventer* Jenkins, 1967. Sample H2-3283.0 × 440.
6. *Cyathochitina jenkinsi* Neville, 1974. Sample H2-3282.5 × 200.
7. *Cyathochitina* cf. *varennensis* Paris, 1981. Sample H2-3282.5 × 410.

Pterograptus elegans graptolite Zone, indicating a late middle Abereiddian age.

Subfamily Tanuchitininae Paris, 1981
Genus *Tanuchitina* Jansonius, 1964 emend. Paris, Grahn, Nestor and Lakova, 1999

Tanuchitina cf. *bergstroemi* (Laufeld, 1967)
(Plate II, 7)

Biometry: Average obtained from sample K5-4112.0: $D_p = 81$ μm, range 65–97 μm, $N = 5$, SD = 14.4; length of carina measured on one specimen: 10 μm.
Remarks: Biometry and overall appearance of the recorded specimens appear consistent with the original description of *Tanuchitina bergstroemi*; however, because of scarce and poorly preserved material, we prefer to adopt an open nomenclature.
Stratigraphic range: In Baltoscandia, *T. bergstroemi* is an important index species for the upper Vormsi and lower Pirgu stages (corresponding to the Pusgillian, early Ashgill, in terms of the British Standard). The species also occurs in the latest Caradoc to the earliest Ashgill of the Brabant Massif, which is part of the palaeocontinent Avalonia (Van Grootel et al., 1997; Samuelsson and Verniers, 2000).

Subfamily Belonechitininae Paris, 1981
Genus *Belonechitina* Jansonius, 1964

Belonechitina micracantha (Eisenack, 1931)
(Plate II, 5)

Biometry: Average obtained from samples K5-4007.5, K5-4013.0, K5-4095.1, K5-4096.5, K5-4099.0 and K5-4112.0: $L = 137$ μm, range 87–190 μm, $N = 41$, SD = 21.3; $D_p = 72$ μm, range 53–100 μm, $N = 40$, SD = 10.1; $D_c = 46$ μm, range 33–65 μm, $N = 41$, SD = 6.9; $L_p = 89$ μm, range 46–125 μm, $N = 36$, SD = 18.2.
Remarks: A large number of specimens from the H 2 and K 5 boreholes, as well as from other Ordovician sections of the Rügen area (Samuelsson et al., 2000; Samuelsson and Servais, 2001) belong to the genus *Belonechitina*. Based on their variable vesicle shape, simple spines, and constriction above the basal margin, they can be attributed to *B. micracantha*. However, *B. micracantha* is ambiguously defined, and allow for large morphological variability. For this reason, Grahn et al. (1994) argued that, in Baltoscandia, more than one chitinozoan species is probably represented within *B. micracantha*. This also seems to be the case with the present specimens. Some poorly preserved specimens placed in *B. micracantha* could as well be attributed to *B.* cf. *wesenbergensis* or *B.* cf. *robusta*. The present material, abundant but poorly preserved, is clearly not suitable for taxonomic reassessment of *B. micracantha*.
Stratigraphic range: In Baltoscandia, *B. micracantha* ranges from the upper Volkhov to the uppermost Pirgu (Whitlandian, middle Arenig to Rawtheyan, upper Ashgill; Nõlvak and Grahn, 1993). The species ranges from the middle Arenig to the lower Llanvirn in North Gondwana (Paris, 1981).

Belonechitina robusta (Eisenack, 1959)
(Plate II, 1, 3)

Biometry: A single specimen in sample K5-4007.5 (Plate II, 1, 3): $L > 155$ μm (incomplete); $D_p = 70$ μm; $D_c < 40$ μm; $L_p = 135$ μm.
Remarks: Following Paris (1979), only those specimens that clearly show a rounded margin and multi-rooted, rather than λ-shaped, spine bases have been attributed to *Belonechitina robusta*. Some fragmented specimens showing the characteristic multi-rooted spines were grouped under *Belonechitina* cf. *robusta*.
Stratigraphic range: Nõlvak and Grahn (1993) reported *B. robusta* from the upper Idavere to the lower Nabala Baltoscandian stages (equivalent to, respectively, lower Burrellian, middle Caradoc, and upper Streffordian, upper Caradoc). According to Paris (1990), the species has a slightly narrower stratigraphic range in North Gondwana, occurring only since the late Burrellian.

