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Ecole Doctorale 104 - Sciences de la Matière, du Rayonnement et de l'Environnement

Doctorat de l'Université de Lille 1

Paléontologie

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**Tester le potentiel d'un puissant outil stratigraphique, les
chitinozoaires, pour détecter le début de l'âge glaciaire du
Paléozoïque Inférieur durant l'Ordovicien Inférieur à
Moyen**

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Ph. D. of Lille 1 University

Palaeontology

Chloé AMBERG

**Testing the potential of a powerful stratigraphical
instrument, the chitinozoans, to track the start of an Early
Palaeozoic Ice age during the Early-Middle Ordovician.**

Ph. D. thesis directed by Thomas Servais and supervised by Thijs
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Taxonomic disclaimer:

This report is not deemed nor intended to be valid for publication for the naming of new taxa as stipulated in the article 8.2 of the International code of zoology, 4th edition, 2000, eds. W. D. Ride *et al.*

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I will start in English to thank the jury who kindly accepted to read my manuscript and come and judge my PhD defense, I am very grateful and almost feel like I added my little piece to the Ordovician puzzle!

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Abstract

The Ordovician (485-443 Ma) witnessed major changes in biodiversity including ‘the Great Ordovician Biodiversification Event’ (GOBE), but also the first of the “Big Five” mass extinction events, related to the End Ordovician glaciation. It was long thought to be a greenhouse period, with a short glaciation during the Hirnantian (c. 444 Ma) but recent evidence based on stable isotopes, sequence stratigraphy, plankton provinces and climate models, suggests that this global cooling and the onset of the “Early Palaeozoic Icehouse” may have started much earlier than previously assumed, during the Early-Middle Ordovician. However, each of these methods is inconclusive on its own.

The aim of this study is (1) to find additional evidence for pre-Hirnantian glaciations, focusing on the earliest of the suggested phases of cooling, i.e., in the Floian (early-middle Arenig), assumed to coincide with the onset of the GOBE, and (2) to test if we can apply chitinozoan micropaleontology as a proxy to detect climate variations during the Ordovician.

We first used palynology to test for the primary nature of Ordovician limestone-mudstone alternations in the Oslo-Asker area, the oldest one of these of Arenig age, but could not exclude a potential diagenetic origin for these deposits. Secondly, we built a chitinozoan-biostratigraphic framework for the type Arenig in Wales to get a better understanding about the spatial distribution of key taxa through the interval; comparing the Tremadoc to the Arenig, an increased provincialism was observed across the globe. Thirdly, new chitinozoan data from the near field in Morocco serve to constrain an erosional event potentially related to glacioeustasy.

Résumé:

L’Ordovicien (485-443 Ma) a été témoin de changement majeurs au niveau de la biodiversité marine, tel que la « Grande Biodiversification Ordovicienne » (GOBE), mais aussi la première des cinq grande extinctions de masse lié à la glaciation de l’Hirnantien (env. 444 Ma), mais de nouvelles évidence tel que des isotopes stables, la stratigraphie séquentielle, les provinces planctoniques et les modélisations climatiques suggèrent que ce refroidissement global aurait commencé bien plus tôt que ce que l’on pensait, pendant l’Ordovicien Inférieur-Moyen. Mais ces études ne sont pas concluantes par elles-mêmes.

Le but de cette étude est donc (1) de trouver des preuves supplémentaires d’une période glaciaire pré-Hirnantienne, en se concentrant sur la période la plus ancienne suggérée c.à.d. le Floien (Arenig inférieur-moyen), supposé coïncider avec le début de la GOBE, et (2) tester si les chitinozoaires peuvent être utilisé comme outil pour détecter les variations climatique de l’Ordovicien. Nous avons d’abord utilisé les chitinozoaires pour déterminer la nature d’alternances marno-calcaires de l’Ordovicien dans la région d’Oslo Asker, la plus vieille formation étudiée étant d’âge Arenig tardif, mais nous n’avons pas pu exclure une origine potentiellement diagénétique de ces dépôts. Deuxièmement, une biostratigraphie des chitinozoaires a été établie pour l’Arenig type au Pays de Galles pour observer la répartition spatiale des espèces-clés. En comparant le Trémadoc à l’Arenig, une augmentation du provincialisme est observée. Troisièmement, de nouvelles données palynologique nous permettent de dater des incisions potentiellement liée à des événements glaciaire au Maroc.

Contents

1. Introduction	17
1.1 The Ordovician System	18
1.1.1 History of research	18
1.1.2 Palaeogeography	20
1.1.3 Biodiversity and extinctions	22
1.2 The Ordovician climate, proxies and application	25
1.2.1 Stable isotope proxy data	27
1.2.2 Physical and sequence stratigraphy	32
1.2.3 Plankton provinces	34
1.2.4 General Circulation Models	35
2. Aim of the project	36
2.1 Research questions	37
2.2 Objectives	38
2.3 Implementation and methods	40
2.3.1 The nature of Ordovician limestone-mudstone alternations in the Oslo-Asker area (Norway): primary or diagenetic rhythms?	41
2.3.2 Chitinozoan biostratigraphy and carbon isotope stratigraphy from the Upper Ordovician Skogerholmen Formation in the Oslo Region. A new perspective for the Hirnantian lower boundary in Baltica.	41
2.3.3 Chitinozoan biostratigraphy of the historical Arenig series in Wales (Early-Middle Ordovician)	42
2.3.4 Description of Arenig fauna in the Lake District, Northern England	43
2.3.5 Description of Arenig fauna in the Anti-Atlas, Morocco	43
3. The nature of Ordovician limestone-marl alternations in the Oslo-Asker District(Norway): witnesses of primary glacio-eustasy or diagenetic rhythms?	47
3.1 Supplementary information	61
4. Chitinozoan biostratigraphy and carbon isotope stratigraphy from the Upper Ordovician Skogerholmen Formation in the Oslo Region. A new perspective for the Hirnantian lower boundary in Baltica.	69
4.2 Introduction	71
4.3 Material and methods	73
4.4 Existing stratigraphic framework	74
4.5 Results	75
4.5.1 Biostratigraphy	75
4.5.2 Description of selected species	76
4.5.2.1 <i>Belonechitina gamachiana</i>	76
4.5.2.2 <i>Spinachitina</i> cf. <i>taugourdeau</i>	76

4.5.3	Carbon isotopes	77
4.6	Discussion	77
4.7	Conclusion.....	79
4.8	References :	80
4.9	Figures.....	87
5.	Chitinozoan biostratigraphy of the historical Arenig series in Wales (Lower-Middle Ordovician).	94
5.1	Introduction	96
5.2	Geological overview.....	97
5.2.1	Carmarthen area	98
5.2.1.1	<i>Lithology and sampling</i>	98
5.2.1.2	<i>Fauna and age</i>	98
5.2.2	Whitland area	99
5.2.2.1	<i>Lithology and sampling</i>	99
5.2.2.2	<i>Fauna and age</i>	99
5.2.3	Arenig Fawr area	100
5.2.3.1	<i>Lithology and sampling</i>	100
5.2.3.2	<i>Fauna and age</i>	100
5.3	Results	101
5.3.1	Carmarthen area (Fig. 6).....	101
5.3.2	Whitland area (Fig. 7)	101
5.3.3	Arenig Fawr area (Fig. 8).....	102
5.4	Chitinozoan assemblages and their correlation	102
5.4.1	Assemblage 1	103
5.4.2	Assemblage 2	104
5.4.3	Assemblage 3	105
5.4.4	Assemblage 4	107
5.5	Discussion and palaeogeography	108
5.6	Conclusion.....	109
5.7	References:	109
5.8	Figures.....	117
6.	Chitinozoans from the Tremadocian/Floian boundary (Lower Ordovician) of the Watch Hill Formation, Lake District (Northern England)	129
6.1	Introduction	130
6.2	Material and methods	131
6.3	Results	132

6.4	Taxonomic notes	133
6.5	Stratigraphic discussion.....	133
6.6	Conclusions	135
6.7	References:	135
6.8	Figures.....	138
7.	Description of chitinozoan assemblages from Arenig formations in the Anti-Atlas, Morocco	141
7.1	Geological setting.....	144
7.2	Studied areas and sampling	145
7.3	Description of the assemblages and correlation	145
1.2.5	Jbel Signit Nord.....	145
1.2.6	Meteorite Hotel.....	147
7.4	Conclusions	148
7.5	References:.....	155
8.	General discussion and perspectives.....	158
9.	Conclusions	164
10.	References introduction and conclusion:	167

Résumé étendu en français :

L'Ordovicien (485-443 Ma) est une période très importante et intéressante dans l'histoire de la vie; Il a connu des changements majeurs de la biodiversité avec le plus grand rayonnement de la vie marine, la « Grande Biodiversification Ordovicienne », mais aussi le premier des cinq grands événements d'extinction de masse du Phanérozoïque, associé à la glaciation de l'Ordovicien terminal. On a longtemps pensé que l'Ordovicien était une période à effet de serre, avec une courte glaciation pendant l'âge Hirnantien (c. 444 Ma), mais de nouvelles preuves suggèrent maintenant que ce refroidissement global et le début de l' "Age Glaciaire du Paléozoïque" (EPI) a peut-être commencé beaucoup plus tôt que ce que l'on pensait précédemment, à savoir au début du Katian, avant la Sandbien ou même pendant l'Ordovicien Inférieur-Moyen.

Un certain nombre d'études examine les variations climatiques au cours de l'Ordovicien en utilisant différents outils tels que (1) Les isotopes stables du carbone et de l'oxygène: les données de $\delta^{13}\text{C}$ indiquent une importante excursion isotopique du carbone à l'Ordovicien final, l'Excursion d'Isotope de Carbone de l'Hirnantien, qui est considéré comme un événement isochrone global et un outil de corrélation utile pour l'Hirnantien mais aussi pour tenter de déterminer les variations climatiques antérieures. Plusieurs excursions de moindre amplitude ont été enregistrées dans le Katian, le Sandbien et Darriwilien. Les données $\delta^{18}\text{O}$ dérivées d'apatite de conodontes situés à des paléolatitudes équatoriales suggèrent que les températures de surface de la mer aux tropiques a refroidi au cours de L'Ordovicien Inférieur-Moyen, pour se stabiliser proche des valeurs modernes pendant la Floien; (2) La stratigraphie séquentielle: Plusieurs sections ont été étudiées, telles que la Formation Peninsula en Afrique du Sud, qui expose des strates allant du Floien au Darriwilien, les formations Darriwiliennes de Hiswah et Dubaydib en Jordanie et la Formation Postolonnec en France, datée du Darriwilien et ont été interprétées comme contenant des changements du niveau marin du 3ème et 4ème ordre correspondant à des cycles glacio-eustatiques; (3) La répartition des provinces planctoniques: Certains groupes de zooplancton fossile tels que les chitinozoaires ou les graptolites attestent d'un gradient faunistique relativement abrupt avec un changement rapide de province de l'équateur au pôle, suggérant que le refroidissement global vers le maximum glaciaire de l'Hirnantien était déjà en cours durant le Sandbien; et (4) Les modèles de circulation générale pour l'Ordovicien Inférieur-Moyen qui suggèrent aussi une longue période de refroidissement durant l'Ordovicien.

Cependant, aucune de ces méthodes n'est concluante en elle-même: La signification exacte des excursions d'isotopes de carbone n'est pas encore totalement comprise, mais elles sont toutefois reconnues pour représenter des changements importants dans le cycle du carbone et la chimie des océans. De plus, il n'y a pas de courbes $\delta^{13}\text{C}$ globale et continues pour chaque paléocontinent, car il n'y a pas de section continue exposant l'Ordovicien en entier. En outre, des données paléoclimatiques évoquées plus haut sont souvent limitées aux faibles paléolatitudes et donc peuvent ne pas refléter l'enregistrement du climat global. Les variations du niveau marin durant l'Ordovicien sont difficiles à quantifier et sont sujets à des interprétations de faciès relativement complexes et des problèmes de datations se posent

souvent. Les études biogéographiques de graptolites et de chitinozoaires, bien que potentiellement concluante pour l'Ordovicien Supérieur, n'ont pas encore été réalisées pour l'Ordovicien Inférieur et Moyen. En outre, la mesure dans laquelle les résultats obtenus avec les modèles de circulation générale se rapprochent de la réalité des paléoclimats est limitée par la précision avec laquelle nous pouvons quantifier les paramètres déterminant des modèles pour des temps aussi anciens.

Le but de cette étude est donc de trouver des preuves supplémentaires de glaciations pré-Hirnantien, en se concentrant sur la première des phases proposées de refroidissement, à savoir, dans le Floien (Arénig-Darriwilien) qui est supposé coïncider avec le début de la « Grande Biodiversification Ordovicienne », mais aussi tester l'utilisation des assemblages de chitinozoaires comme outil pour détecter ces variations climatiques pendant l'Ordovicien Inférieur et Moyen. L'étude a suivi 3 objectifs: (1) Déterminer la nature d'alternances marno-calcaires ordoviciennes dans la région d'Oslo-Asker en Norvège présentes dans quatre sections du Darriwilien moyen au Katian supérieure. Ces rythmites sont interprétées comme correspondant à des événements de bas niveau marin et pourraient représenter des variations glacioeustatiques ou, alternativement, être le résultat de diagenèse différentiel; (2) Dater des incisions potentiellement d'âge Arénig au Maroc, région proximale d'une supposée calotte glaciaire, et les corrélérer avec le type zone Arenig du Pays de Galles, zone plus distale de cette supposée calotte glaciaire, et (3) Décrire les assemblages de chitinozoaires de type zone Arenig au Pays de Galles pour permettre une corrélation potentielle avec Gondwana et examiner la paléobiogéographie générale de cette intervalle de temps.

L'étude détaillée des assemblages de chitinozoaires de l'Ordovicien Inférieur et Moyen au Maroc, Pays de Galles, Angleterre et en Norvège, et de l'Ordovicien supérieur en Norvège, a amélioré notre compréhension de la biostratigraphie des chitinozoaires dans cet intervalle, et un cadre biostratigraphique a été établi permettant des corrélations entre Baltica et Laurentia d'une part, et Avalonia et Gondwana de l'autre. Malgré les informations accrues désormais disponibles auprès de la zone de type Arenig, il n'y a pas encore suffisamment de données pour déterminer l'influence des fluctuations climatiques sur les assemblages de chitinozoaires, ou provinces l'Ordovicien Inférieur à Moyen, à la fois à l'échelle globale, entre des zones séparées comme Gondwana, Avalonia et Baltica, comme à l'échelle plus locale comme cela a été tenté pour les rythmites Norvégiennes. Cependant, les nouvelles données biostratigraphiques obtenues au Maroc servent à dater un événement de forte érosion potentiellement glacioeustatique au Gondwana.

Pour conclure, ma contribution à la compréhension du système Ordovicien est la suivante: En ce qui concerne le potentiel des chitinozoaires pour suivre les variations climatiques et peut-être le début d'une période glaciaire Paléozoïque pendant l'Ordovicien Inférieur et Moyen, les résultats sont variables: En Norvège, les résultats ne sont pas concluants ; les assemblages de chitinozoaires du Darriwilien, Sandbien et Katian ne permettent pas de détecter des variations dans les rythmites qui pourraient être liés aux variations des températures de surface de l'océan et aux fluctuations climatiques. Une seule espèce dans le Sandbien supérieur montre une différence significative d'abondance dans les deux lithologies, étant plus abondant dans les marnes que dans les calcaires, mais cela ne suffit pas pour confirmer l'expression de

variations climatiques. Au Maroc, les résultats sont probants ; les assemblages de chitinozoaires récupérés dans les incisions indiquent clairement un événement de courte durée au milieu de l'Arénig qui est au moins régionale, et donc pourrait être lié à glacioeustasie. Toutefois, d'autres mécanismes expliquant la formation de ces incisions existent et l'hypothèse glaciogénique nécessite une confirmation supplémentaire avec l'analyse en cours des dépôts sédimentologique. Les quatre assemblages définis au Pays de Galles permettant une corrélation solide avec Gondwana, révèlent une faune similaires pour le Tremadoc supérieur et l'Arénig moyen-supérieur, mais certaines espèces clés présentes dans le domaine péri-Gondwanien font défaut au Pays de Galles. La nouvelle faune décrite permet également une interprétation paléobiogéographique, quoique limitée, lorsque l'on compare avec la faune de Gondwana, Baltica et Laurentia, montrant qu'un ensemble de données plus important est nécessaire pour une analyse complète.

1. Introduction

1.1 The Ordovician System

1.1.1 History of research

The Ordovician System was born from a compromise between two different interpretations of the strata overlying the – in modern usage - Cambrian and underlying the Silurian. The Cambrian has been studied by Cambridge University Professor Adam Sedgwick (1785-1873) in Wales and the Silurian rocks by the British Geological Survey director Roderick Murchison (1792-1871) in Shropshire and South Wales in a joint study (Sedgwick and Murchison, 1835). As their work advanced and the strata they studied started to overlap, they both claimed the appartenance of the strata to ‘their’ studied system (Fig. 1, Murchison, 1954; Sedgwick, 1955) and this eventually led to a stratigraphic dispute that was not resolved until after their deaths.

The British geologists remained divided until a solution was proposed by Charles Lapworth (1842-1920) in 1879 while he was still on an assistant-mastership in the Madras College, St Andrews, before he was appointed in 1881 as the new chair of Geology at Birmingham University. Lapworth’s proposal was to erect a separate system containing the controversial strata, the Ordovician, which according to him was clearly identifiable on the basis of its fossil contents. Three distinct Lower Palaeozoic fauna were already defined by Barrande (1852) in Bohemia from what he called the Silurian, the “Primordial Fauna”, roughly corresponding to the present day Middle and Upper Cambrian, the “Second Fauna” roughly corresponding to the present day Ordovician and the “Third Fauna” corresponding to the present day Silurian and Devonian (Fig. 1). The Ordovician eventually became a universally recognized system after ratification during the International Geological Congress in 1960. However confusion remained, as the base of the Ordovician in the Anglo-Welsh basin was defined by Lapworth at the base of the Arenigian rocks, therefore assigning the Tremadocian rocks to the Cambrian. The controversy of where to draw the Cambrian-Ordovician is well explained in Henningsmoen (1973) with all the historical arguments from the authors that attempt to define it. Williams *et al.* (1972) provided the first international correlation chart of the British and Irish Ordovician and proposed a subdivision of the Ordovician that did not include the Tremadoc. A working group on the Cambrian-Ordovician boundary was formed in 1974 by the International Commission on Stratigraphy (ICS) that eventually lead to the inclusion of the Tremadoc into the Ordovician, as part of a decision of the International Union of Geological Sciences (IUGS, Norford, 1988). In Fortey *et al.* (1991), six series were defined in the Anglo-Welsh basin, in ascending order, the recently added Tremadoc, the Arenig, the Llanvirn, the Caradoc and the Ashgill (Fig. 1, the four latter originally described in Williams *et al.*, 1972 and Whittington *et al.*, 1984) that remained the standard for chronostratigraphy for many years.

As the original definition of the series’ boundaries were often drawn at major unconformities and their type sections were dispersed over England and Wales, Fortey *et al.* (1991) tried to redefine the base of the series into continuous sequences and widespread fauna to identify stratotype to enable international correlation. A revision of these series’ boundaries was later

made by Fortey *et al.* (1995) as their series proposed in 1991 were not accepted and more precision on their definitions were asked, considering that the type localities that gave their name to the series did not fulfill the IUGS standards required for stratotype. A last revision of the Ordovician British series was made by Fortey *et al.* (2000) that still consider the historical sections in the Anglo-Welsh basin to be appropriate to define standard stratotypes for the Ordovician.

BRITAIN				BOHEMIA		
Sedgwick 1855	Murchison 1859		Lapworth 1879	Modern usage		Barrande 1852
				DEVONIAN		étages E, F, G & H (Third Fauna)
SILURIAN	UPPER SILURIAN	"Ludlow" "Wenlock" "Upper Llandovery"	SILURIAN Downtonian Salopian Valentian	SILURIAN	Pridoli Ludlow Wenlock Llandovery	
UPPER CAMBRIAN	"Caradoc" "Llandeilo"		ORDOVICIAN Caradoc Llandeilo Arenig	ORDOVICIAN	Ashgill Caradoc Llanvirn Arenig Tremadoc	étages D (Second Fauna)
MIDDLE CAMBRIAN	LOWER SILURIAN		↓ ?	CAMBRIAN	Upper Middle Lower	
LOWER CAMBRIAN (Longmyd)	CAMBRIAN (Longmyd)			CAMBRIAN		étages A & B (Azoic schists)
				PRECAMBRIAN		

Figure 1: The historical and modern subdivisions of the Early Palaeozoic, as proposed by the different authors (From Vandembroucke 2008, unpub. PhD thesis, modified after Webby (Fig. 1, 1998).

The Subcommittee on Ordovician Stratigraphy of the ICS was created in 1978 to establish a standard and international geochronological/chronostratigraphical framework because the inability to precisely correlate the British series elsewhere resulted in the establishment of the regional series on different continents that created confusion and lead to imprecise correlation (Webby 1998; Finney 2005). It led to the ratification by the ICS of new global stages, each defined by a Global Boundary Stratotype and Point (GSSP), in ascending order (Fig. 1): the Tremadocian (Cooper *et al.*, 2001), the Floian (Bergström *et al.*, 2004), the Dapingian (Wang *et al.*, 2005; Chen *et al.*, 2009), the Darriwilian (Mitchell *et al.*, 1997), the Sandbian (Bergström *et al.*, 2000), the Katian (Goldman *et al.*, 2007) and the Hirnantian (Chen *et al.*, 2006).

In this study, the names of the global series will be used except for the project in the type Arenig in the Anglo-Welsh basin where the British series will be used.