Belonechitina cf. *wesenbergensis* (Eisenack, 1959)
(Plate II, 6)

Biometry: Average obtained from samples K5-4007.5 and K5-4096.5: $L = 148$ μm, range 115–185 μm, N = 4, SD = 34.5; $D_p = 65$ μm, range 53–80 μm, $N = 4$, SD = 12.1; $D_c = 44$ μm, range 36–55 μm, $N = 4$, SD = 8.2; $L_p = 102$ μm, range 82–125 μm, N = 4, SD = 21.0.
Remarks: Only those specimens with a distinct neck

PLATE II

and a clearly recognisable fringed aperture have been placed in this species. In the original description of *Conochitina micracantha wesenbergensis* (Eisenack, 1959), parallel flanks are also regarded as an important taxonomic feature, but only rarely do the present specimens show this morphological character. The present specimens might represent a new species, recovered also in the Rügen 5/66 borehole (Samuelsson et al., 2000), but are too scarce to allow for its formal establishment. Grahn et al. (1994) hypothesised that several species are grouped together in the current conception of *B. wesenbergensis*.

Stratigraphic range: B. wesenbergensis ranges from the Abereiddian, lower Llanvirn to the Ashgill (Grahn and Bergström, 1984), although Grahn (pers. comm.) points out that typical *B. wesenbergensis* do not occur until the Caradoc. Specimens comparable to the present are recovered from the borehole Rügen 5/66, in intervals independently dated by graptolites to the Llandeilan, upper Llanvirn and Aurelucian, lower Caradoc (Samuelsson et al., 2000; Maletz, 1998). Other specimens similar to the ones described herein occur in the *Siphonochitina formosa* Biozone of the well Binz 1/73 in the Rügen area (Samuelsson et al., 2000).

Family Lagenochitininae Eisenack, 1931 emend. Paris, 1981
Subfamily Lagenochitininae Paris, 1981
Genus *Lagenochitina* Eisenack, 1931 emend. Paris, Grahn, Nestor and Lakova, 1999

Lagenochitina cf. *cybaea* (Umnova, 1969)

Biometry: One specimen from sample H2-3282.5: $L = 152\ \mu m$; $D_p = 65\ \mu m$; $D_c = 41\ \mu m$; $L_p = 95\ \mu m$.

Remarks: Specimens of *Lagenochitina* cf. *cybaea* (Umnova) identical to the present one also occur in the Lohme 2/70 borehole (Samuelsson and Servais, 2001). Umnova's (1969) description and illustrations of *L. cybaea* are rather poor, and without access to the type-material, confident attribution of the present specimen to *L. cybaea* appears impossible. Therefore, we prefer to place this specimen in open nomenclature.

Stratigraphic range: Umnova (1969) reported *L. cybaea* from upper Arenig through upper Llanvirn levels of the Rybinskaya borehole, Kalinin Province, Russia. In the Rügen area, the species is an important constituent of the *Siphonochitina formosa* Biozone in the Lohme 2/70 borehole (Samuelsson and Servais, 2001).

Subfamily Cyathochitininae Paris, 1981
Genus *Cyathochitina* Eisenack, 1955 emend. Paris, Grahn, Nestor and Lakova, 1999

Cyathochitina campanulaeformis (Eisenack, 1931)

Biometry: Average obtained from samples H2-3276.4 and H2-3278.5: $L = 184\ \mu m$, range 113–250 μm, $N = 14$, SD = 43.1; $D_p = 93\ \mu m$, range 75–115 μm, $N = 15$, SD = 12.0; $D_c = 53\ \mu m$, range 42–64 μm, $N = 13$, SD = 7.1; $L_p = 114\ \mu m$, range 80–175 μm, $N = 15$, SD = 26.0.