1.1.2 Palaeogeography

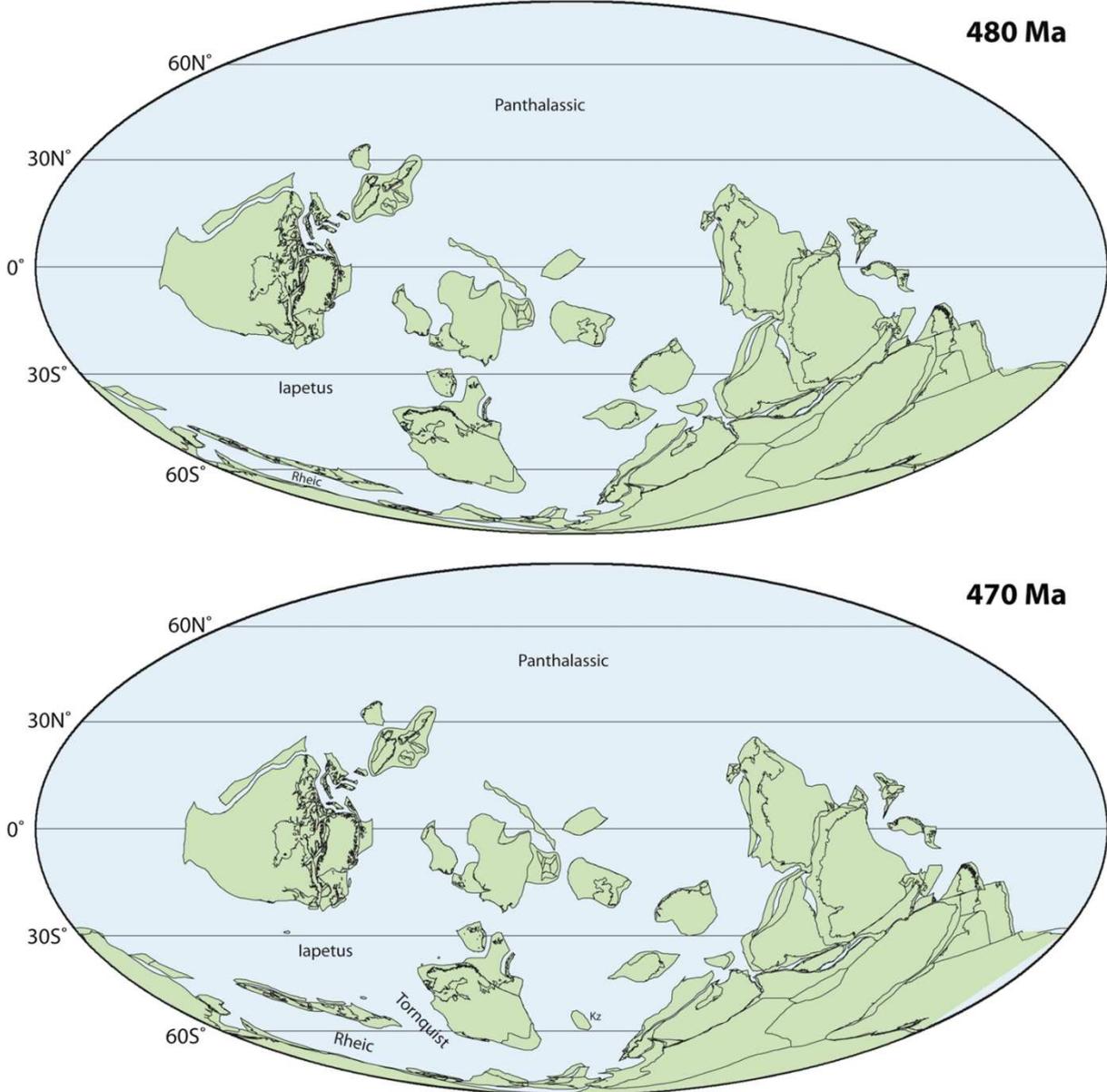
The Ordovician System was a period of major and increasing dispersion of the Palaeocontinents separated by wide oceans, resulting from the breakup of the Neoproterozoic super continent Rodinia. The first reconstructions of the palaeogeography were realized by Smith et al (1973) for the entire Phanerozoic and were almost exclusively based on palaeomagnetic data. Since then, refined studies for the Palaeozoic, combining paleontological, stratigraphical and tectonic evidence, were published, such as those of Scotese and McKerrow (1990) and many others followed (i.e. Harper et al., 1996; Torsvik, 1998; Cocks, 2001; Cocks and Torsvik, 2002, 2005, 2007, 2011; Torsvik and Cocks, 2004, 2005, 2009, 2011, 2013). Four major palaeocontinents were present: Gondwana, Laurentia, Baltica and Siberia and the microcontinent Avalonia. The location and displacements of the Palaeocontinents is shown in figure 2.

The Gondwana Palaeocontinent included the present day South America, Africa, Madagascar, Arabian Peninsula, India, Antarctica and Australasia (Torsvik and Cocks, 2013). It was the largest continent during the Lower Palaeozoic, until the Carboniferous. It extended across all southern-hemisphere paleolatitudes, from the South Pole in Africa to the equator in Australasia, and remained at high latitudes during most of the Lower Palaeozoic.

The Laurentia Palaeocontinent included the present day North America, Greenland and Scotland and occupied a relatively stable paleoequatorial position throughout the Ordovician. There were many peri-Gondwana and peri-Laurentia terranes including island complexes and microcontinents across the Iapetus Ocean and associated to Avalonia, the largest microcontinent, that were accreted to Laurentia during the Ordovician, and whose presence was neglected in the past (Harper, 1996). It grouped various present day areas, such as Cape Cod in Massachusetts, Newfoundland in Canada, southern Ireland, southern Britain (England and Wales), Belgium, northwestern Germany and part of Poland. It was first attached to Gondwana and separated from it during the Tremadocian. It started to drift towards Baltica, creating and opening the Rheic Ocean between Gondwana and Avalonia (Cocks and Fortey, 2009). The Tornquist Sea between Avalonia and Baltica therefore decreased in size as well as the Iapetus Ocean between Avalonia and Laurentia. Eventually Avalonia docked into Baltica near the end of the Ordovician ending its status of independent microcontinent.

The Baltica palaeocontinent comprised most of the present day Scandinavia, Eastern Europe and the Russian platform. It was first situated at middle-high palaeolatitudes (about 50 S°) during the Early-Middle Ordovician and moved to more temperate latitudes (about 40 S°) in the latest Darriwilian. Baltica underwent a significant counterclockwise rotation of 120° during the late Cambrian and Early Ordovician. Following its collision with Avalonia at the end of the Ordovician, the merged continents collided with Laurentia during the middle Silurian, which created the Caledonian orogenic belt.

The Ordovician was a tectonically very active period with drifting and colliding continents and terranes, spreading ridges, subduction zones, orogenic belts and island arcs. Therefore, explosive volcanism eruptions were common at that time, spreading ash deposits widely over the seafloor such as the Caradocian Kinnekulle K-bentonite in Sweden correlated to the Millbridge K-bentonite in the USA (Saltzman *et al*, 2003; Huff 2008; Sell and Samson, 2011). This dynamic Palaeogeography might have induced major changes in the ocean and atmosphere geochemistry during the Ordovician, which are thought to have triggered one of the major episodes of climate and biodiversity changes of the Phanerozoic (e. g. Servais et al., 2010).



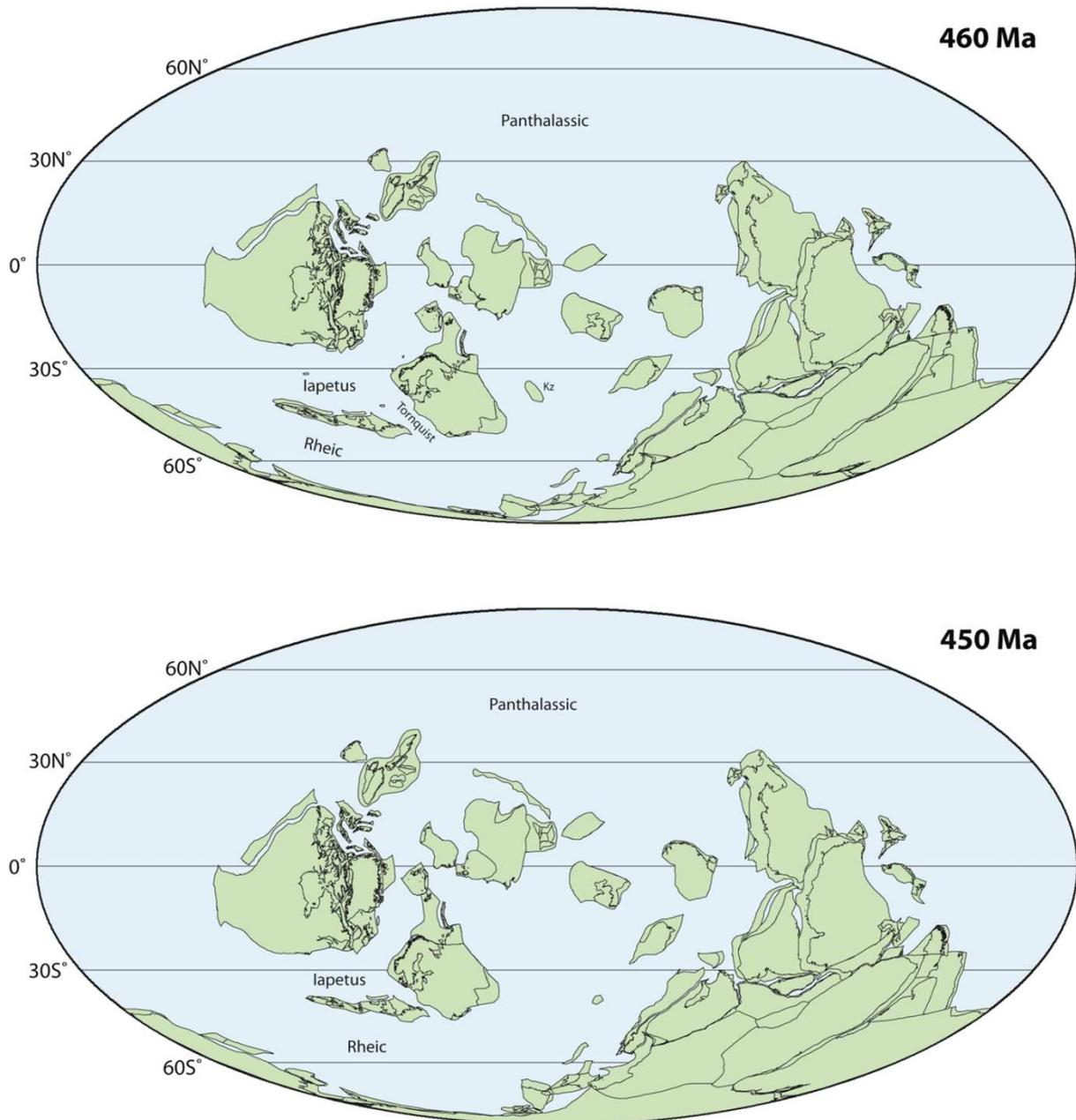


Figure 2: Palaeogeographical reconstructions of the Early Ordovician (Tremadocian, 480 Ma) Middle Ordovician (Dapingian, 470 Ma) and Late Ordovician (Sandbian, 460 Ma, Katian, 450 Ma), from Torsvik and Cocks (2013).

1.1.3 Biodiversity and extinctions

One of the more interesting and intriguing aspects of the Ordovician period is that it witnessed a major radiation of the marine life during the Early Middle Ordovician, but also one of the big five mass extinctions (Raup and Sepkoski, 1982) associated with an important glacial event, the Hirnantian glaciation at the end Ordovician. The Ordovician was long considered to be a super-greenhouse world interrupted only by a short glaciation at the end of the Period, during the Hirnantian (Brenchley *et al.*, 1994, 2003) and recorded high sea levels

sustaining this hypothesis, considered to be the highest of the whole Palaeozoic Era (Ross and Ross 1992; Nielsen 2004; Haq and Schutter, 2008). Nowadays, emerging evidence suggests that prolonged cooling must have preceded the end Ordovician glaciation and maybe fostered conditions for the establishment of the Great Ordovician Biodiversification Event (GOBE, i. e. Trotter *et al.*, 2008, Rasmussen *et al.*, 2016).

The Ordovician is the period that witnessed the greatest marine diversification on record. After the Cambrian Explosion, where most of the metazoan groups appeared and started to increase in diversity (Budd, 2008; Munnecke *et al.*, 2010), marine invertebrates truly diversified during the GOBE (Webby *et al.*, 2004; Harper 2006), giving rise to the Palaeozoic Evolutionary Fauna described by Sepkoski (1981, Figure 3). Those two events are sometimes considered to be one single evolutionary trend, but approximately 40-80 Myr separate the Cambrian Explosion and the GOBE, which is still challenging this 'single-event' hypothesis (Servais *et al.*, 2009, 2010).

Important changes in the ecological evolution occurred, characterized by the rise of the suspension feeders that started to occupy the water column (Figure 4) and the expansion of zooplankton (i. e. graptolites and chitinozoans). During the early Middle Ordovician, marine plankton biodiversity increased dramatically and these organisms started to colonize the planktonic realm (Trotter *et al.*, 2008); tiering strategies also (further) developed in the Palaeozoic Evolutionary Fauna, the development of hardgrounds permitted the encrustment of organisms and the seafloor became densely populated as the bioturbations in the sea floor, even in deep sea, became very common (Servais *et al.*, 2010). The high sea level associated with widespread epicontinental seas favored the colonization of the shelves by reefs, including a shift from the microbial-dominated reefs in the Early Ordovician to metazoan-dominated reefs in the Middle Ordovician.

This Early Palaeozoic radiation may have had various associated causes, such as the breakup of the super continent Rodinia, part of the super-continent cycle that is notoriously correlated to 1st order sea level movements and marine biodiversity: the periods with the presence of a supercontinent corresponds to lower diversity whereas maximal spreading of continents are associated to high diversity (Servais *et al.*, 2009). The Ordovician plate tectonic context would have produced widespread continents that promote a high degree of provincialism (Harper 2006), high sea levels and extended epicontinental seas, that in modern days also are biodiversity hotspots. The highest phytoplankton diversity was also observed during the GOBE. The diversity curves of the phytoplankton show a correlation with the diversification of the suspension feeders and zooplankton. The number of acritarch species started to increase during the Late Cambrian and reached its maximum diversity in the Darriwilian (Strother 1996, Mullins *et al.*, 2006, Servais *et al.*, 2004, 2008, 2009, 2010). It is thought to be related to high sea level and dispersed positions of the continents, but also to orogeny and the intense volcanic activity providing nutrients (Servais *et al.*, 2008). It is not proven whether the increasing diversity of phytoplankton can be related directly to bioproductivity, but it shows major changes in the trophic chain, which is why we also speak of plankton revolution (Servais *et al.*, 2010). The paleoclimate in the Early-Middle Ordovician, when the GOBE took place, was believed to be relatively stable, and despite of new evidence suggesting an

early cooling starting much before the end Ordovician glaciations (e. g. Trotter *et al.*, 2008), some authors believed that a warm climate may have favored the GOBE (Servais *et al.*, 2008). Extraterrestrial cause has also been invoked as many meteorites and craters are recorded in Baltica in the appropriate levels (Schmitz *et al.*, 2008).

Therefore the GOBE is seen as a revolution in the history of life that is due to a combination of factors from different origins, biological, geological and climatological and our modern ecosystems still witness those established then (Servais *et al.*, 2008).

The Ordovician radiation was interrupted by the End Ordovician extinction, one of the most severe extinctions of the Phanerozoic (Fig. 3, Sepkoski 1981, Sheehan, 2001) correlated to the Hirnantian glaciation, although the long-standing one-to-one causative relation between cooling and extinction currently is challenged (Hammarlund *et al.*, 2012; Harper *et al.*, 2014; Ghienne *et al.*, 2014; Vandenbroucke *et al.*, 2015). About 20% of the families, 40 % of the genera and up to 85 % of the species went extinct, and the phytoplankton and zooplankton forming the base of the food chain and playing an important role in driving the GOBE, were severely affected. The end Ordovician extinction is thought to comprise two pulses (Brenchley, 1984, Brenchley *et al.*, 2006), the first one just below the *Normalograptus extraordinarius* graptolite Biozone, which mainly affected the nektonic and planktonic organisms living on the shelf and deep sea, as the falling sea level provoked the demise on the large shelf area established during the Middle Ordovician. The second pulse, found within the *N. persculptus* graptolite Biozone had a more global effect on every organism (Harper *et al.*, 2014). The driving mechanism of the first extinction pulse is still matter of debate, as the timing of events, such as temperature and sea level drop, is not clear, but there is an agreement that the second pulse correspond to a widespread transgression due to the melting ice cap. The extinctions were followed by the establishment of a survival/recovery fauna during the *N. extraordinarius* graptolite Biozone and in the lowermost Silurian *ascensus* graptolite biozone.

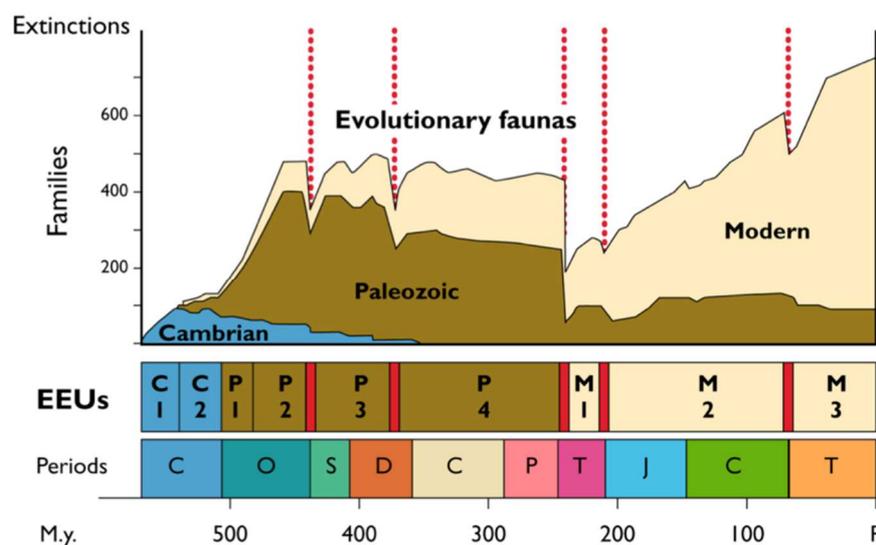


Figure 3: Ecologic evolutionary units and faunas as defined by Sepkovski (1981) with the revised Ecologically Evolutionary Units (EEUs Sheehan, 1996) and the major mass extinctions events in red (From Harper, 2006).

As for the GOBE, the factors that triggered this glacial event and above all, the timing of the events involved are debated, but the hypothesis of a combination of different causes is generally accepted (Harper *et al.*, 2014). The research community's perception about the global climate during the Ordovician has greatly evolved during the last twenty years and many studies were carried out using a great variety of proxies leading to new scenarios for the onset of the Early Palaeozoic Ice age (EPI); these will be discussed in detail in the next section.

1.2 The Ordovician climate, proxies and application

The end Ordovician glaciation was first described in Morocco by Destombes (1968 a, b, 1971; Destombes *et al.*, 1985) based on sedimentological evidence such as stratigraphic unconformities. This glacial event was considered as very anomalous compared to more recent glaciations (e. g. during the Cenozoic) as, in a first attempt to evaluate the atmospheric CO₂ level over time, Berner *et al.*, (1990) estimated high rates of CO₂ during the Early Palaeozoic. Their models included a combination of parameters, such as: sedimentary burial of organic matter (calculated using carbon isotopes from ancient rocks), silicate weathering (calculated using estimated past elevation and the effect of rivers and land plants on weathering), variation in ocean ridges and volcanoes degassing (estimated from seafloor spreading) and the deposition of carbon moving from platform to deep sea. They modelled a curve indicating high CO₂ for the Early Palaeozoic and Mesozoic and low for the Permo-Carboniferous and Late Cenozoic. Subsequently, in 1991, Berner published the results from a new model with a higher complexity of the geological, geochemical, climatological and biological parameters, which confirmed the earlier results. Crowley and Baum (1991) were amongst the first to identify the contradiction of having a glaciation in a greenhouse period, as suggested by the high CO₂ values indicated in the models of Berner (1990, 1991) and high sea levels (e. g. Brenchley and Newall, 1980; Fortey, 1984, Ross and Ross, 1992). Therefore they simulated the condition of an icecap growing during the Hirnantian with such conditions, and only 0% to 47% of the known ice volume in the Hirnantian could be simulated when the parameters (orbital forcing and snow albedo) were forced to their maximum (Crowley and Baum, 1991).

This lead Brenchley *et al.* (1994) to think there were other parameters involved, so they obtained new stable isotopes data from Late Ordovician and early Silurian brachiopods to test the hypothesis of a glaciation during a greenhouse period. Their oxygen isotopes data show changes in sea water temperatures and ice cap volume that made them believe that there was a short glacial event during the Hirnantian of approximately 0.5 to 1.5 Myr, and the ice cap grew and melted very rapidly, unlike the progressive growth in several cycles of the Cenozoic

glaciation, which would be consistent with the high CO₂ levels. They also assumed that a significant change in the carbon cycle, indicated by carbon isotope excursion during the Late Ordovician, may represent a reduction in *p*CO₂ and may have provoked the glaciation.

In 1994, Berner revised his model from 1991 and the GEOCARB II emerged with similar conclusions. Later, Berner and Kothavala (2001) produced a revised version of his model, the GEOCARB III, including the latest update of the parameters, amongst which new data from general circulation model, a weathering-uplift factor based on strontium isotopes, a more accurate estimation of the effect of the emerging land plants during the Devonian, the latest updates in (changes in) palaeogeography and new δ¹³C data. The results obtained were similar to the first studies, indicating a very high CO₂ level for the Early Palaeozoic following by a large drop during the Devonian.

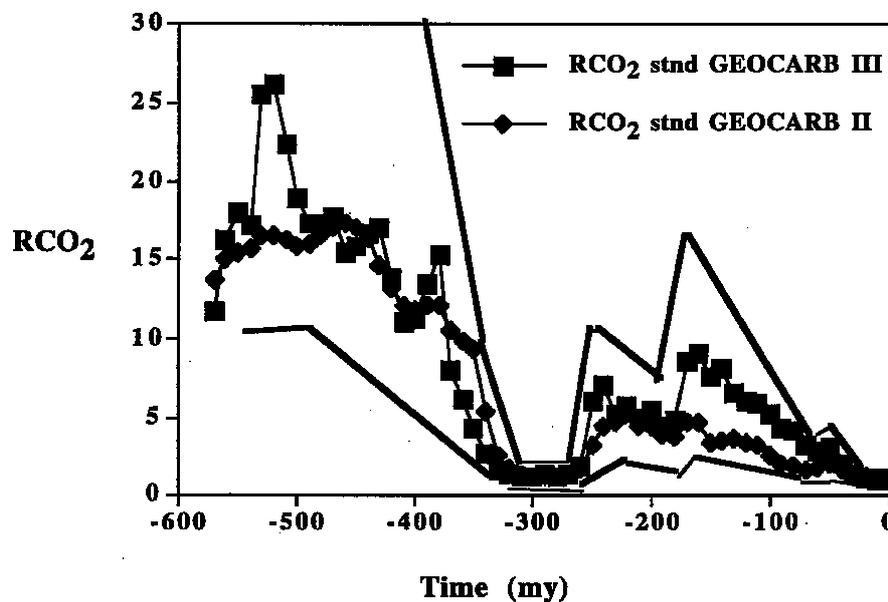


Figure 4: High level of CO₂ calculated for the Early Palaeozoic with the GEOCARB II and III models from Berner and Kothavala (2001).

Other evidence, based on high relative global sea levels and implausibly high sea surface water temperatures (SSTs) derived from marine δ¹⁸O_{carb} values from limestones and brachiopods (Veizer, 1999, 2000; Shields *et al.* 2003), also supported the postulated super greenhouse state during the Early-Middle Ordovician. Assuming sea water (SMOW) had a similar stable isotopic value to present day, equatorial temperatures were calculated as reaching ~70°C. This is implausibly high and has led to the view that seawater chemistry has changed significantly from the Ordovician (Shields *et al.*, 2003).

However, at about the same time a radically different view has emerged from new stable isotope data (e. g. Ainsaar *et al.*, 1999; Ludvigson *et al.*, 2000, 2004; Saltzman and Young,

2005, Bergström *et al.*, 2006, 2009a, 2011) containing a largely correlatable carbon isotope excursion (the Chatfieldian Excursion, latter named the Guttenberg Isotope Carbon Excursion, GICE) coupled to sedimentological evidence, demonstrating that the Hirnantian glaciation was actually part of a “long-lived Late Ordovician glaciation” that was initiated during the early Katian and therefore that a brief episode of CO₂ draw-down may have been missed in previous studies.

More recently, some authors even suggested an early cooling starting already during the Early-Middle Ordovician, such as Trotter *et al.* (2008) using $\delta^{18}\text{O}$ values from conodont apatite, suggesting decreasing temperatures throughout the Tremadocian and the Floian. Rasmussen *et al.* (2016) used $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ data from brachiopods that suggest the onset of the Early Palaeozoic Ice age (EPI) during the Middle Darriwilian. Other proxies such as sequence stratigraphy also demonstrate the existence of an EPI starting during the Darriwilian, based on eustatic cycles (Turner *et al.*, 2011, 2012). General circulation models are also used to model an early cooling, starting at the Middle Ordovician (Nardin *et al.*, 2011). In addition, Pohl *et al.* (2014) demonstrated that when the CO₂ is decreased from 8 times the pre-industrial atmospheric level (PAL) to 6 times PAL at 470 Ma (Middle Ordovician), an abrupt icehouse can be induced and that, unlike previously assumed, an drastic drop of CO₂ is not necessarily required to induce an icehouse period (Pohl *et al.*, 2014). Finally, the distribution of fossil groups that are SST dependent, i. e. graptolites or chitinozoans, have been used to establish latitudinally controlled palaeoprovinces in the early Late Ordovician by Vandenbroucke *et al.*, (2009, 2010a) and confirm that the cooling trend toward the Hirnantian had started before or during the Sandbian (Vandenbroucke *et al.*, 2010b).

In addition, Ghienne *et al.* (2014) refined the timing of events in Gondwana during the Hirnantian glaciation with sequence stratigraphic correlations between the Anti-Atlas, Morocco (Gondwana) and sections on Anticosti Island, Canada (Laurentia). This study reveals three main glacial cycles during the end-Ordovician and multiple higher order cycles, suggesting a non-unique Cenozoic-style glaciation for the Hirnantian.

It is becoming clear that the Early-Middle Ordovician was not the long-assumed greenhouse state previously described and that the Hirnantian was rather the maximum expression of the EPI (Page *et al.*, 2007). However, depending on the proxy data used, the timing of the onset of the EPI slightly varies, and therefore the methods and their limits will be fully described in the next sections 1.2.

1.2.1 Stable isotope proxy data

Stable carbon isotope stratigraphy has become an important tool in our science and was a key element in how the scientific community's perception on the duration of Ordovician cold period changed stepwise over the last decades. The view of a very short-lived Hirnantian glaciation, ‘unique in Earth history’ gave way to other interpretations: in the newly

established paradigm, the Hirnantian glaciation (~444 Ma) is a discrete event of a few 100.000 years during a much longer EPI. The early Katian global positive $\delta^{13}\text{C}$ GICE was suggested to represent an interval of cooling by Saltzman and Young (2005) based on its coincidence with low-stand deposits and the presence of similar isotope signatures in the Hirnantian. The GICE was previously called the Chatfieldian excursion when it was first described in Northern America (Hatch *et al.*, 1987; Saltzman *et al.*, 2003, Saltzman and Young, 2005). The GICE is reported from sections around the world, e.g., in the upper part of the Baltic Keila Stage (Middle Caradoc) in Estonia (Aisaar *et al.*, 1999; Kaljo *et al.*, 2003), in the Mjøsa Formation in Sweden and in the Frognerkilen Formation in Norway (Bergström *et al.*, 2011). In the view of Page *et al.*, (2007), it represents the onset of a prolonged Early Palaeozoic Ice Age (EPI), culminating in the Hirnantian glacial maximum *c.* 10 Ma later. Causal hypotheses drawing on Cenozoic scenarios propose changes in Mid-Ordovician mountain building as a result of continental collision, and enhanced silicate weathering as a sink for atmospheric CO_2 and as a mechanism for the initial onset of cooling (Page *et al.*, 2007). Cooling continued through the Sandbian and resulted in a first glaciation at the GICE, followed by several (smaller) Katian glaciations. A late Katian ‘snow gun’ effect (\approx the Boda event) may have finally pushed the system into the Hirnantian glacial maximum and the ice sheet became subject to orbital tuning (Page *et al.*, 2007). This stepped sequence of events is much like the one suggested for Cenozoic glaciation (Armstrong 2007). However, recent studies suggest that the climate already started cooling before the GICE (see next sections). Yet others, such as Bergström (2009a) argue that there is no evidence that the GICE excursion is directly linked to a glaciation in Gondwana, but that it remains a useful tool for global stratigraphical correlation.

Since the discovery of the GICE, many more positive excursions have been found in the upper Ordovician, most of them in the Katian (Ainsaar *et al.*, 2010; Bergström *et al.*, 2010, 2011, 2014, 2015, Holmden *et al.*, 2013) but also in the Darriwilian (Rasmussen *et al.*, 2009; Ainsaar *et al.*, 2007, 2010; Bergström *et al.*, 2010) A general $\delta^{13}\text{C}$ curve (Fig. 5) has been established (Bergström *et al.*, 2009a) based on data from Argentina, Estonia and North America and at least five excursions are suggested to be correlatable across several palaeocontinents (Ainsaar *et al.*, 2010; Bergström *et al.*, 2014, 2015), although it remains uncertain whether these excursions represent glacial or cooling events.

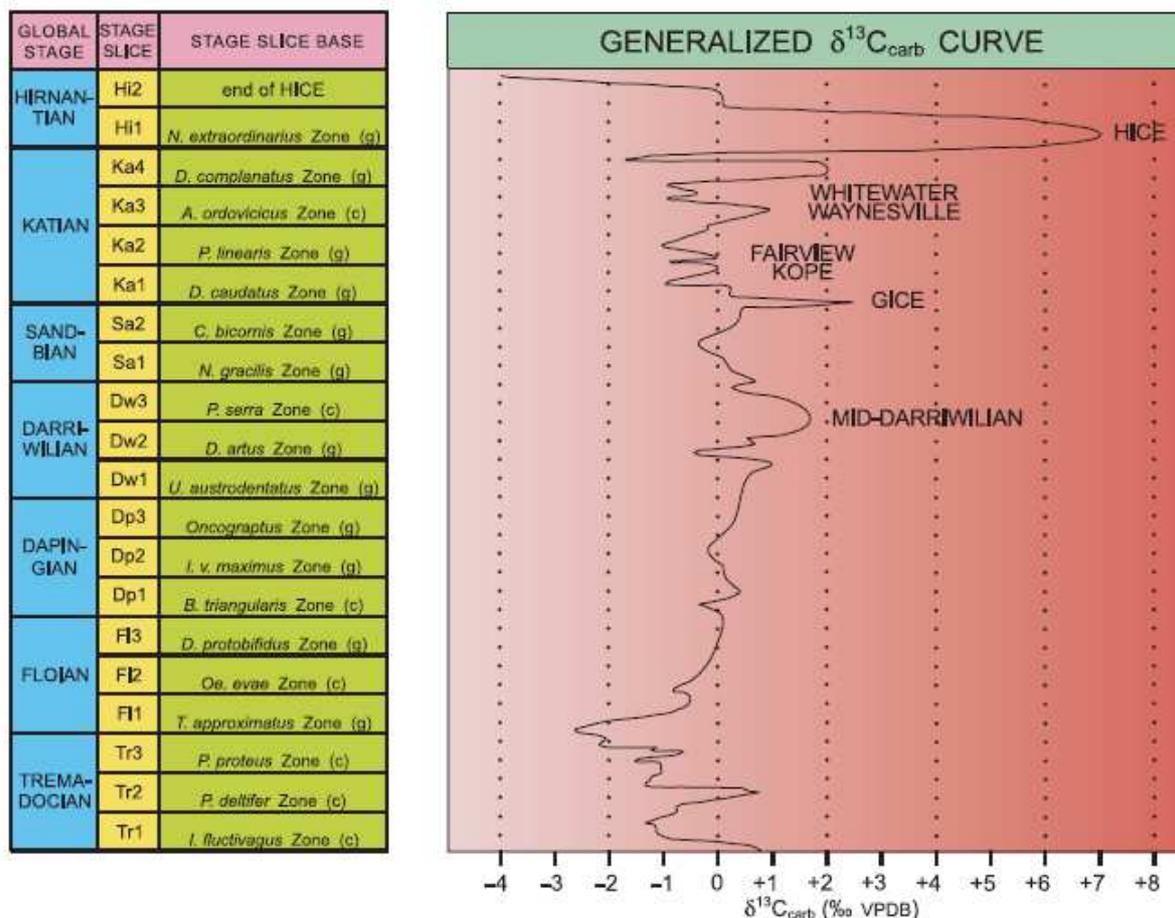


Figure 5: The graptolite and conodont biozones used to define the stage slice and a general composite $\delta^{13}\text{C}_{\text{carb}}$ curve from Bergström *et al.* (2009a)

It is relatively well accepted (e.g., Cramer and Saltzman 2005), that these elevated $\delta^{13}\text{C}$ values may indicate enhanced burial of organic matter in the deep ocean derived from an increased primary productivity. Other explanations exist, such as the carbonate weather hypothesis during sea level drop of Kump *et al.* (1999) for the HICE. The main difference between those two scenarios is the timing of changes in $p\text{CO}_2$ and the onset of $\delta^{13}\text{C}$ excursion. In the first scenario, the glaciation is triggered by the increasing primary productivity that removed an important amount of organic carbon from the surface water (Brenchley *et al.*, 1994, 2003). Therefore, the $\delta^{13}\text{C}$ excursion would coincide with $p\text{CO}_2$ lowering, the SST and sea level drop, the expansion of an ice cap and the onset of an extinction event. In the second scenario, the Taconic orogeny caused a lowering of the $p\text{CO}_2$ during the late Middle Ordovician with the weathering of continental silicate rocks acting as a sink for CO_2 , triggering the expansion of an icecap and the sea level drop. The $\delta^{13}\text{C}$ excursion would thus correspond to an increase in weathering of the carbonate exposed during the regression and follow the lowering of the $p\text{CO}_2$. As the ice was expanding, the weathering decreased and the $p\text{CO}_2$ start to rise again and eventually the glaciation ceased (Brenchley *et al.*, 2003).

The various interpretations for the $\delta^{13}\text{C}$ excursions (in terms of their relation to the palaeoclimate) can be traced back to the complexity of the C-cycle. Many processes can lead

to carbon cycle variations, but major positive or negative $\delta^{13}\text{C}$ excursions nevertheless indicate major changes in the ocean's geochemistry.

Variations in the $\delta^{18}\text{O}$ record are easier to interpret although this record is more prone to diagenetic processes and other secondary alterations that are common in ancient rocks and that can alter the isotopic signal. Oxygen isotope fractionation depends on the temperature during the precipitation of the carbonates and the $\delta^{18}\text{O}$ of the surrounding sea water. As such, the $^{16}\text{O}/^{18}\text{O}$ ratio can be used as a tool to detect glaciations, as during glacial event, oceans are enriched in the heavier ^{18}O and the lighter ^{16}O is preferentially incorporated in snow and icecaps. But the proxy is sensitive to evaporation and precipitation, therefore interpretation of the variations of the ratio must be treated carefully interpreted.

Most of the deep-time studies of interest have been focused on the Upper Ordovician, such as those of Brenchley *et al.* (1994, 2003) for example. However, Trotter *et al.* (2008) established a new $\delta^{18}\text{O}$ curve from the lowermost Ordovician to the lowermost Silurian (Fig. 6), with oxygen isotopes derived from conodont apatite, the mineralogy of which is more stable than that of the calcitic brachiopods, thus more resistant to diagenetic alteration. The data suggests a global cooling during the Early-Middle Ordovician that already started in the Tremadoc from temperatures around 40 °C, to reach the modern equatorial SST during the Floian/Dapingian. Then, a relative stability is observed in the Middle-Late Ordovician and finally the end Ordovician is characterized by a rapid temperature drop corresponding to the classic Hirnantian glaciation. These data are in contradiction with the previous studies suggesting a stable greenhouse state for most of the Ordovician. However, it is important to note that relatively few conodont samples were used and that all of them were exclusively collected in Australia (Gondwana) and Canada (Laurentia), at paleotropical latitudes during the Ordovician, and tropical sea surface temperatures (SST) may not be representative of the global SST REF. In addition, the conodont apatite, although it is more stable than marine carbonate because of its crystalline structure (Trotter *et al.*, 2008), can still be altered during its burial history, or even during the extraction (Wheeley *et al.*, 2012).

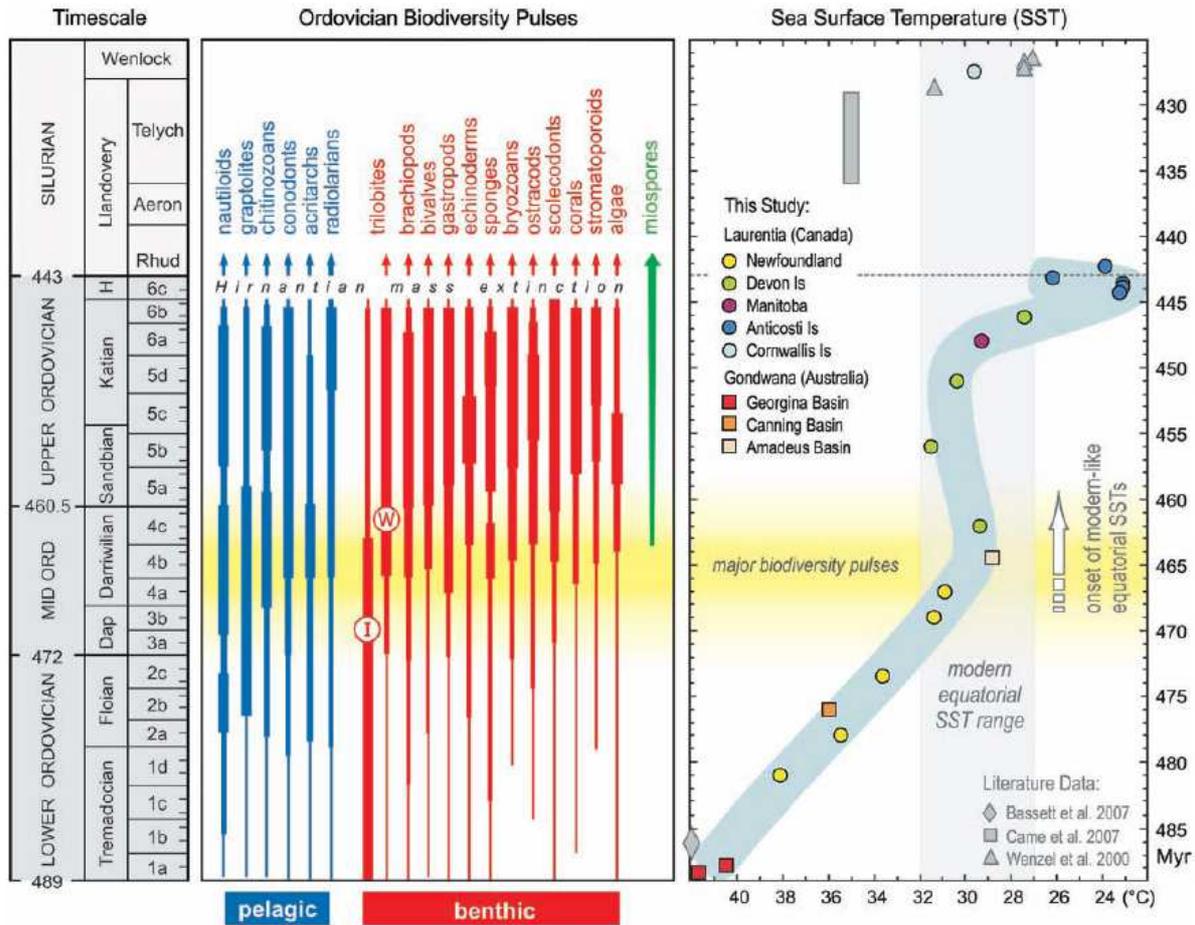


Figure 5: Global diversity of several pelagic and benthic groups plotted against the sea surface temperatures calculated from conodont oxygen isotopes from Trotter *et al.* (2008) suggesting an early cooling starting during the Early Middle Ordovician.

More recently, Rasmussen *et al.* (2016) demonstrated that the onset of the Ordovician icehouse period took place in the Early-Middle Ordovician based on stable isotope data (Fig. 6). They combined paleobiological data from brachiopods and trilobites with stable isotopes (brachiopods $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) and trace element from samples collected bed-by-bed in western Russia, situated at middle palaeolatitudes during the Early-Middle Ordovician. They built a high resolution (3rd and 4th order) sea level curve based on the biofacies established with the macrofossils and they estimated at least 150 m sea level drop from the upper Floian highstand to the lower Darriwilian. They also detected a short warming interval indicated by the rapid drop of oxygen isotope values in the uppermost Floian and then, in the lower Darriwilian, the values increased again, suggesting a 4 to 5°C cooling. They argue that only glacioeustatic variations could have produced such a large sea level drop, and, combining with the isotopic data, propose that the onset of the EPI is around the Lower-Middle Ordovician boundary. This is concordant with the proposed Darriwilian Ice Age proposed by Turner *et al.* (2012).

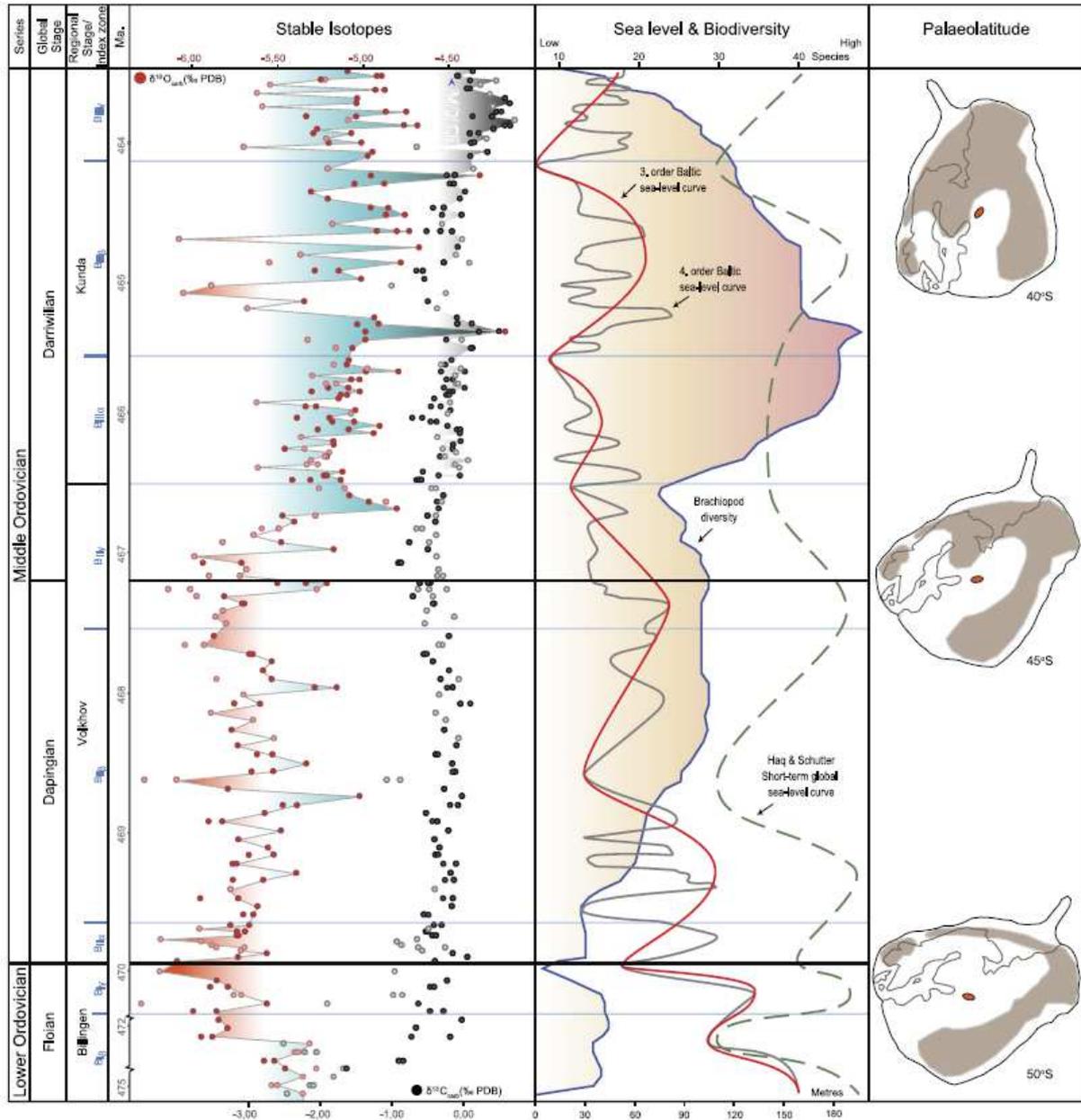


Figure 6: Oxygen and carbon isotopes calculated from brachiopods plotted against the sea level and biodiversity curve of the rynchoellifomean brachiopods from Rasmussen *et al.* (2016) indicating an early cooling during the middle Darriwilian.

1.2.2 Physical and sequence stratigraphy

The oldest method to track climate changes is to look at the sedimentary record in the field. A relatively new method of interpreting the accumulation of the sediments, based on the analysis of the nature and sequences of the deposits, is sequence stratigraphy. In the near field sections, close the hypothesized icecap (i.e. in Gondwana), we can observe direct sedimentological evidence of glaciations, such as glacial deposits (tillites or diamictites) or erosional features (striae, glacial pavement, incised valleys) that are witnesses of the waxing and waning of the ice cap. And in addition, we can interpret the cyclicity in the sedimentary

rocks using sequence stratigraphy and cyclostratigraphy to reconstruct the sea level variations, depending on the order, or sequence, in which the strata were deposited in the accommodation space, their sedimentary structures and the limits between the sequences. A sequence, or an entire sea level cycle, is described as follow by Catuneanu (2006): “onset of a base-level fall, the end of a base level-fall, end of regression and end of transgression”. However, different methods are currently applied and the lack of international consensus between the models and terminology used, can hamper correlations. Nevertheless, it has been widely used in Ordovician series (Videt *et al.*, 2010; Loi *et al.*, 2010; Turner *et al.*, 2011, 2012; Dabard *et al.*, 2015). It has to be noted that a backstripping procedure (Allen and Allen, 1990; Watts 2001) has to be applied on the results to calculate and remove the effect of the tectonic subsidence, compaction and sediment load on the eustatic curve, which distort the signal.

Loi *et al.* (2010) subdivided the upper Ordovician succession in Morocco into two packages, the lower corresponding to a shelf succession and the upper to a glacial related succession. They identified six sequences, or genetic units, interpreted as representing glacioeustatic oscillations in the Anti-Atlas in Morocco, and reconstructed a sea level curve based on the changing facies. It shows three remarkable episodes of sea level fall or forced regressions in the Katian, interpreted as glacial episodes preceding the Hirnantian, but direct sedimentological evidence (such as subglacial erosion or diamictites) is missing. Two glacial events were also identified during the Hirnantian. Loi *et al.* (2010) correlated the first sea level drop in the early Katian with the GICE in Laurentia, associated with the “Eureka Quartzite” a lowstand deposit, interpreted by Saltzman and Young (2005) as the potential onset of a glaciation in Gondwana. It can also be correlated to the “Solvang Lowstand Event” of Nielsen (2004) in Baltica. The second sea level drop occurred in the middle Katian and was correlated with a major regressive event in Baltica (Calner *et al.*, 2010) and the third sea level fall in the Latest Katian with an unnamed lowstand event of Nielsen (2004) in the lower Skogerholmen Formation, between the “Grimsøya Regressive Event” and the “Spanslokket Drowning Event”. The stratigraphic position of this formation, however, is studied in detail by Amberg *et al.* (2016, *subm.*) who reassigned it to the Katian-Hirnantian Boundary (see chapter 4).