PLATE II
SEM photographs of selected chitinozoans from the K5 Oderbank well, east of Rügen Island, northern Germany.

1. *Belonechitina robusta* (Eisenack, 1959). Sample K5-4007.5 × 400.
2. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Sample K5-4013.0 × 510.
3. *Belonechitina* cf. *robusta* (Eisenack, 1959). Detail of specimen of Fig. 1, showing detail of base with the typical λ- and multipodal spines. Sample K5-4007.5 × 2700.
4. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Detail of specimen of Fig. 2, showing detail of base with typical rounded, irregularly shaped granules, sometimes with multipode bases. Sample K5-4013.5 × 1430.
5. *Belonechitina micracantha* (Eisenack, 1931). Sample K5-4112.0 × 380.
6. *Belonechitina* cf. *wesenbergensis* (Eisenack, 1959). Sample K5-4096.5 × 370.
7. *Tanuchitina* cf. *bergstroemi* (Laufeld, 1967). Sample K5-4112.0 × 340.
8. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Sample K5-4095.1 × 440.
9. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Sample K5-4095.1 × 450.
10. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Sample K5-4095.1 × 520.
11. *Eisenackitina* aff. *lagenomorpha* (Eisenack, 1931). Sample K5-4095.1 × 450.

Remarks: These specimens have their maximum diameter at the margin; the relatively long neck is connected to the chamber by a more conspicuous flexure than in *Cyathochitina jenkinsi*.
Stratigraphic range: Known stratigraphic range of *C. campanulaeformis* in the Algerian Sahara is from lower Llanvirn (Paris, 1981) through upper Ashgill strata (Oulebsir and Paris, 1995). In Baltoscandia, *C. campanulaeformis* apparently occurs over a wider stratigraphic range, occurring from the Aseri local Stage (corresponding to the upper Abereiddian, middle Llanvirn) through lower Silurian (Grahn et al., 1994).

Cyathochitina jenkinsi Neville, 1974
(Plate I, 6)

Biometry: Average obtained from samples H2-3276.4, H2-3278.5 and H2-3282.5: $L = 191$ μm, range 133–330 μm, $N = 11$, SD = 53.2; $D_p =$ 91 μm, range 50–136 μm, $N = 20$, SD = 21.2; $D_c =$ 55 μm, range 30–85 μm, $N = 13$, SD. = 13.5; $L_p =$ 128 μm, range 75–190 μm, $N = 18$, SD = 29.6.
Remarks: Although morphologically variable, all the recorded specimens reach their maximum diameter at approximately one-third of the total length, measured from the base. The neck is short.
Stratigraphic range: The *C. jenkinsi* type-material (Neville, 1974) is of early Abereiddian, early Llanvirn age (Paris, 1981, p. 384). Oulebsir and Paris (1995) ascribed their local (Algerian Sahara) *C. jenkinsi* Biozone to the late early Llanvirn. Their *C. jenkinsi* Biozone falls between the *Siphonochitina formosa* and the *Armoricochitina armoricana* Biozones sensu Paris (1990).

Cyathochitina cf. *varennensis* (Paris, 1981)
(Plate I, 7)

Biometry: Measurements on two specimens recovered from sample H2-3282.5: $L = 150$ and 132 μm; $D_p =$ 75 and 70 μm; $D_c = 55$ and 46 μm; $L_p = 100$ and 95 μm.
Remarks: The two recorded specimens are significantly shorter than typical *Cyathochitina campanulaeformis* and *Cyathochitina jenkinsi*. They appear instead comparable to the holotype of *C. varennensis*, described by Paris (1981) from the lower part of the lower Llanvirn Pissot Formation, Domfront (Orne), Armorican Massif, France. However, the latter species has a more conspicuous carina and wider chamber than the present specimens, which we prefer to retain in open nomenclature.
Stratigraphic range: (*C. varennensis*). Lower Llanvirn (Paris, 1981).

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