Turner *et al.* (2011) also used sequence stratigraphy in Cape Basin (South Africa) to describe the stratigraphy of the Peninsula Formation, comprising the lower Leeukop Member and the upper Platteklip Member straddling the Lower-Middle Ordovician boundary. The outcrop present coarse sandstones corresponding to fluvial deposits interbedded with thin transgressive marine sediments organized in ten 3rd order (allogenic) sequences. These ten 3rd order sequences are grouped into a lower regressive 2nd order sequence and an upper transgressive 2nd order sequence. Using correlations with the sea level curve from Haq and Shutter (2008) to identify the frequency and ages of their cycles, Turner *et al.* (2011) suggest these are the result of glacioeustatic sea level movements during the basal Middle Ordovician (Floian). Hence, they also suggest and that an icecap should have already been present at the South Pole during the early Middle Ordovician, which is in agreement with the hypothesis of Trotter *et al.* (2008). Another study conducted by Turner *et al.* (2012) in the Darriwilian Hiswah-Dubaydid Formation in Jordan came to the same conclusions, i.e., that the cyclicity

observed in these sediments also has a glacioeustatic origin. In summary, Turner *et al.* (2011, 2012) hypothesize the presence of an icecap during the Floian and the Darriwilian.

Dabard *et al.* (2015) in turn performed a sequence stratigraphic analysis on strata from the Dapingian to the Sandbian from the Armorican Massif in France that was part of Gondwana at that time. They reconstructed a multi order eustatic sea level curve based on facies analysis and stacking patterns, a gamma-ray record, and a chitinozoan biostratigraphic framework. They identified thirty five high frequency 4th order sequences with an approximate 410 kyr duration, which they interpreted as eccentricity cycles. Eleven lower frequency 3rd order sequences with an approximate 1.2 Ma duration interpreted as long obliquity cycles, an orbital forcing parameter which is known to govern icehouse in the Cenozoic and the Quaternary. An eustatic sea level curve was constructed by converting the stratigraphic signal combined with parameters such as compaction, sediment load and tectonic subsidence. A series of abrupt sea level falls and regressive events in the Darriwilian and the Sandbian are interpreted as representing glaciations, one on them corresponding to the Mid-Darriwilian carbon isotope excursion described e. g. in Ainsaar *et al.* (2010) and Bergström *et al.* (2010). This lends support to the EPI starting during the Middle Ordovician.

1.2.3 Plankton provinces

We know that the distribution of the actual planktonic organisms, such as the foraminifera, is predominantly dependent on the SST and thus reflect distinct, largely latitudinal, planktonic provinces (Hart 2000). These provinces shift position when SST start varying and climate belts migrate, and have been used to track the climate variations during the Cenozoic. Several palaeoecological models were developed to test the influence of different parameters on the distribution fossil zooplankton such as graptolites and a strong correlation with SST has been suggested. Vandembroucke *et al.* (2009a) tested this hypothesis during the Ordovician by mapping the spatial distribution of graptolites in order to establish provinces or biotopes for the *Nemagraptus gracilis* graptolite Biozone in the early Sandbian. They ran the TWINSPAN (Two Way indicator species analysis) on the presence/absence matrix of the species and seriated the results to obtain latitudinally constrained sub group of species, defining the Sandbian biotopes. Their effort resulted in the recognition of four provinces divided in biotopes, corresponding to different climatic belts with a steep latitudinal gradient; the latter resembles the distribution patterns of modern plankton, therefore suggesting a non-greenhouse state during the *N. gracilis* graptolite Biozone. The same approach was used by Vandembroucke *et al.* (2010b) on the same *gracilis* biozone, but with chitinozoans. Similar results were obtained, with provinces and biotopes comparable to the graptolites, but the chitinozoans are mainly restricted to middle and high southern latitudes, from 35°S onward. From these studies combined, two climatic fronts were recognized, the first one at approximately 35°S and the second one at 55° - 70°S, corresponding to the present day subtropical front and polar front. It is clear that the fossil zooplankton is controlled by SST, alike the modern foraminifera, and therefore can be used to track climate belt variations. The authors conclude that the cooling trend toward the Hirnantian was initiated before the

Sandbian, as suggested by Trotter *et al.* (2008) and challenge the notion of a uniform greenhouse climate prior to the Hirnantian glaciation.

1.2.4 General Circulation Models

Numerical models are powerful tool to simulate the atmospheric and oceanic conditions in the past and to recreate the environmental conditions of ancient life, but rely on many parameters for their boundary conditions, which are often hard to calculate, quantify or estimate, especially in the older times such as the Palaeozoic. Therefore this tool also has important limitations and key uncertainties associated with its output. The earlier investigations of numerical model were mostly focused on the Hirnantian glaciation (Hermann *et al.*, 2004), trying to understand the paradox of high $p\text{CO}_2$ during a glaciation.

Nardin *et al.* (2011) used a coupled climate-geochemistry GEOCLIM numerical model to simulate the Palaeozoic climate. They investigated a time period from the Furongian to the Early Devonian divided in five time slices. For each time slice, a reconstruction was applied to test the potential influence of two forcing parameters: the changes of palaeogeographical position with the drifting of the continents, and the weathering of the siliciclastic rocks. These simulations allowed the authors to postulate an EPI, as they noted the onset of an early cooling during the Middle Ordovician until the Llandovery, with a drop in the mean annual continental temperatures (MAT) from 15°C to 13°C, which does not correspond to the large range of decreasing SSTs from approximately 40°C to 30°C calculated by Trotter *et al.* (2008) during the Early Ordovician. They also suggest that the northward drifting of the continents could have caused the drop in atmospheric CO_2 level during the upper Cambrian to the Lower-Middle Ordovician. The same conditions were modeled until the middle Silurian, at which point the $p\text{CO}_2$ level started to rise again.

Pohl *et al.* (2014) tested the response of the Ordovician climate to CO_2 variations and palaeogeography using a general circulation model (GCM), FOAM, with coupled component for the ocean, the atmosphere and sea ice. They used different CO_2 levels (from 2 to 12 PAL) with different Palaeogeographical configurations, at 470 Ma (Middle Ordovician) and 450 Ma (Upper Ordovician). Their results indicate that at 470 Ma and 450 Ma, a decrease to 8 PAL and 6 PAL is sufficiently sudden to induce runaway icehouse conditions. At 450 Ma, the tipping point is observed when the CO_2 is decreased from 8 PAL to 6 PAL, leading to a ~9°C temperature drop. Pohl *et al.* (2015) use the same GCM runs to map the Ordovician ocean surface circulation, as a series of base maps for palaeobiogeographical studies.

2. Aim of the project

2.1 Research questions

The research community's perception of the Ordovician climate has significantly evolved during the last twenty years. From a supposed super greenhouse period with a short glacial event at the very end, during the Hirnantian, there is now increasing evidence from various proxies suggesting that the onset of an EPI occurred during the Middle Ordovician, i.e., the Darriwilian (e. g. Nardin *et al.*, 2011; Turner *et al.*, 2012; Dabard *et al.*, 2015; Rasmussen *et al.*, 2016) or even during the Early Ordovician, i. e. the Floian (Trotter *et al.*, 2008). However, none of these studies were conclusive at the start of the project, and to some extent still are not today.

For instance, the issues with the various lines of evidence summarized in section two are:

1. The exact significance of the carbon isotope excursions are not clear yet, although they are known to represent important changes in the carbon cycle and the ocean chemistry. In addition, there are no continuous, general $\delta^{13}\text{C}$ curves for each palaeocontinent, as there is no continuous section from the Lower to Upper Ordovician. Consequently, composites from different region that were relatively distant, are used instead, such as the generalized composite curve of Bergström *et al.* (2015), which is a combination of the chemostratigraphy in Clear Springs, (Maryland) from Leslie *et al.* (2011) for the Middle Ordovician, the chemostratigraphy in the Cincinnati Region from Bergström *et al.* (2007, 2010) for the lower Upper Ordovician and the chemostratigraphy in Anticosti Island from Young *et al.* (2010) for the uppermost Ordovician. Therefore these could include local variations in the carbon cycle rather than global climatic events. For example, Bergström *et al.* (2009) mentioned that the Mid-Darriwilian excursion is not visible in the Great Basin (Saltzman and Young, 2005) whereas it appears clearly in Baltica in Kaljo *et al.* (2007). Alternatively, such signatures could also reflect stratigraphic gaps (hiatuses) or even a combination of both phenomena. The relation between oxygen isotopes and climate variations is more clear, but the seminal study of Trotter *et al.* (2008) which first suggested an early cooling of the SSTs temperatures during early Middle Ordovician used samples from low tropical paleolatitudes exclusively, i. e., Canada and Australia, which may not be representative of the global SST variations. However, the recent study from Rasmussen *et al.* (2016) from Baltica shows very interesting results connecting the GOBE with an early global cooling during the Darriwilian.

2. Sequence stratigraphic methodology, to some degree lacks the international consensus in the terminology that is necessary to avoid confusions. The quantification of sea level variations in deep time is no mean feat. In addition, the studies suggesting an early cooling and the presence of an ice cap in Gondwana during the Darriwilian, such as in Saudi Arabia or South Africa (Turner *et al.*, 2011, 2012) is difficult to correlate into middle or high paleolatitudes.

3. The biogeographical studies with graptolites and chitinozoans are conclusive for the Late Ordovician, but we lack data from the Early and Middle Ordovician especially in the middle latitude occupied by the palaeocontinent Avalonia.

4. The general circulation models show promising results (Nardin *et al.*, 2011, Pohl *et al.*, 2014) to help unravel the conditions of the onset of the EPI, but their boundary conditions are difficult to constrain, especially in ancient times such as the Ordovician.

The research question addressed in this PhD thesis, builds on the aforementioned uncertainties, and is a dual one:

1. Can we find additional evidence for pre-Hirnantian glaciations? We focus on the earliest of the suggested phases of cooling, i.e., the episode in the Floian which is suggested to coincide with the onset of the GOBE.

2. Can we use data from a group of organic-walled planktic microfossils, the chitinozoans, to track this climatic change?

2.2 Objectives

My aim is to investigate whether we can use chitinozoan microfossils (as part of a multidisciplinary methodology) to help unveil the Early-Middle Ordovician climate state, and to add to emerging evidence of potential icehouse condition during that period. My focus is on the Floian-Darriwilian (or the ‘Arenig’ in UK regional chronostratigraphic terminology) which has been suggested as the period of the potential onset of cooling in the Ordovician, and on the middle to high paleolatitudes that are underexplored as discussed higher in this chapter. The specific objectives of this study are identified as the following research targets as shown in the figure 7:

Objective 1: The nature of Ordovician limestone-mudstone alternations in the Oslo-Asker area

In the Oslo Region in Norway, several rhythmites of alternating limestone and marl beds occurring in the Middle and Upper Ordovician are interpreted as corresponding to lowstand events observed in the Ordovician eustatic sea level curve for Baltica (Nielsen 2004), and could possibly represent glacioeustatic variations. Alternatively these could also simply be the result of differential diagenesis, as explained by Hallam (1986), Munnecke *et al.* (1996), Biernacka *et al.* (2005) or Westphal *et al.* (2010, 2008). We here aim to discriminate between these two hypotheses using a coupled geochemical and palynological study. Interestingly, the lowest rhythmite from the Huk Formation seems to coincide with the suggested early phases of Ordovician cooling in the Floian and the rhythmite straddling the Sandbian-Katian boundary has been described by Bergström *et al.* (2011) to record the GICE. A corollary of

these investigations is that that they provide the potential better to correlate these key sections using chitinozoans biostratigraphy.

Objective 2: Date potential Arenig near field glacial sedimentary features in Morocco and correlate them with the type Arenig area in the Anglo-Welsh basin

In the near field sections to the Ordovician Austral ice sheet, in modern Morocco, there are several incisions into the Ordovician sedimentary successions of the Anti-Atlas, which were long interpreted as related to the Hirnantian glaciations. An emerging revised sedimentary architecture suggests that some of these incisions may be significantly older, and may even date back to the Floian. Our aims here are to date these incisions, and to constrain the duration of their formation by studying microfossil assemblages in the incised succession as well as in the incision infill. A better constrained duration will help shed light on the mechanisms that lay at the basis of these structures. I.e., short durations would point towards a purely erosional origin, potentially linked to lowered base levels, while long time gaps in the unconformities would open up the possibility for a tectonic origin (uplift followed by erosion).

Likewise, if these are sedimentary structures that are the expressions of glacio-eustatic sea level lows, we predict they should correlate with lowstand deposits over long distance, which is tested by comparing the sedimentary expressions of the same biochrons in the Morocco with other areas. Our first data on one of the key incisions, in Jebel Signit, suggested a Floian age, which we aim to correlate with, e.g., the type Arenig area in the UK which is the subject of Objective 3.

Objective 3: The type Arenig area in the Anglo-Welsh basin and chitinozoan palaeobiogeography

As demonstrated by Vandembroucke *et al.* (2010 a,b) the fossil zooplankton provinces are a robust proxy to detect climate variations, as they are SST-dependent and therefore can be used to track migrating climate belts and oceanic fronts. However, at the onset of the project, there is no chitinozoan database available from the literature for the period that we want to investigate, i. e. the Arenig (Early-Middle Ordovician) in the Anglo-Welsh basin, whose potential is proven but uninvestigated (Molyneux 1990). This area was situated on the palaeocontinent Avalonia, which is of particular importance as it (high to) middle paleolatitudes during the Early to Mid Ordovician, i.e., those latitudes where Vandembroucke *et al.* (2010a, b) demonstrate that the signature of the migrating polar front was detectable.

However, further complications arose when Nowak *et al.* (2016, i. e. near the end of my project) as they suggested re-assigning an originally Arenig chitinozoan Biozone to the upper Tremadoc, suggesting that the assumed 'Arenig' from the near field may not correlate into the Type Arenig from the Anglo-Welsh basin. Obviously, this issue needs to be resolved first, before palaeobiogeographic issues can be approached.

Therefore the first step was to establish a chitinozoan database for the type Arenig to build a robust biostratigraphical framework, in order to evaluate if there are similarity with the assemblages of the high latitudes as a second step, and finally try to find time-equivalent strata to those containing the incisions in Morocco, and if so, look at their sedimentology to see if it is consistent with a low stand deposits from the near field sections.

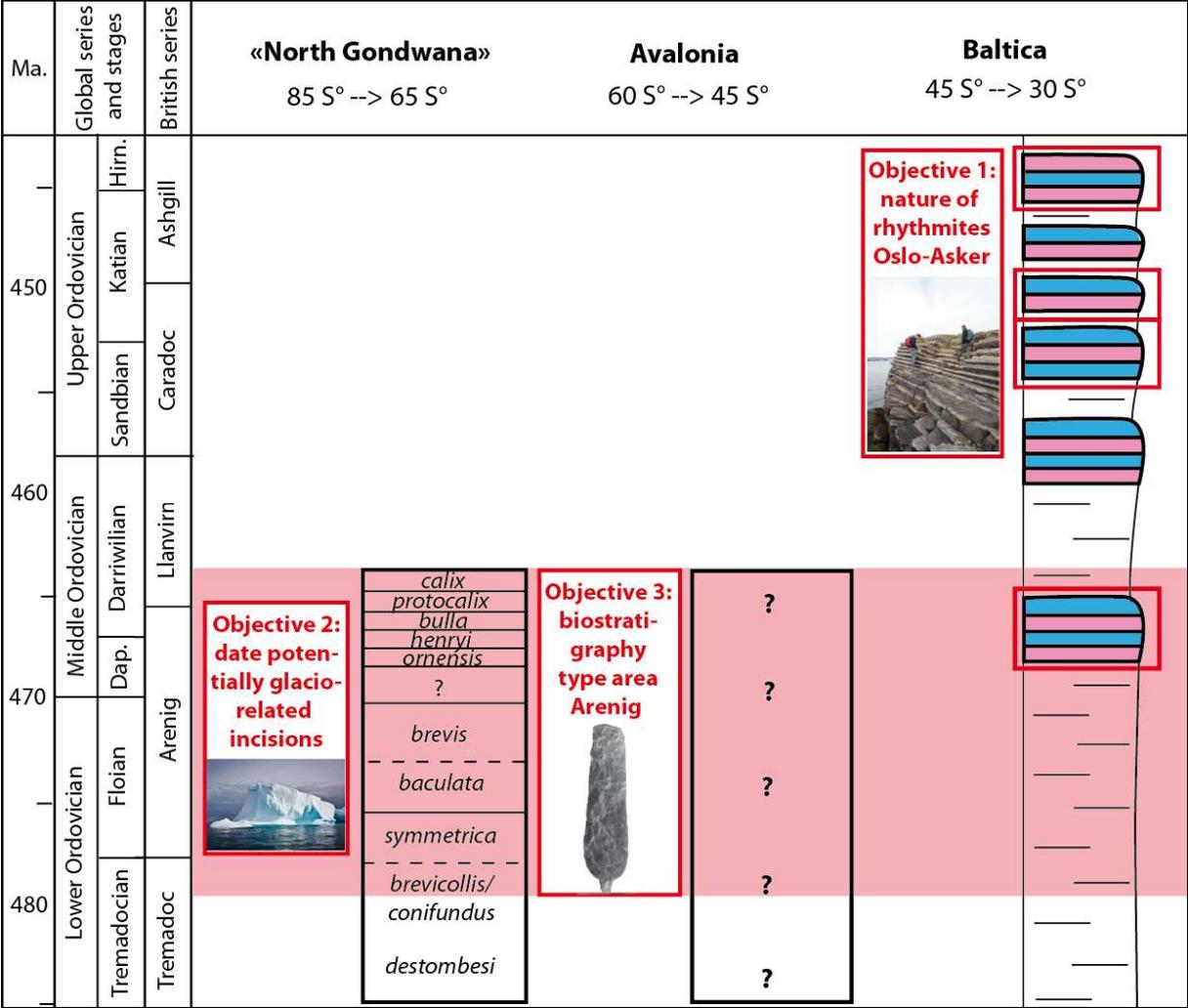


Figure 7: the objectives of my thesis at a glance: Focus on the earliest of the suggested phase of cooling in the Floian-Darrivilian interval (the Arenig, pale red box) and side project.

2.3 Implementation and methods

To meet these objectives, I performed a series of chitinozoan analyses, the results of which are presented here as a series of research papers and manuscripts. In total, I analyzed 240 samples (amongst which 102 from the Oslo-Asker Area, 40 from Morocco and 98 from Wales and the English Lake District), identified 15462 specimens (amongst them 7386 from the Oslo-Asker Area, 3798 from Morocco and 4278 from Wales and English Lake District).

In addition, 53 samples from the English Lake District were processed but not analyzed. The results obtained are compiled into four publications, the first one been published, the second one submitted and the two last one in preparation. A last chapter summarizing the results obtained in Morocco and will not be the subject of a publication yet, as we miss the sedimentological analysis which is currently in progress.

2.3.1 The nature of Ordovician limestone-mudstone alternations in the Oslo-Asker area (Norway): primary or diagenetic rhythms?

By: Amberg, C. E. A., Collart, T., Salenbien, W., Egger, L. M., Munnecke, A., Nielsen, A. T., Monnet, C., Hammer, Ø., and Vandenbroucke, T. R. A.

Publication status: Published, Scientific Reports, n°6; URL:

<http://www.nature.com/articles/srep18787>

Seven rhythmites from the Oslo-Asker area were sampled bed by bed, one in the Darriwilian, one in the Sandbian and three in the Katian and analyzed in detail (Fig. 8.1-4). We conducted a multiproxy study on four of them, the Darriwilian and the Katian ones (Amberg *et al.* 2016) with statistical analyses of the biostratigraphical data coupled to chemostratigraphy. This paper meets ‘Objective 1’.

All the analyses, sampling methods, results and interpretations are fully detailed in Amberg *et al.* (2016), reproduced here as chapter 3. My contribution to this multi-authored paper included the palynological analyses (laboratory processing of the samples and hand picking of the residues) of the samples from the Huk and Skogerholmen formations, the revision of the palynomorph data from the Arnestad, Frognerkilen and Solvang formations (originally collected by Tim Collart and Wout Salenbien respectively, as part of their MSc work at Ghent University) and the analyses and interpretation of the XRF data (collected by Lisa M. Egger, as part of her MSc work at Erlangen-Nuremberg University). Øyvind Hammer and Claude Monnet performed the statistical analyses. Arne Nielsen led the field work, and sampled the section with TRAV, WS and TC.

2.3.2 Chitinozoan biostratigraphy and carbon isotope stratigraphy from the Upper Ordovician Skogerholmen Formation in the Oslo Region. A new perspective for the Hirnantian lower boundary in Baltica.

By: Amberg, C. E. A., Vandenbroucke, T. R. A., Nielsen, A. T., Munnecke, A., and McLaughlin, P. I.

Publication status: Submitted, under review, RPP

There are different points of view regarding position of the Katian/Hirnantian boundary when correlating Laurentia and Baltica. Some studies place this chronostratigraphical limit at the base of the *Belonechitina gamachiana* chitinozoan Biozone, whereas others consider it to be at the base of the *Spinachitina taugourdeaui* chitinozoan Biozone. In one of the Katian rhythmites described in the previous project from the Oslo Region, i. e. the youngest one, we identified the species *B. gamachiana*. We calibrate the biostratigraphy with stable carbon isotopes and propose a new stratigraphic position for the Hirnantian lower boundary in Baltica that can be correlated with a section in Anticosti Island in Canada (Amberg *et al.*, *subm.*). This paper was not in our original objectives, but was motivated by the palynological results obtained from the “Objective 1”, coupled to carbon isotope data that show a significant stratigraphical interest.

All the analyses and sampling methods are fully detailed in Amberg *et al.* (2016), reproduced here as chapter 3. All the results and interpretations are fully detailed in Amberg *et al.* (*subm.*) here as chapter 4. My contribution to this multi-authored paper included the palynological analyses (laboratory processing of the samples, hand picking of the residues and SEM picturing of the specimens) of the samples from the Skogerholmen Formation and the analyses and interpretation of the carbon isotope data (collected by Axel Munnecke at Erlangen-Nuremberg University). Arne Nielsen led the field work, and sampled the section with TRAV and Øyvind Hammer.

2.3.3 Chitinozoan biostratigraphy of the historical Arenig series in Wales (Early-Middle Ordovician)

By: Amberg, C. E. A., Vandenbroucke, T. R. A., Molyneux, S. and Zalasiewicz, J. A.

Publication status: In preparation for submission to Geol Mag.

A field work campaign was conducted in South Wales in the Carmarthen and Whitland areas where four Arenig sections that were considered as potential stratotype by Fortey and Owens (1978, 1987) were sampled (Fig. 9) continuously and two other areas more scatteredly (see maps in Amberg *et al.*, *in prep.* a). In addition, samples from the Tremadoc were collected at the British Geological Survey (BGS) and few samples from the historical type area, the Arenig Fawr area, collected during a previous field campaign by Thijs Vandenbroucke and Richard Ramsey completed the sampling. Four chitinozoan assemblages were described and correlated with similar faunas from Gondwana, Avalonia and Baltica and we attempted to find an explanation for the correlations observed. This paper meets ‘Objective 3’.

All the analysis are fully detailed in Amberg *et al.* (2016), reproduced here as chapter 3. The sampling methods, results and interpretations are fully detailed in Amberg *et al.* (*in prep.* a), reproduced here as chapter 5. My contribution to this multi-authored paper

include the palynological analyses (laboratory processing of the samples, hand picking of the residues and SEM picturing of the specimens) of the samples from the Carmarthen, Afon Ffynnant, Colomendy, Cwmfelin Boeth, Pontyfenni and Llanfallteg formations. TRAV led the field work and sampled the sections with CEAA and the samples were recovered at the BGS by CEAA.

2.3.4 Description of Arenig fauna in the Lake District, Northern England

By: Amberg, C. E. A., Vandembroucke, T. R. A., Molyneux, S. and Servais, T.

Publication status: In preparation for submission to *Palynology*?

We also collected samples from the BGS from the Tremadoc Watch Hill Formation in the Skiddaw Group in the Lake District. No chitinozoan biostratigraphy of the Early Ordovician was attempted in Northern England before, and here we report the first specimens of *Euconochitina symmetrica*, indicating the eponymous chitinozoan biozone classically considered to be of early Arenig age, although this formation has been described as Tremadoc, based on the “*messaoudensis-trifidum*” acritarch assemblage (Amberg *et al.* in prep. b). This problem has been encountered before in Nowak *et al.* (2016) and may point to the need for the recalibration of the biozone’s chronostratigraphic position and, above all, to a general questioning about the identification of different species that are morphologically very similar. This paper meets ‘Objective 3’.

All the analysis are fully detailed in Amberg *et al.* (2016), reproduced here as chapter 3. The sampling methods, results and interpretations are fully detailed in Amberg *et al.* (in prep. b), reproduced here as chapter 6. My contribution to this multi-authored paper includes the palynological analyses (laboratory processing of the samples, hand picking of the residues and SEM picturing of the specimens) of the samples from the Watch Hill Formation. SM led the field work and sampled the Watch Hill Formation used for the study of the English Lake District found in the BGS Memoir from Cooper *et al.* (2004).

2.3.5 Description of Arenig fauna in the Anti-Atlas, Morocco

Several samples were collected in two areas in the Anti-Atlas in Morocco: At the Meteorite Hotel in Alnif, where the Arenig Fezouata Formation and the Tachilla Formation, straddling the Arenig Llanvirn boundary are expected to crop out, and at Jebel Signit Nord (Mssissi), where a large-scale incision of unknown age is observed (Figure 8.5-6). The palynological content was described and permitted to confirm the Arenig age of the sediments in Alnif but also of the incision, as the samples taken below and inside the incision were estimated as middle Arenig. We are working in

collaboration with colleagues from Lyon and Strasbourg University, which attempt to establish the setting up of the sedimentary glacial deposits in the Anti Atlas. However, as this stratigraphical framework in which the present palynological study takes place is not established, the results described in chapter 7, are not meant to be published yet. This chapter meets “Objective 2”.

All the analysis are fully detailed in Amberg *et al.* (2016), reproduced here as chapter 3. The sampling methods, results and interpretations are fully detailed in chapter 7. My contribution to this study includes the palynological analyses (hand picking of the residues and SEM picturing of the specimens) of the samples from the Upper Fezouata, Zini and Tachilla formations. Jean Francois Ghienne led the field work and sampled the sections with TRAV.



Figure 8: Pictures of selected outcrops. 1: Lysaker Member (bounded in red) of the lower Darriwilian (upper Arenig) Huk Formation in Vollen, Norway; 2: The upper Sandbian Arnestad and Frognerkilen formations in Nakkholmen Island, Norway; 3: The lower Katian Solvang Formation in Bygdøy, Norway; 4: The lowermost Hirnantian Hovedøya Member of the Skogerholmen Formation in Hovedøya Island, Norway; 5-6 Incision (in bold red) in the Arenig upper Fezouata Formation in Jbel Signit Nord, Morocco.

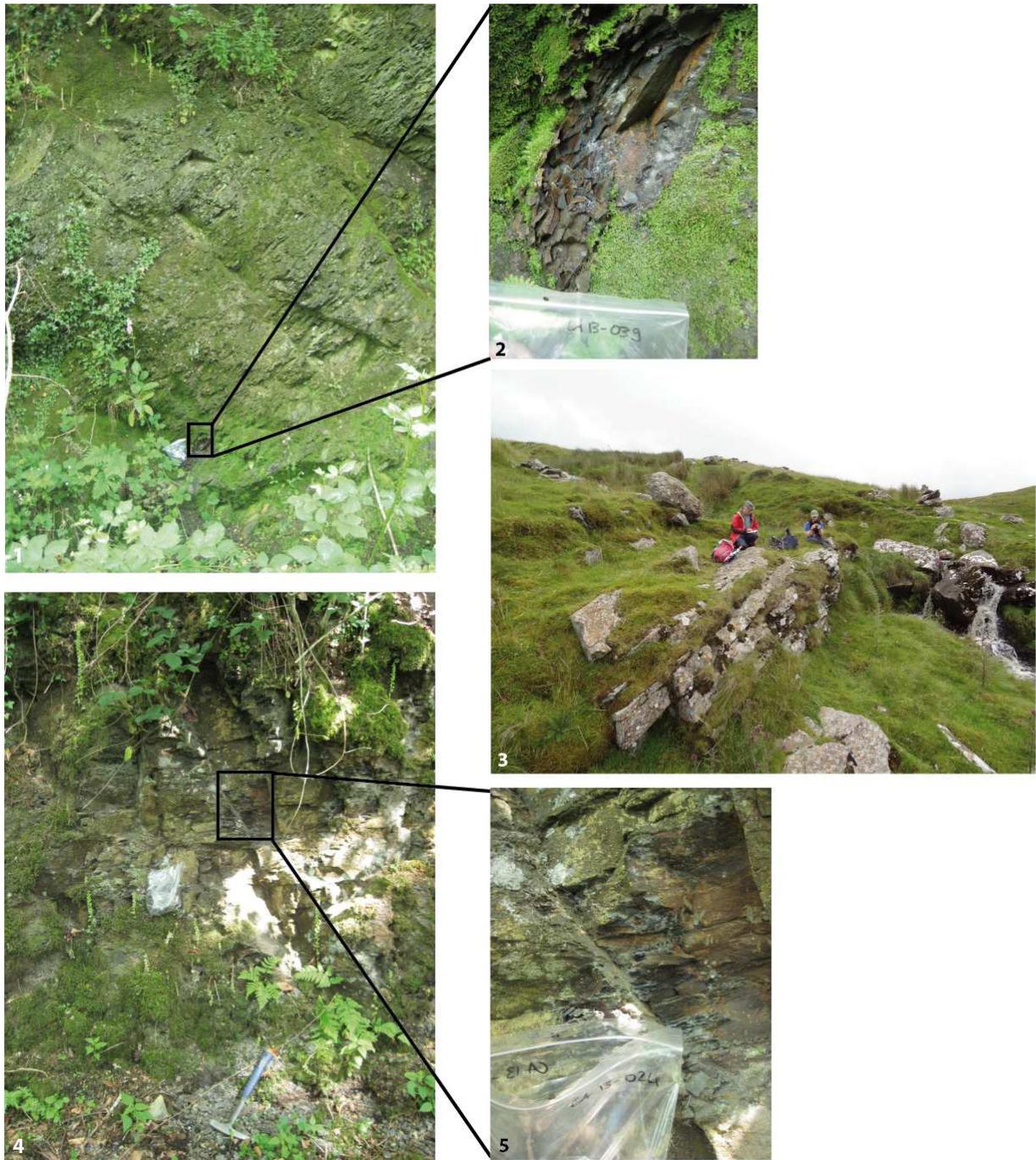
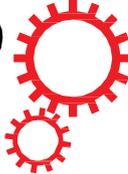


Figure 9: Pictures of selected outcrops in Wales. 1-2 Pontyfenni old quarry in the area of Whitland exposing the upper Arenig Pontyfenni Formation; 3: Hafotty Ffilltirgerig River in the area of the Arenig Fawr exposing the Llyfnant Member of the Carnedd Iago Formation; 4-5: Llanfallteg old railway in the area of Whitland exposing the Llanfallteg Formation straddling the Arenig-Llanvirn boundary.

**3. The nature of Ordovician
limestone-marl alternations
in the Oslo-Asker District
(Norway): witnesses of
primary glacio-eustasy or
diagenetic rhythms?**

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The nature of Ordovician limestone-marl alternations in the Oslo-Asker District (Norway): witnesses of primary glacio-eustasy or diagenetic rhythms?

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Ordovician limestone-marl alternations in the Oslo-Asker District have been interpreted as signaling glacio-eustatic lowstands, which would support a prolonged “Early Palaeozoic Icehouse”. However, these rhythmites could alternatively reflect differential diagenesis, without sedimentary trigger. Here, we test both hypotheses through one Darriwilian and three Katian sections. Our methodology consists of a bed-by-bed analysis of palynological (chitinozoan) and geochemical (XRF) data, to evaluate whether the limestone/marl couplets reflect an original cyclic signal. The results reveal similar palynomorph assemblages in limestones and marls. Exceptions, which could be interpreted as reflecting palaeoclimatological fluctuations, exist at the species level: *Ancyrochitina bornholmensis* seems to be more abundant in the marl samples from the lower Frognerkilen Formation on Nakkholmen Island. However, these rare cases where chitinozoans differ between limestone/marl facies are deemed insufficient for the identification of original cyclicality. The geochemical data show a near-perfect correlation between insoluble elements in the limestone and the marls, which indicates a similar composition of the potential precursor sediment, also in the Frognerkilen Formation. This is consistent with the palynological data. Although an original cyclic pattern could still be recorded by other, uninvestigated parameters, our palaeontological and geochemical data combined do not support the presence of such a signal.

The Ordovician (485–443 Ma) has long been known as a greenhouse period, with a short glaciation during the Hirnantian age (c. 444 Ma)¹. This terminal Ordovician glaciation coincided with the first of the “Big Five” mass extinction events of the Phanerozoic². An emerging body of evidence now suggests that this global cooling and the onset of the “Early Palaeozoic Icehouse” (EPI) may have started much earlier than previously assumed³, i.e. during the early Katian^{4–6}, before the Sandbian⁷ or even during the Early-Middle Ordovician³. This has fundamental importance, because an early phase of cooling could provide a driving mechanism for the major changes in biodiversity during the Great Ordovician Biodiversification Event (GOBE)³.

As compelling as these new ideas are, they remain to be tested. So far, the studies in support of a protracted EPI comprise: (1) $\delta^{18}\text{O}$ data derived from conodont apatite at equatorial palaeolatitudes³ suggesting that the tropical sea surface temperatures (SST) cooled during Early-Middle Ordovician, to stabilize close to modern values of SSTs; (2)

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the sequence stratigraphic architecture of various Ordovician packages, such as those treated herein⁸, the Peninsula Formation (Floian to Darriwilian) in South Africa⁹ and the Darriwilian Hiswah and Dubaydib formations in Jordan¹⁰, which have been suggested to record 3rd and 4th order sea level changes corresponding to glacio-eustatic cycles; (3) microfossil evidence with relatively steep graptolite and chitinozoan equator-to-pole faunal gradients that suggest cooling towards the Hirnantian glacial maximum was already underway in the Sandbian^{7,11}; and (4) General Circulation Models (GCMs) for the Early-Middle Ordovician¹² that suggest a long-term cooling trend through the Ordovician. However, each of these methodologies is inconclusive on its own. Climate proxy data that are limited to the low palaeolatitudes may not be the best recorder of global climate¹³. Ordovician sea level variations are difficult to quantify and often are subject to complex facies interpretations and dating issues. Biogeographical studies of graptolites and chitinozoans, although potentially conclusive for the Late Ordovician, do not yet exist for the Early and Middle Ordovician. Furthermore, the degree to which GCM output approximates real palaeoclimates is limited by the accuracy with which we can quantify the prevailing boundary conditions in deep-time. The aim of this study is to discuss the nature of the Middle-Late Ordovician background climate by scrutinizing some of the stratigraphical evidence.

The large-scale alternation between limestone and marl dominated formations is one of the main features observed in the Ordovician succession of the Oslo-Asker District in Norway¹⁴. According to Nielsen⁸, these alternating formations are the result of changes in depositional depth, potentially representing lower order glacio-eustatic sea level fluctuations. The calcareous formations often are composed of, or include, decimeter scale alternations of limestones and marls. Such fine-grained calcareous rhythmites appear in large epeiric seas through the entire Phanerozoic^{15–17}. The rhythmites in the Oslo-Asker District consist of uncompacted continuous or nodular limestone beds separated by marl (or shale, which is a field-descriptive term and has no meaning in terms of absolute carbonate content) interlayers that are strongly compacted. Transitions between continuous limestone beds and isolated nodular limestone in a marly matrix are observed throughout the succession. The origin of the limestone nodules in the Oslo-Asker District has been long debated. Some authors considered that the nodules formed by dissolution of continuous carbonate layers exposed to undersaturated sea-water¹⁸. Others argued that the nodular limestone are early diagenetic concretions formed by carbonate precipitation in pore space underneath the water-sediment interface¹⁹, eventually collating into limestone beds. The latter interpretation is supported by the majority of authors^{20–22}. Yet other scenarios²³ consider that the nodules are the result of bacterial activity where the sulfate reduction and fermentation by the bacteria led to the production of bicarbonate and sulfide eventually turned into carbonate and pyrite, commonly found in the rhythmites.

In Nielsen's model⁸, these rhythmites, internally, may represent a higher order palaeoclimatological control, in turn driven by orbital forcing. Others argue that such lithologies could be the result of differential diagenesis, i.e., a process of redistribution of calcium carbonate from marl layers to emergent limestone beds by dissolution, migration, and re-precipitation of ions²⁴ regardless of the presence or absence of primary sedimentary rhythms^{17,25–27}. In this scenario, aragonite dissolves in the shallow marine burial environment and eventually cements the uncompacted limestone beds^{24,28}.

Many of the Ordovician Oslo-Asker District rhythmites, if not all, are characterized by large positive excursions in $\delta^{13}\text{C}$ values, as evidenced by data from the Frognerkilen⁶, Solvang⁶ and Skogerholmen (unpubl. data) formations in the Oslo Region and other districts. Bergström *et al.*⁶ identified the excursions in the Frognerkilen and Solvang formations as the Guttenberg Isotope Carbone Excursion (GICE) and Kope (or Rakvere) excursions, respectively. The systematic coincidence between rhythmites and stable isotope excursions suggest that the rhythmites have been deposited under different environmental conditions than the intertonguing dark shale formations, and may thus well represent packages deposited during times of lower order glacio-eustatic lowstands as suggested by Nielsen⁸. Alternatively, one could argue that the environmental conditions that caused the isotope excursions also were responsible for differential diagenesis and the production of rhythmites in those particular intervals: for instance, aragonite is necessary as source to fuel differential diagenesis²⁹, and aragonite is mostly produced on and exported from shallow-water platforms during sea-level high-stands ("Highstand Shedding")^{30,31}. The times of peak isotope values may thus well have been times of aragonite production in the Oslo Region, hypothetically driven by changes in water composition (more oligotrophic) or sea-level (in this case, a relative increase). In this context, and even for the well-documented Hirnantian isotope excursion, it is debated whether the $\delta^{13}\text{C}$ peak values correspond to peak glaciation³². In summary, although the isotope excursions suggest changes in the palaeo-environment, they do not exclude a diagenetic origin for the limestone/marl couplets.

To investigate the depositional conditions of the Oslo rhythmites, we conducted bed-by-bed analyses using palynomorph assemblages (chitinozoans), which are diagenetically inert compounds, combined with x-ray fluorescence (XRF) measurements of insoluble oxides and elements. An original cyclic signal should be reflected in the chitinozoan microfauna, as they are thought to have a planktic mode of distribution and characterize latitudinally restricted water masses that are inferred to be SST-controlled and as such track episodes of major climate change, much like modern zooplankton^{11,33}. We should thus observe different palynomorph assemblages for the two lithologies, if the rhythmites are reflecting a primary environmental signal. Palynomorph assemblages are relatively robust against the effects of differential diagenesis, unlike calcareous microfossils that might be destroyed in the marl interlayers by dissolution and compaction²⁶. However, they do suffer compaction in marls, obscuring some of their morphological characters, in comparison to their limestone-hosted counterparts³⁴. Likewise, when plotting the diagenetically stable oxides and elements percentages and their linear fit, we should observe two distinct populations for the two lithologies, with each regression line having a different slope, pointing to different ratios of these constituents in the precursor sediments of limestones and marls and thus to an original cyclic signal²⁶. The most suitable relation to detect this signal is $\text{TiO}_2/\text{Al}_2\text{O}_3$. However, if such a systematic difference is not observed, i.e., the two populations plot along a similar or equal trend line, the rhythmites can be either a diagenetic enhancement of a primary rhythm, with original differences in parameters that have not been measured or have been destroyed

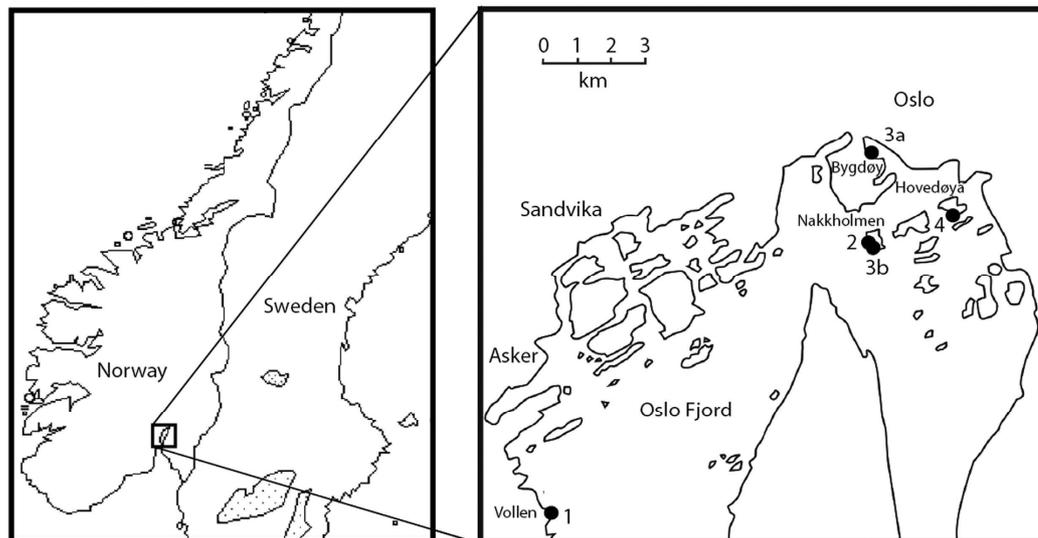


Figure 1. Map of the Oslo-Asker District showing the sampled locations. 1: Huk Formation in Vollen, 2: Arnestad and Frognerkilen formations on Nakkholmen Island, 3a Solvang Formation on the Bygdøy Peninsula, 3b: Solvang Formation on Nakkholmen Island, 4: Skogerholmen Formation on Hovedøya Island. Modified after Grahn *et al.*⁴⁹.

during diagenesis (e.g. primary porosity, permeability, TOC content), or are entirely diagenetic²⁶. This inability to demonstrate unambiguously a diagenetic origin is referred to as the “diagenetic dilemma”²⁶.

We sampled four separate intervals of alternating limestone and marls in different outcrops in the Oslo-Asker District (Fig. 1), i.e., the Lysaker Member of the Huk Formation (Darriwilian), the transition between the Arnestad and the Frognerkilen formations (Sandbian-Katian), the Solvang Formation (lower Katian), and the Hovedøya Member of the Spannslokket Formation (upper Katian) (Fig. 2). A summary of the stratigraphy and sampled sections is presented in the methods section. If the oldest marl-limestone rhythmite in the Oslo-Asker District, the Huk Formation, proves to be an expression of glacioeustasy, this would correlate well with the postulated stabilization of a cool climate by the Middle Ordovician as suggested by Trotter *et al.*³, or with the early cold snap of Turner *et al.*⁹, and would become an important argument for a protracted Ordovician icehouse condition.

Results

In total, 77 samples have been investigated for palynology and 7062 specimens of chitinozoans are recorded (Fig. 3). The section on Hovedøya Island yields the best preserved specimens (Fig. 4) whereas the sections at Vollen, Bygdøy and on Nakkholmen Island contain rather poorly preserved specimens, which hampers identification. This is likely due to the presence of Permian intrusions in the area¹⁴, and, notably for the Huk Formation, the tectonic deformation of the sediments. Differential preservation is also a factor, as the specimens found in limestones are better preserved than the ones found in marls. Sampled sections on Bygdøy and Nakkholmen Island yielded a higher amount of chitinozoans, in general about four specimens per gram of rock, whereas the sections from Vollen and Hovedøya Island yielded only half as many. The results of the palynological (see also Supplementary Figs S1, S3, S5, S7) and XRF analyses (Supplementary Figs S2, S4, S6, S8) are summarized for each stratigraphic interval.

Huk Formation. Sixty samples were collected in the Lysaker Member of the Huk Formation. A first batch was almost barren, and only 22 samples from the second batch, yielding a significant amount of chitinozoans, were retained for further analyses. They yielded 1394 chitinozoans in total, of which 891 were identified to the species level. Five genera and eight species were distinguished in this lowly diverse section (Fig. 3a). *Cyathochitina* is the most abundant genus (73% of the assemblage). It is present throughout the section but becomes increasingly abundant towards the top. The other genera with a marked abundance are *Conochitina*, *Desmochitina*, *Lagenochitina* and *Rhabdochitina*. Their abundance is low but constant through the section. The HCA (Supplementary Fig. S1) shows a complete intermixing of the chitinozoan taxonomic composition between the two lithologies. The DCA (Supplementary Fig. S1) also shows a strong overlap of the taxonomic components between the different lithologies, suggesting a rather similar chitinozoan composition between limestone and marl. Furthermore, the ANOSIM ($R = -0.06$; $p = 0.812$) and PERMANOVA (Pseudo- $F = 0.06$; $p = 0.535$) both show that chitinozoan assemblages are not significantly different between the two lithologies for the entire section. The most abundant species are *Cyathochitina calix* and *Cy. campanulaeformis* (Fig. 4.2). In the lower part of the section *Cy. calix* dominates, and *Cy. campanulaeformis* progressively appears and finally becomes more abundant towards the upper part of the section. The species for the other genera are left in open nomenclature (as ‘sp.’) due to poor preservation. Similar to the analyses at the genus level, we observe no lithology-specific assemblages at the species level, as shown by the HCA and DCA (Supplementary Fig. S1); the ANOSIM ($R = 0.03$; $p = 0.294$) and PERMANOVA (Pseudo- $F = 0.10$; $p = 0.233$) confirm this result.

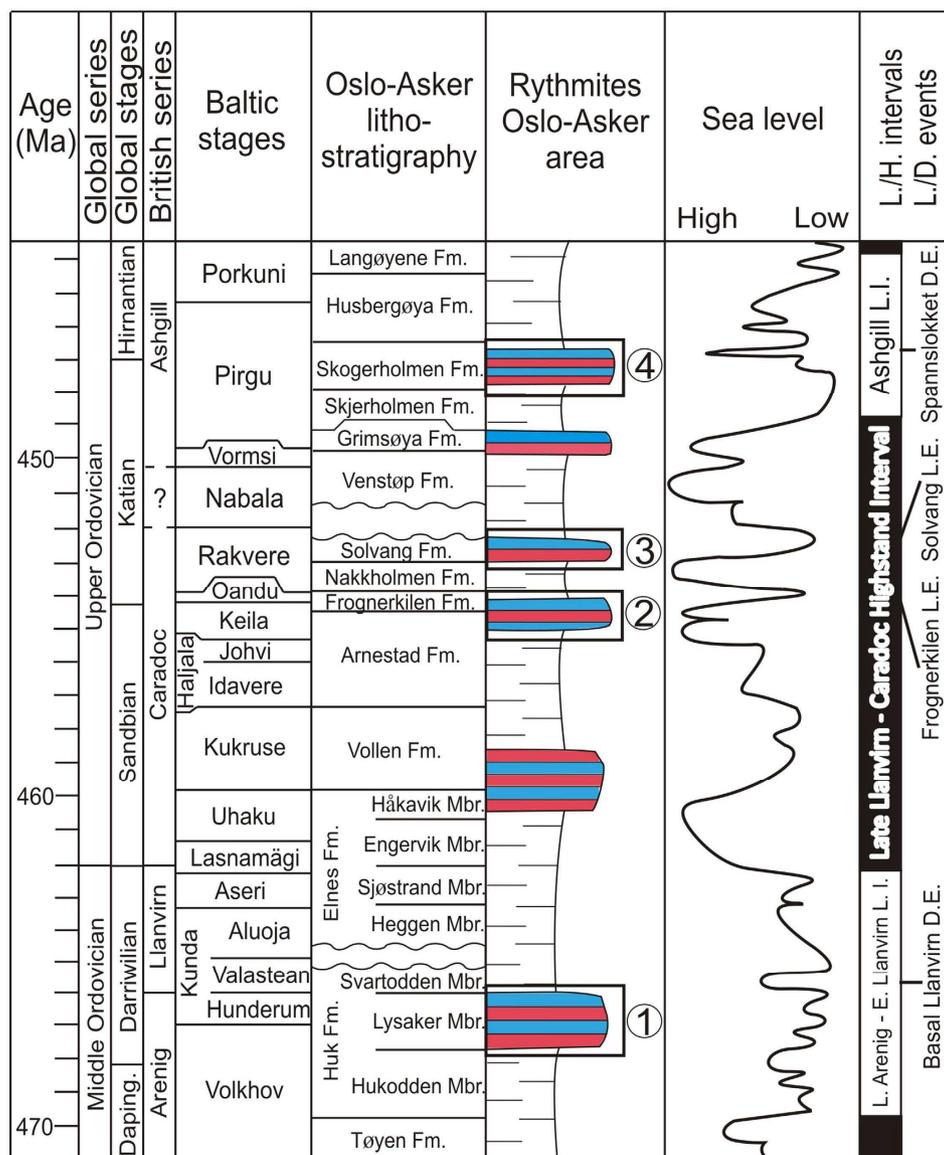


Figure 2. Lithostratigraphical chart of the Oslo-Asker District with the regional Baltic stages, the sea level curve and lowstand/highstand intervals (L./H.I) and lowstand/drowning events (L.E./D.E.) modified from Nielsen²⁷. The black and white bars represent 2nd order oscillations. The numbers refer to the four studied intervals corresponding to an interpreted lowstand event or interval. The red/blue alternations schematically represent the limestone/marl alternations.

The same 22 samples were used for XRF analysis. The bivariate scatter plots of TiO_2 and Al_2O_3 percentages show two groups representing the limestones and marls. Their regression lines show no significant difference in slope ($p = 0.179$, Fig. 5a). This absence of significant difference in slopes between the lithologies is confirmed by the data for the other elements and oxides that are preferentially bound to clay minerals (K_2O , SiO_2 , and Rb), the data for the oxides and elements bound to both clay and calcite minerals (Fe_2O_3 , Zn , MgO), and the data for the elements and oxides bound only to calcite minerals (Sr), except for the MnO values, which show a significant ($p = 0.035$) difference in slopes between the lithologies. All the charts are uploaded as supplementary material (Supplementary Fig. S2).

Arnestad/Frognerkilen formations. Of the 34 samples collected, 24 contain a significant number of palynomorphs. In total, 2712 specimens were identified to 12 genera and 22 species (Fig. 3b). The genus *Spinachitina* is the most abundant throughout the section, comprising 57% of the assemblage, followed by *Conochitina*, *Ancyrochitina*, *Belonechitina*, and *Desmochitina* with much lower and sporadic abundances (respectively, 18%, 9%, 8% and 6%). The other genera present have a very low relative abundance and are not considered (see Fig. 3b). The HCA and DCA show that there is no clear separation between the two lithologies regarding assemblage composition at the genus level throughout the section (Fig. 6). Furthermore, ANOSIM ($R = 0.12$; $p = 0.029$) and

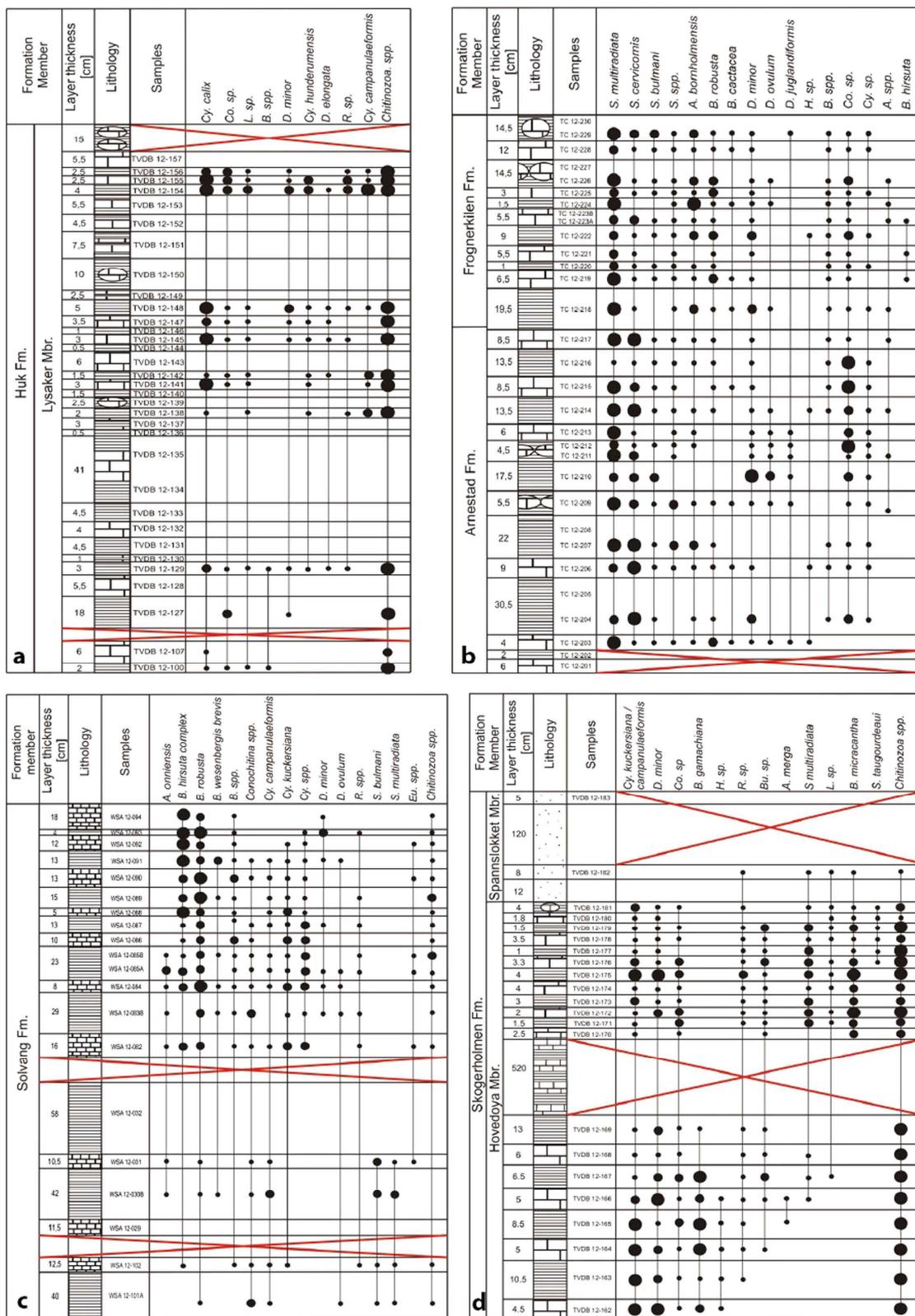


Figure 3. Stratigraphic log and palynomorph assemblages of the investigated sections. (a) Huk Section, (b) Nakkholmen Section, (c) Bygdøy Section, (d) Hovedøya Section. Small dots: <10 specimen per sample, medium dots: 10–40 specimen, big dots: >40 specimen.

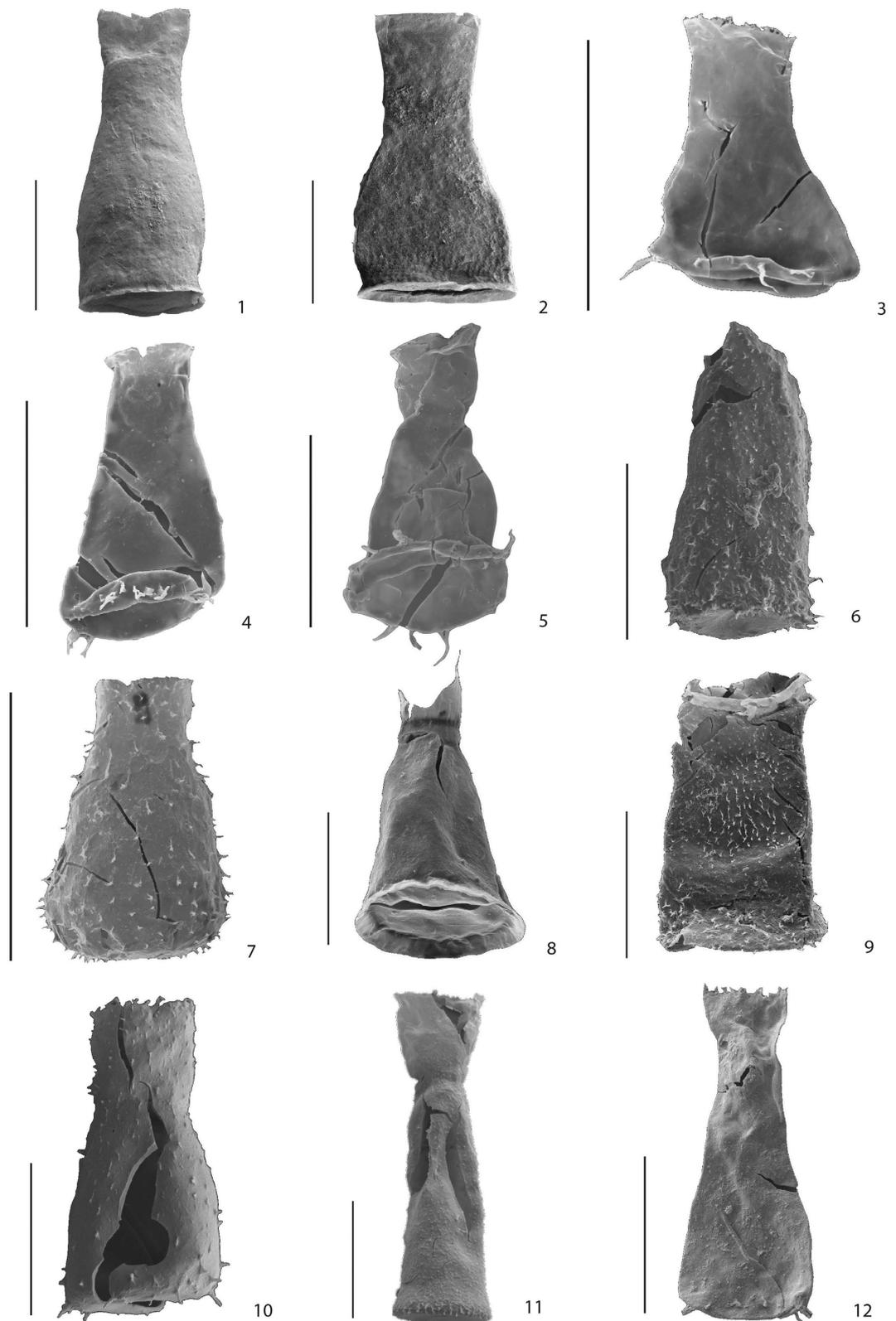


Figure 4. SEM images of selected chitinozoans. 1–2: Huk Formation. 1. *Cyathochitina calix*. 2. *Cyathochitina campanulaeformis*. 3–6: Arnestad/Frognerkilen formations. 3. *Ancyrochitina bornholmensis*. 4. *Spinachitina cervicornis*. 5. *Spinachitina multiradiata*. 6. *Belonechitina robusta*. 7–9: Solvang Formation: 7. *Belonechitina hirsuta* complex. 8. *Cyathochitina campanulaeformis*. 9. *Belonechitina robusta*. 10–12: Skogerholmen Formation: 10. *Belonechitina gamachiana*. 11. *Belonechitina micracantha*. 12. *Spinachitina* cf. *taugourdeau*. Scale bar: 100 μ m.

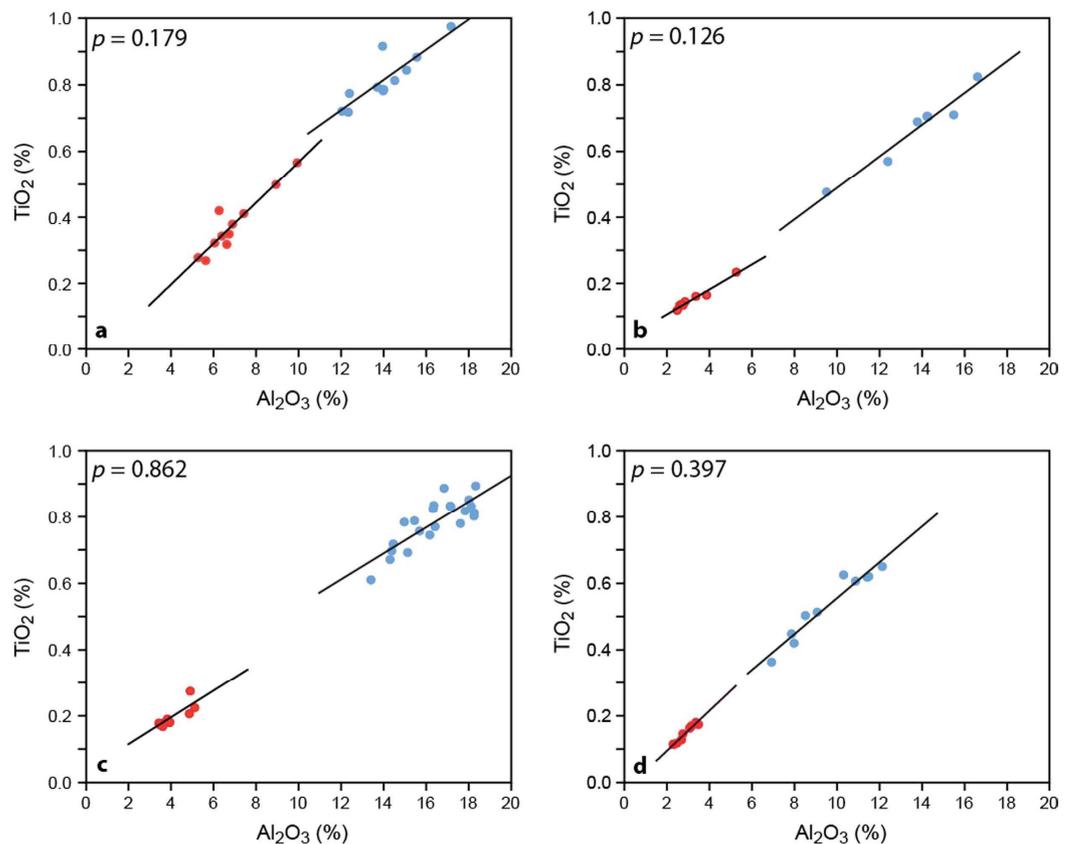


Figure 5. $\text{TiO}_2/\text{Al}_2\text{O}_3$ data for: (a) Huk Formation, (b) Arnestad/Frognerkilen formations, (c) Solvang Formation, (d) Skogerholmen Formation. The data in each sections plot on regression lines with a high correlation between the two lithologies. Limestones are in red and marls in blue. P values <0.05 would indicate a significant difference between the slopes.

PERMANOVA (Pseudo- $F = 0.15$; $p = 0.012$) confirm that the chitinozoan assemblage is not influenced by the lithology (Fig. 6). Although these two tests indicate a significant difference ($p = 0.029$) in composition between limestone and marl, the R value of the ANOSIM indicates that the groups are barely distinguishable ($R = 0.12$). This pattern indicates that one or a few taxa within the assemblage may have different abundances between lithologies. The ANOVA performed on each taxon separately (Supplementary Fig. S3) indicates that only one genus has a significant difference in mean abundance between the two lithologies ($F = 6.21$; $P = 0.015$): *Ancyrochitina* thus has a lower relative abundance in limestones and a higher relative abundance in marls. Interestingly, the genus *Conochitina* has a different relative abundance, although this is not significant ($F = 3.25$; $p = 0.075$). In contrast, the genus *Spinachitina*, which is the most abundant, is clearly not affected by the lithology ($F = 0.04$; $p = 0.840$).

At species level, *Spinachitina multiradiata* (Fig. 4) is the most abundant (35%) and ranges throughout the section. The second most abundant species is *Conochitina* sp. with 18%. We observe a biostratigraphic separation between the upper part of the section, corresponding to the Frognerkilen Formation, and the lower part of the section, corresponding to the Arnestad Formation: *S. cervicornis* (Fig. 4) is abundant in the latter formation and decreases towards the top (Fig. 3) while *Ancyrochitina bornholmensis* and *Belonechitina robusta* (Fig. 4) become more abundant. Much as observed at the genus level, the HCA and DCA show no clear separation between the two lithologies regarding assemblage composition at the species level throughout the entire section (Fig. 6). Similarly, ANOSIM ($R = 0.11$; $p = 0.049$) and PERMANOVA (Pseudo- $F = 0.11$; $p = 0.023$) confirm that chitinozoan assemblages are not generally influenced by the lithology, bar perhaps a few taxa. The ANOVA (Supplementary Fig. S4) indicates that only one species has a significant difference in mean abundance between the two lithologies ($F = 4.19$; $p = 0.044$), i.e., *A. bornholmensis*. Again, the most abundant taxon, *Spinachitina multiradiata*, does not display a significantly different relative abundance between lithologies ($F = 0.27$; $p = 0.869$).

Out of the 24 samples analyzed for palynology, 15 were used for XRF. As for the Huk Fm., the slopes of the regression lines from limestones and marls are not significantly different for $\text{TiO}_2/\text{Al}_2\text{O}_3$ ($p = 0.126$, Fig. 5b), as also observed for K_2O , but the other elements and oxides bound to clay minerals present a significant difference ($p(\text{SiO}_2) = 0.009$, $p(\text{Rb}) = 0.003$) between the limestones and marls. The elements bound to both clay and calcite minerals display no difference between the limestone group and the marl group for Zn and Fe_2O_3 , after removing two outliers of Fe_2O_3 in samples TC 12-226 and TC 12-203, but the trend lines from MgO present a significant difference ($p = 0.035$) between the lithologies. The elements bound to calcite minerals show a significant difference

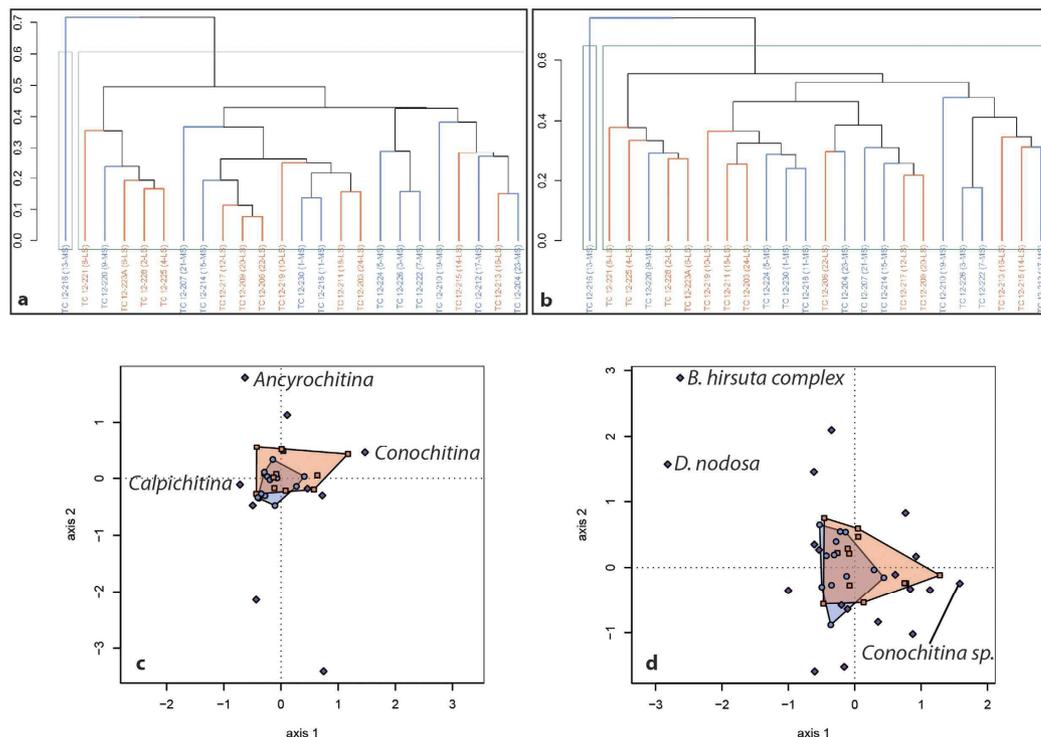


Figure 6. Statistical analyses for the chitinozoan assemblages of the Arnestad/Frognerkilen formations. **(a)** Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at the genus level shows no grouping. **(b)** Hierarchical Cluster Analysis at species level, showing no grouping, same as for genus level. **(c)** Detrended Correspondence Analysis (Bray-Curtis index) at genus level shows overlapping of the assemblage from both lithologies indicating a globally similar composition. **(d)** Detrended Correspondence Analysis at species level indicating a similar composition, same as for genus level. Limestones are in red and marls in blue.

in slopes for Sr ($p = 0.047$), when two peak values of Sr from the samples TC 12-226 and TC 12-203 were removed, but not for MnO (Supplementary Fig. S4).

Solvang Formation. In this section, 18 of the samples collected yielded palynomorphs. Out of 1612 chitinozoans found, 1535 specimens were successfully identified to the genus level and 1209 specimens down to species level (Fig. 3c). In total, 11 different genera have been encountered and 16 different species were identified with confidence. *Belonechitina* is the most abundant genus (56% of the assemblage) and *Cyathochitina* is the second most abundant, representing 20% of the assemblage. The genus *Spinachitina* is moderately abundant (7%) and is only present in the four first samples of the lower part of the section (WSA 12-101B, WSA 12-102, WSA 12-030B, WSA 12-031), where the overall abundance and diversity of palynomorphs are low. Other genera occur in low abundance (Fig. 3c). All the genera are equally present in limestones and marls as shown by the HCA, DCA, ANOSIM ($R = -0.05$; $p = 0.684$) and PERMANOVA (Pseudo- $F = 0.03$; $p = 0.647$) (Supplementary Fig. S5). At the species level, the *Belonechitina hirsuta* complex (Fig. 4) is the most abundant 'species'³⁵ (27%). The second most abundant species is *Belonechitina robusta* (Fig. 4) representing 23% of the assemblage. *Cyathochitina campanulaeformis* and *C. kuckersiana* (Fig. 4) have been grouped together as their onerous differentiation mainly revolves around the length of a fragile carina. They are present throughout the section with a low relative abundance. The species *Spinachitina bulmani* and *Spinachitina multiradiata* are found only in the four basal samples, which clearly separates them from the rest of the section. At the species level, there is no evidence of lithofacies control on the palynomorph assemblages as suggested by the HCA, DCA, ANOSIM ($R = -0.01$; $p = 0.443$) and PERMANOVA (Pseudo- $F = 0.05$; $p = 0.516$) (Supplementary Fig. S6).

The same micropalaeontology samples were used for XRF except for the lowest two: WSA 12-101B and WSA 12-102. Once again, the slopes of the trend lines of both limestone and marls are similar for TiO_2/Al_2O_3 ($p = 0.862$, Fig. 5c), thus showing no difference in slopes between the two lithologies, nor do the other elements bound to clay minerals (K_2O , SiO_2). The Rb data, when removing an outlier from the sample WSA-074A, are an exception, displaying a significant difference in slopes ($p = 0.029$). There is no difference in slopes for both lithologies in the elements included in both crystal lattices of calcite and clay minerals such as Zn and Fe_2O_3 , even when removing two peak values of Fe_2O_3 from WSA-12-090 and WSA-12-074A, but MgO present a significant difference in slopes of $p = 0.0003$ between the limestones and the marls. The elements only bound to calcite minerals present a significant difference in slopes for Sr ($p = 0.001$), but not for MnO. (Supplementary Fig. S6).

Skogerholmen Formation. Out of 31 samples collected from this section, 21 yielded sufficient amounts of palynomorphs. In total, 2445 specimens of chitinozoans were identified, and 10 genera were encountered representing 13 species (Fig. 3d). In the Hovedøya Section, *Cyathochitina* is the most common genus (25%) and it is found throughout the section although in very variable abundances. The second most abundant genus is *Belonechitina* (24%). It is also present throughout the section but its concentration is rather constant, except in the upper part where it becomes rare. The genus *Desmochitina* comprises 16% of the assemblage. Its abundance in the section is very variable, half of the total population being found in three samples. The genus *Spinachitina* (13%) is found almost exclusively in the upper part of the section, except for five specimens scattered in the lower part of the section. Similar to the three other intervals studied, the HCA and DCA reveal no specific grouping of palynomorphs between marls and limestones at the genus level, and the statistical analysis is in agreement (ANOSIM: $R = -0.06$; $p = 0.737$; PERMANOVA: Pseudo- $F = 0.01$; $p = 0.925$), indicating that the lithology has no influence on the assemblages (Supplementary Fig. S8). At the species level, the most abundant species are *Cyathochitina kuckersiana* and *C. campanulaeformis*, grouped together (25%). *Belonechitina micracantha* and *B. gamachiana* (Fig. 4) are rather abundant (13% and 12% of the assemblage, respectively). *Belonechitina micracantha* appears when *B. gamachiana* disappears. The species *Spinachitina multiradiata* appears in the lower part of the section with only five specimens and becomes relatively abundant (12%) in the upper part of the section. *Desmochitina ovulum* is moderately abundant (11%) throughout the section. *Spinachitina* cf. *taugourdeau* (Fig. 4) has a very low abundance, but is remarkable as a biostratigraphical index species of the basal Hirnantian or Porkuni Baltic stage. The confirmation of this species, here in open nomenclature, would be important for the further interpretation of this section. Much like at the genus level, the HCA, DCA, ANOSIM ($R = -0.07$; $p = 0.833$) and PERMANOVA (Pseudo- $F = 0.01$; $p = 0.932$) (Supplementary Fig. S8) show no significant difference in species assemblages between the two lithologies.

The same 21 samples were used for XRF. As in the sections discussed above, the two lithologies present no significant difference in their regression slopes for $\text{TiO}_2/\text{Al}_2\text{O}_3$ ($p = 0.397$, Fig. 5d), as for the other elements and oxides bound to clay minerals (Rb, SiO_2), except for the K_2O data that show a significant difference in slope ($p = 0.016$) between the limestones and marls. The elements and oxides that can be included both in the calcite lattice and in clay minerals present a relatively similar trend line with no significant difference in slopes between both lithologies for MgO and Fe_2O_3 . Zn is the exception, where the trend lines of limestones and marls are significantly different ($p = 0.015$), and the same applies for the elements and oxides bound to calcite minerals ($p(\text{Sr}) = 0.015$, $p(\text{MnO}) = 0.0003$). (Supplementary Fig. S9).

Discussion

In the four intervals studied, the assemblages of chitinozoans are generally independent of the lithology sampled (in terms of relative abundance). The HCA and DCA fail to demonstrate a clear separation in composition of assemblages between the limestones and the marls. The ANOSIM and PERMANOVA confirm this result, with very low R values between -0.10 to 0.15 indicating no difference between the lithologies, except for the Nakkholmen section. All these methods indicate that the lithology does not control the total taxonomic composition of the samples. However, one exception is observed: the ANOVA reveals that the genus *Ancyrochitina* and the species *Ancyrochitina bornholmensis*, found in the Arnestad/Frognerkilen Formation interval, are significantly more abundant in the marls. It is important to note that the ability to accurately identify species sometimes depends on differential preservation in certain lithologies: limestones, for instance, notably allow for fine details and relief to be preserved, whereas specimens in marls are often flattened and fine ornamental details destroyed. The identification of *A. bornholmensis*, however, does not rely on such vulnerable criteria, suggesting that the systematic difference in relative abundance of this species could reflect primary differences. Such a signal could support Nielsen⁸ who interpreted the Frognerkilen Formation as a lowstand event, identified by Bergström^{6,36} as the GICE, one of the first glacial episodes in the EPI^{4,37}. However, the cyclic variation of only one species amongst many, in a very restricted part of the section (10 samples) remains unconvincing.

Another potential problem linked to differential preservation is observed in the lower part of Skogerholmen Formation, relating to the species *Belonechitina gamachiana* and how it appears in limestones and marls. The shape and size of the specimens are the same, but the specimens from limestones have long basal spines combined with short ones along the chamber, whereas in marls they just carry a few remains of spines and often appear almost glabrous.

To identify a primary signal from the geochemical XRF analyses from the rhythmites, we should expect two trend lines with different slopes for the limestones and marls when plotting the diagenetically stable trace elements and oxides³⁸. In all of our four intervals, the $\text{TiO}_2/\text{Al}_2\text{O}_3$ data, which is the most suitable to detect a primary difference in the sediment, show no significant difference in the slopes of the trend lines between the limestones and marls. The other oxides and elements bound to clay minerals present more contrasted results in all the intervals except for the Huk Formation, where we found no difference in slopes for the four elements and oxides tested: The Arnestad/Frognerkilen formations and the Hovedøya Member display significant differences in slopes for K_2O . The Arnestad/Frognerkilen formations and the Solvang Formation also show significant differences in slopes for Rb. These differences in slopes can be explained either by the fact that the Huk Formation is the most diagenetically overprinted section, or because the three other sections had slight differences in their precursor sediments. The elements and oxides that can be included in both the calcite lattice and in clay minerals display mixed results as well as the elements and oxides only bound to carbonates. This is mainly due to the high dispersion of the data. The overall results are in good agreement with the process of carbonate redistribution by differential diagenesis. The high correlation of diagenetically stable elements in limestones and marls indicates that the original clay mineral composition was rather homogeneous, which suggests no major difference in clay mineral input during “limestone times” and “marl times”. Even when plotting the data from the Frognerkilen Formation (where minor differences are observed in the palynomorph assemblages), we observe an excellent correlation between the lithologies, which

is consistent with our interpretation that the cyclic signal in the abundances of a single species, *A. bornholmensis*, probably is not significant. The outlier XRF results we removed, from TC 12-203 (limestone) and TC 12-226 (marl) in Nakkholmen and WSA-12-090 (limestone) and WSA -12-074A (marl) in Bygdøy, represent a mix of both lithologies, so this does not influence the results.

In summary, in the dataset we collected, there is no evidence suggesting a primary rhythm. Nevertheless, as indicated in the introduction, this does not prove that these rhythmites are entirely of diagenetic origin. Differences may have existed that have been destroyed during diagenesis, or the proxies we measured may have been insensitive to the environmental cycles at work. For instance, chitinozoans do not respond directly to water depth or sea level changes (much less so than, e.g., acritarchs³⁹) but the distribution of their assemblages is driven by SST¹¹. So in order to observe a systematic difference in the palynomorph assemblages between limestone and marl beds, in a scenario where these reflect a glacial/interglacial climate signal, our sampling site, the Oslo-Asker District, would have needed to be positioned at a certain latitude, prone to be crossed by the shifting boundary between the latitudinal chitinozoan biotopes in every climate change cycle. If our zone of investigation stays within the same latitudinal biotope, even while it is contracting and expanding, those faunal variations will not be recorded in the cyclic sediment, and the environmental signal will not be clearly expressed. Nevertheless, during the time slabs investigated, the palaeolatitudinal position of the Oslo-Asker District shifted from approximately 50–45°S during the Early Ordovician to 30°S in the Late Ordovician^{40,41}. The study site thus occupied the mid-latitudes during much of the Ordovician, which should constitute an appropriate position to detect polar front migrations during periods of extreme climate change, as we know from studies on the Pleistocene⁴² as well as on the Ordovician^{11,33}. A last aspect where chitinozoans may be useful to elucidate the nature of the rhythmites is as a high-resolution biostratigraphic marker. If the interpreted glacio-eustatic lows can be correlated to similar events in other epicratonic basins, this considerably strengthens the case for the rhythmites to be records of glaciations. Unfortunately, due to the poor preservation of the specimens recovered, we did not obtain sufficiently high-resolution data to make valid comments in this context for most of the rhythmites.

Conclusion

In this study, we used different diagenetically inert parameters as a proxy to determine the origin of limestone-marl alternations, previously interpreted as the result of palaeoclimatic variations. Although the cyclicity is obvious in the outcrop, our data does not allow us to prove a primary origin of the signal, but rather suggests a diagenetic scenario: The micropaleontological analyses reveal no significant differences in palynomorph assemblages between the two lithologies, and the geochemical analyses show trend lines (linear fit) with similar slopes for limestones and marls, with a high correlation of diagenetically stable elements normalized to Al₂O₃. In the Frognerkilen Formation, one species seems to have different concentrations in each of the lithologies. However this result is considered insignificant in comparison to the overlarge majority of the palynological data, and it is not supported by the geochemical study. It is important to re-state, however, that lack of evidence for an original cyclic signal does not necessarily imply an entirely diagenetic origin of the rhythmites.

Methods

Stratigraphy and Sample location. During the Early Palaeozoic, the Oslo-Asker District⁴³ (Fig. 1) was a cratonic basin on the Baltica palaeoplate⁴⁴. A detailed review of its Ordovician stratigraphy by Owen *et al.*¹⁴ summarized the available data^{45,46,47}. Nølvak & Grahn⁴⁸ and Grahn *et al.*⁴⁹ gave a preliminary account of the chitinozoan biostratigraphy. The stratigraphy of the four studied intervals is summarized below:

- (1) The oldest interval comprises the Huk Formation and its three members¹⁴ (Fig. 2). The formation is about 6 m thick at the sampling location, and consists of massive limestones of the Hukodden Member and the Svar-todden Member, bracketing the middle Lysaker Member, which is an alternation of nodular limestone and tectonised marl, and is the interval studied here. The formation ranges from the early Volkhov Baltic Stage to upper part of the Kunda Baltic Stage⁵⁰. The Huk Formation was sampled and measured about one km south of Vollen (Fig. 1), at the junction of Elnesknausene road and Øvre Elnes Vei road (N59°47'49.2" E10°29'17.9").
- (2) The second interval comprises the Arnestad Formation⁵¹ – Frognerkilen Formation transition (Fig. 2). The former formation is 17.5 m thick and consists mainly of thick marl beds (30–40 cm) with only thin nodular orbbed limestone layers in between. It belongs to the Haljala and Keila Baltic stages⁸. The overlying Frognerkilen Formation¹⁴ comprises about 9.5 m of rubbly limestone changing upwards into nodular limestone and marls, and belongs to the Keila and Oandu Baltic stages⁸. This interval was measured and sampled at the southwestern edge of Nakkholmen Island in the Oslo Fjord (N59°53'17.48" E10°41'29.17") (Fig. 1).
- (3) The Solvang Formation⁴⁷ (Fig. 2) has a thickness of 12 m at "Rødløkken Shore" and of 14.5 m on Nakkholmen Island, and belongs to the Rakvere Baltic Stage⁸. The Solvang Formation is developed as irregularly bedded and nodular limestone up to 20 centimeter thick with intervening calcareous marl layers that can be up to 60 cm in thickness. This third interval was mainly measured and sampled on the Bygdøy Peninsula, in a locality known as 'Rodeløkken Shore' (N59°54'54.07" E10°41'28.92") (Fig. 1.3a). Because the base of the formation is not well exposed at this location, a second section of the Solvang Formation was measured and sampled on the south-western part of Nakkholmen Island (N59°53'19.03" E10°41'31.52") (Fig. 1.3b). Two samples from the base of the formation from Nakkholmen Island complete the dataset from the 'Rodeløkken Shore'.
- (4) The last interval comprises the Skogerholmen Formation¹⁴ (Fig. 2) and its two members. The formation consists of alternating limestone, marl and siltstone and is about 35 m thick and it represents the Pirgu Baltic Stage⁸. It comprises two members, i.e., the upper Spannslokket Member and the lower Hovedøya Member, the latter studied here. The Skogerholmen Formation was sampled and measured at the south-west corner of Hovedøya Island (N59°53'32.0" E10°43'38.2") (Fig. 1).

Palynological analyses. The samples (50 g to 500 g) were collected bed-by-bed. The palynological analyses were carried out at the University of Lille (France) and Ghent University (Belgium). The protocol involves crushing the rock samples for a first acid treatment of 38% HCl during 24 hours. We used about 40 g for the marls (20 g in UGent) and 100 g for the limestones (30 g in UGent). The residue was then washed, prior to a second acid treatment with c. 200 ml 40–45% HF which was agitated (Lille) or heated to 80 °C (UGent) for 12 to 24 hours. Finally, the residues were washed with warm 38% HCl to remove any newly formed F-compounds before neutralization and filtering at 51 µm. The residues on the sieves were handpicked using a binocular microscope at 25–50 times magnification, and then identified with an SEM: a FEI Quanta 200 (Lille) and a JEOL JSM6400 (UGent).

The chitinozoan taxonomic composition was investigated using multivariate classification and ordination methods, as well as statistical tests. The dataset consists of abundance data (counts of chitinozoan specimens) in each sampled bed. First, a hierarchical cluster analysis (HCA) based on the Bray-Curtis similarity matrix and the UPGMA (Unweighted Pair Group Method with Arithmetic mean) linkage algorithm was performed to initially evaluate if the two lithologies cluster in two different groups or are mixed together. In the former case, this would indicate that the two lithologies have distinct taxonomic compositions. Alongside the HCA, a detrended correspondence analysis (DCA) has been applied. The purpose of this ordination method is to evaluate if some taxa are restricted to a specific lithology and consequently ordered along a gradient. The computed DCA was also based on the Bray-Curtis similarity matrix. Next, in order to have a statistical evaluation of the (dis)similarity of the chitinozoan taxonomic composition between the two lithologies, two multivariate tests have been performed: a one-way analysis of similarity (ANOSIM), and a one-way permutational multivariate analysis of variance (PERMANOVA). These tests were performed based on the Bray-Curtis similarity matrix, with 1000 permutations, and by setting the significance level at $p = 0.05$. Finally, an analysis of variance (ANOVA) has been performed to test whether the difference in mean abundance is statistically different between the two lithologies for each taxon separately. All these methods (HCA, DCA, ANOVA, ANOSIM, and PERMANOVA) are established methods for multivariate data analysis^{52–56}. The descriptive, exploratory and statistical analyses of chitinozoan data have been performed using the environment R⁵⁷ version 3.1.2 with the packages “vegan”⁵⁸ and “epaleo” (C. Monnet, 2015, unpublished). The data analyses have been performed at two different taxonomic levels (genus and species), across the region as well as for each section separately. Due to significantly different sample sizes across the studied strata within and amongst the sections (chi square tests result into $p < 0.001$ for all sections and taxonomic levels), abundances of taxa within sampled beds were converted into relative proportions prior to the analyses.

XRF analyses. In parallel, the samples were processed at the University of Erlangen for geochemistry. The samples were first crushed in a hydraulic press and finely ground and homogenized in a vibratory disc mill (Retsch RS 1, 50 ml agate grinding set). After drying in an oven at 105 °C for about 12 hours, 1.0006 g ± 0.6 mg of the sample was weighted in a porcelain crucible and stored in a muffle furnace at 1030 °C for 12 hours, pre-glowing the sample material, in order to measure the loss of ignition. The pre-glowed material was melted step-by-step with 4.830 g of lithium tetraborate (Li₂B₄O₇) as a flux, and about 230 mg of di-iodine pentoxide (soldering flux), and the liquid was cast into a coquille. For the melting process, the manually homogenized compound was filled into platinum crucibles (98% Pt and 2% Au). The Oxiflux fusion system comprises three oxidation level/burners (450 °C, 550 °C, 650 °C) and two major burners (950 °C and 1050 °C). The quantitative major and trace elements analyses were carried out using a Spectro Xepos He energy-dispersive XRF spectrometer. The KH standard for limestone (Zentrales Geologisches Institut Berlin) and the JLs-1 standard for marls (Geological Survey of Japan) were used for XRF spectrometry. The XRF analyses allow us to test for diagenetic redistribution of major and/or trace elements. The elements that are part of the siliciclastic portion of the sediment, such as elements bound to clay minerals or heavy minerals like rutile, are less mobile than the calcareous components. When the calcite dissolution takes place, it results in a passive enrichment of insolubles like Ti or Al in the marl beds and a passive dilution of insolubles in the limestone beds. The concentrations of the major element (Si, Ti, Al, Fe, Mn, Mg, Ca, Na, K, P) and 12 trace elements (Ba, Cr, Ga, Nb, Ni, Pb, Rb, Sr, Th, V, Y, Zn, Zr) have been measured, specified as oxides (wt. %) for the major elements and single elements (ppm) for the trace elements. The elements are normalized relative to Al, because aluminum oxides do not dissolve at the usual pH and redox conditions during diagenetic alteration of deposits. The major and trace elements can be divided into three groups: the first group includes elements that are preferentially bound to clay minerals, such as Ti, Al, K, Rb and Si. Another group of elements (Mg, Fe, and Zn) can be identified by their preferential inclusion in the crystal lattice of calcite and clay minerals. A last group of elements are preferentially incorporated in the carbonates (Sr, Mn). The ratio between TiO₂/Al₂O₃ is particularly appropriate to detect primary differences in the sediment because TiO₂ shows a wide range for different clay minerals²⁶. If the rhythmites record an environmental signal, we should observe trend lines with different slopes for the limestones and marls, whereas a similar slope suggests they can potentially emerge, diagenetically, from a single progenitor sediment²⁶. The trend lines between the various elements and oxides normalized with Al₂O₃ have been computed by a linear fit with the major axis approach for limestones and marls separately. The difference in the slopes of these trend lines has been assessed statistically using the maximum likelihood estimate for the common slope and the Bartlett-corrected likelihood ratio test⁵⁹, as implemented in the software PAST⁶⁰ version 3.09.

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Author Contributions

T.R.A.V., A.M. and A.T.N. designed the research project; A.T.N., T.R.A.V., T.C., W.S. and O.H. conducted field work; C.E.A.A., T.C., W.S. conducted the palynological experiments; L.M.E. conducted the XRF experiments; C.M. and O.H. performed statistical analyses; T.R.A.V. supervised C.E.A.A. (PhD), T.C. (MSc) and W.S. (MSc), A.M. supervised L.M.E. (MSc). All authors reviewed the manuscript.

Additional Information

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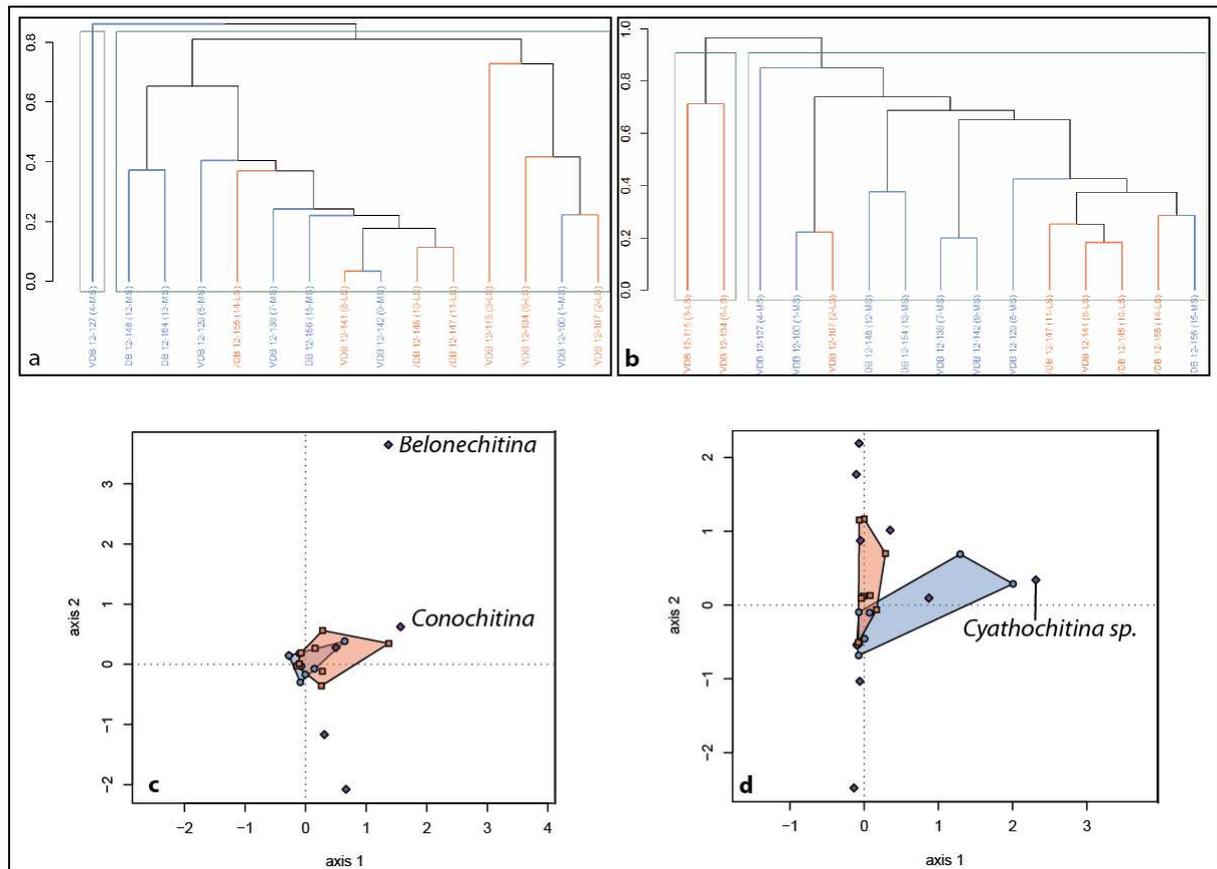
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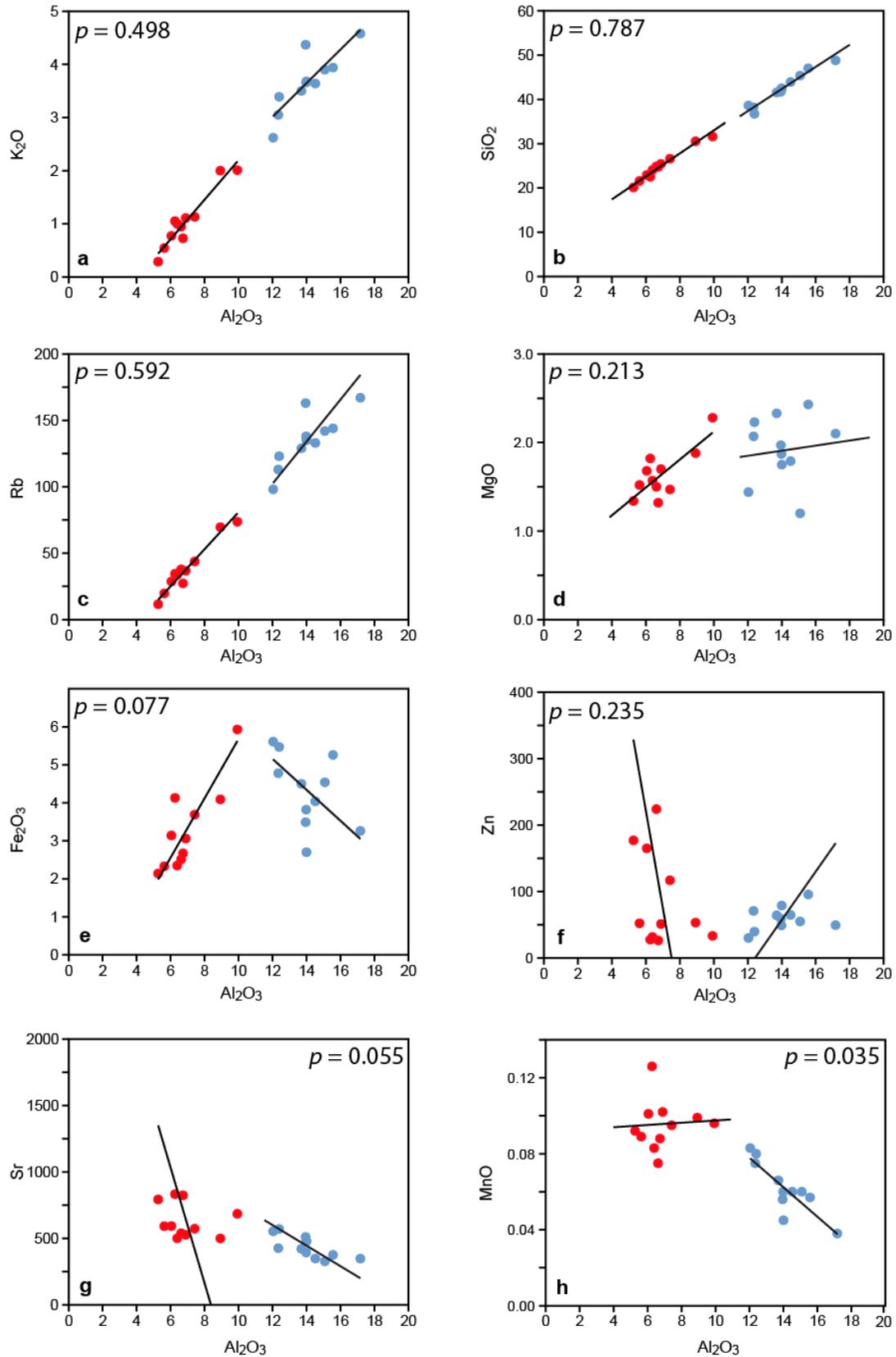
3.1 Supplementary information

The nature of Ordovician Limestone-marl alternations in the Oslo-Asker area (Norway): witnesses of primary glacio-eustasy or diagenetic rhythms?

Chloé E. A. Amberg, Tim Collart, Wout Salenbien, Lisa M. Egger, Axel Munnecke, Arne T. Nielsen, Claude Monnet, Øyvind Hammer & Thijs R. A. Vandenbroucke.



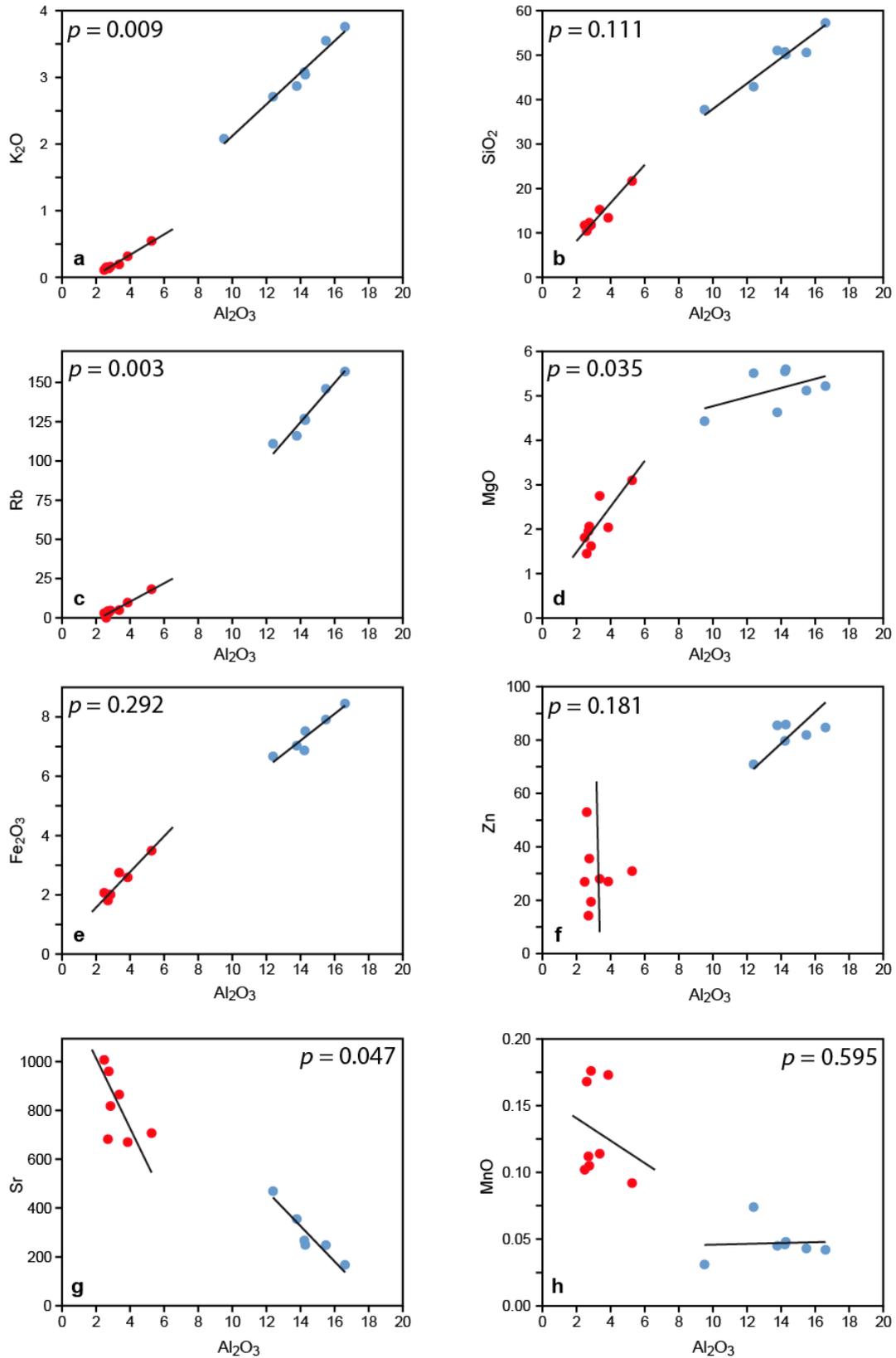
Supplementary Figure S1. Statistical analysis for the chitinozoan assemblages of the Lysaker Member of the Huk Formation. (a) Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at genus level. (b) Hierarchical Cluster Analysis at species level. (c) Detrended Correspondence Analysis (Bray-Curtis index) at genus level. (d) Detrended Correspondence Analysis at species level. The analyses indicate a similar composition of assemblages. Limestones are in red, marls in blue.



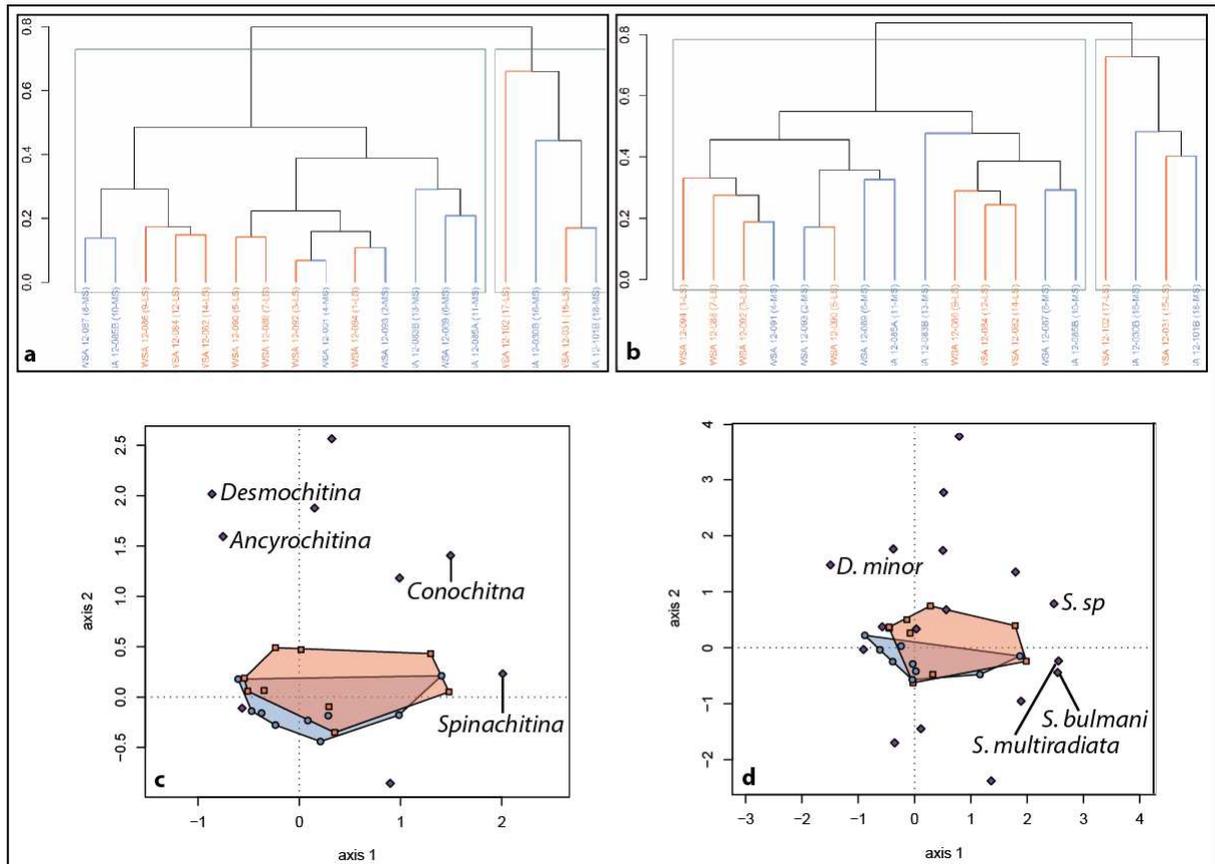
Supplementary Figure S2. XRF element ratios for the Lysaker Member of The Huk Formation. a-c: Elements preferentially bound to clay minerals. d-f: Elements preferentially bound to clay and calcite minerals. g-h: Elements bound to calcite minerals. Limestones are in red and marls in blue. P values < 0.05 indicate significant difference between the slopes.

Taxa	F	P
<i>Ancyrochitina</i>	6.21	0.015
<i>Ancyrochitina bornholmensis</i>	4.19	0.044
<i>Conochitina</i>	3.25	0.075
<i>Belonechitina hirsuta</i>	2.95	0.090
<i>Conochitina sp</i>	2.80	0.098
<i>Rhabdochitina</i>	2.59	0.111
<i>Rhabdochitina sp</i>	2.59	0.111
<i>Ancyrochitina omniensis</i>	2.19	0.143
<i>Lagenochitina</i>	2.17	0.145
<i>Lagenochitina sp</i>	2.17	0.145
<i>Desmochitina ovulum</i>	2.05	0.156
<i>Belonechitina wesenbergis brevis</i>	1.73	0.192
<i>Desmochitina nodosa</i>	1.61	0.208
<i>Belonechitina cactacea</i>	1.60	0.210
<i>Euconochitina</i>	1.48	0.228
<i>Euconochitina sp</i>	1.48	0.228
<i>Bursachitina</i>	1.28	0.261
<i>Bursachitina sp</i>	1.28	0.261
<i>Calpichitina</i>	1.27	0.263
<i>Calpichitina sp</i>	1.27	0.263
<i>Ancyrochitina sp</i>	1.00	0.320
<i>Belonechitina hirsuta complex</i>	0.87	0.353
<i>Cyathochitina</i>	0.86	0.357
<i>Cyathochitina calix</i>	0.82	0.367
<i>Spinachitina bulmani</i>	0.74	0.392
<i>Desmochitina</i>	0.42	0.519
<i>Belonechitina</i>	0.38	0.538
<i>Belonechitina robusta</i>	0.31	0.580
<i>Spinachitina sp</i>	0.23	0.634
<i>Desmochitina minor</i>	0.21	0.645
<i>Cyathochitina huderumensis</i>	0.18	0.674
<i>Cyathochitina gr.campanulaeformis/kuckersiana</i>	0.12	0.733
<i>Desmochitina juglandiformis</i>	0.10	0.745
<i>Conochitina minnesotensis</i>	0.10	0.755
<i>Belonechitina gamachiana</i>	0.06	0.811
<i>Belonechitina micracantha</i>	0.05	0.820
<i>Spinachitina</i>	0.04	0.840
<i>Desmochitina elongata</i>	0.03	0.849
<i>Hercochitina</i>	0.03	0.853
<i>Hercochitina sp</i>	0.03	0.853
<i>Spinachitina multiradiata</i>	0.03	0.869
<i>Spinachitina cf. taugourdeau</i>	0.01	0.919
<i>Belonechitina sp</i>	0.01	0.921
<i>Cyathochitina sp</i>	0.00	0.950
<i>Spinachitina cervicornis</i>	0.00	0.958

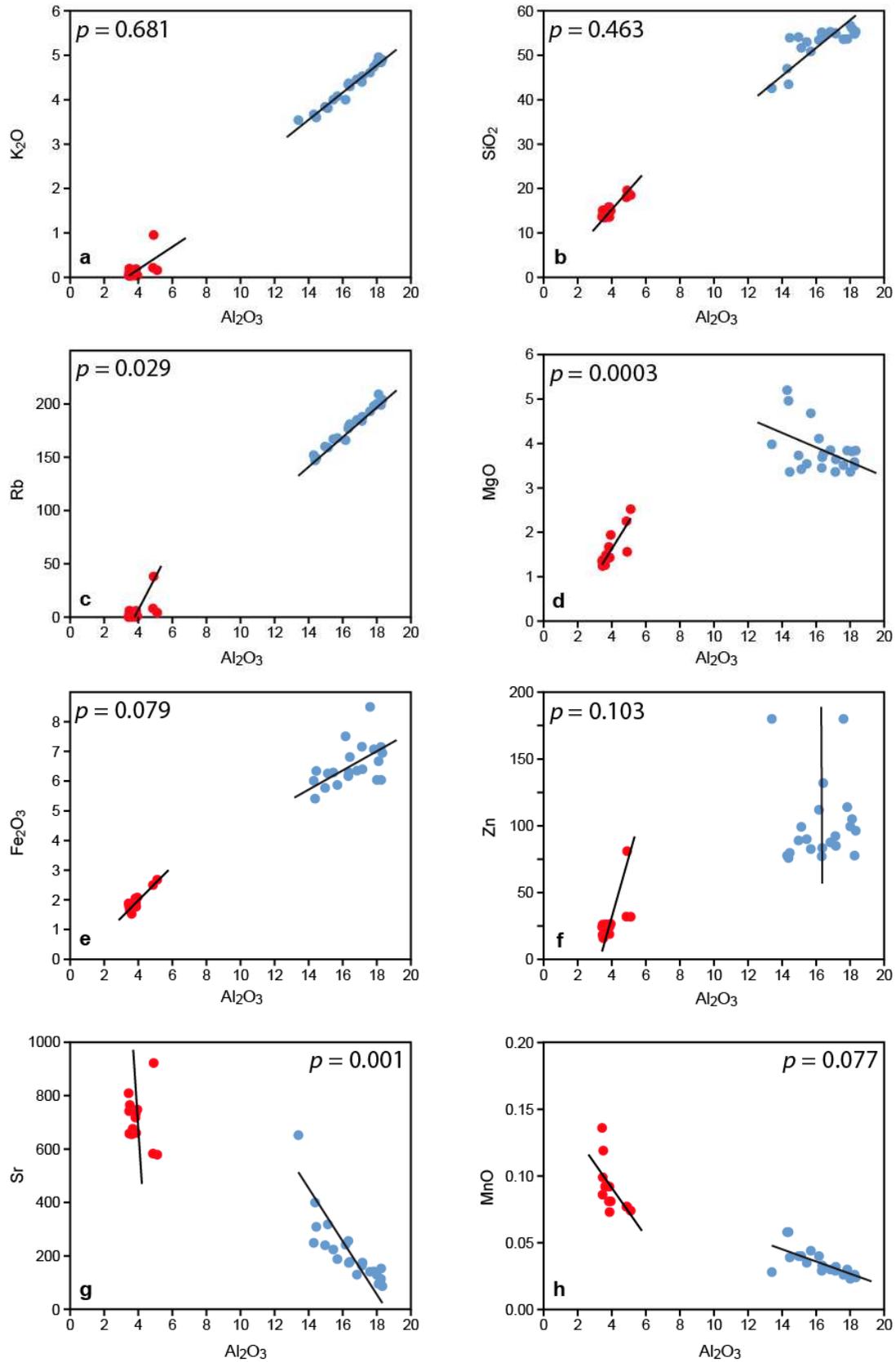
Supplementary Fig. S3: One-way ANOVA of each taxon separately in order to test for their equality of mean relative abundance between the two lithologies (37 samples of limestones and 39 of marls).



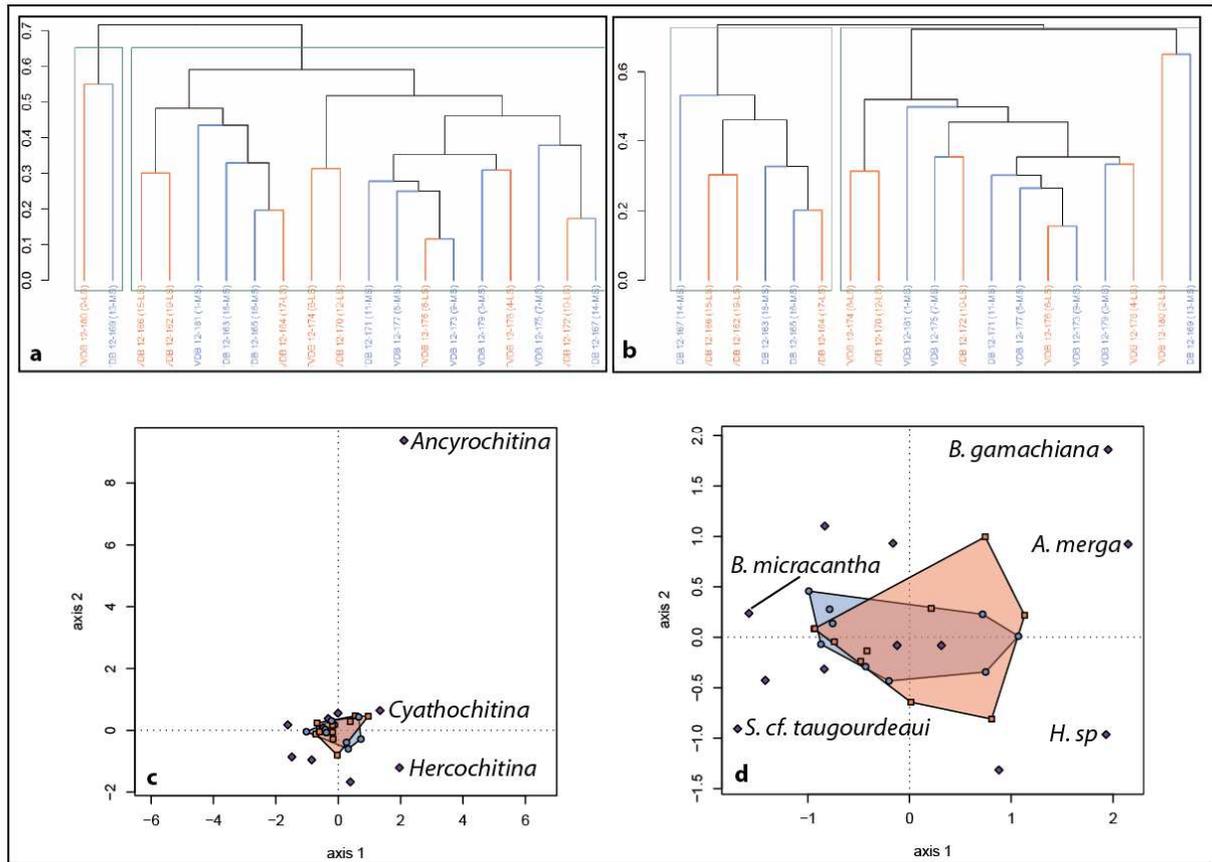
Supplementary Figure S4. XRF element ratios for Arnestad/Frognerkilen Formation. a-c: Elements preferentially bound to clay minerals. d-f: Elements preferentially bound to clay and calcite minerals. g-h: Elements bound to calcite minerals. Limestones are in red and marls in blue. P values < 0.05 indicate significant difference between the slopes.



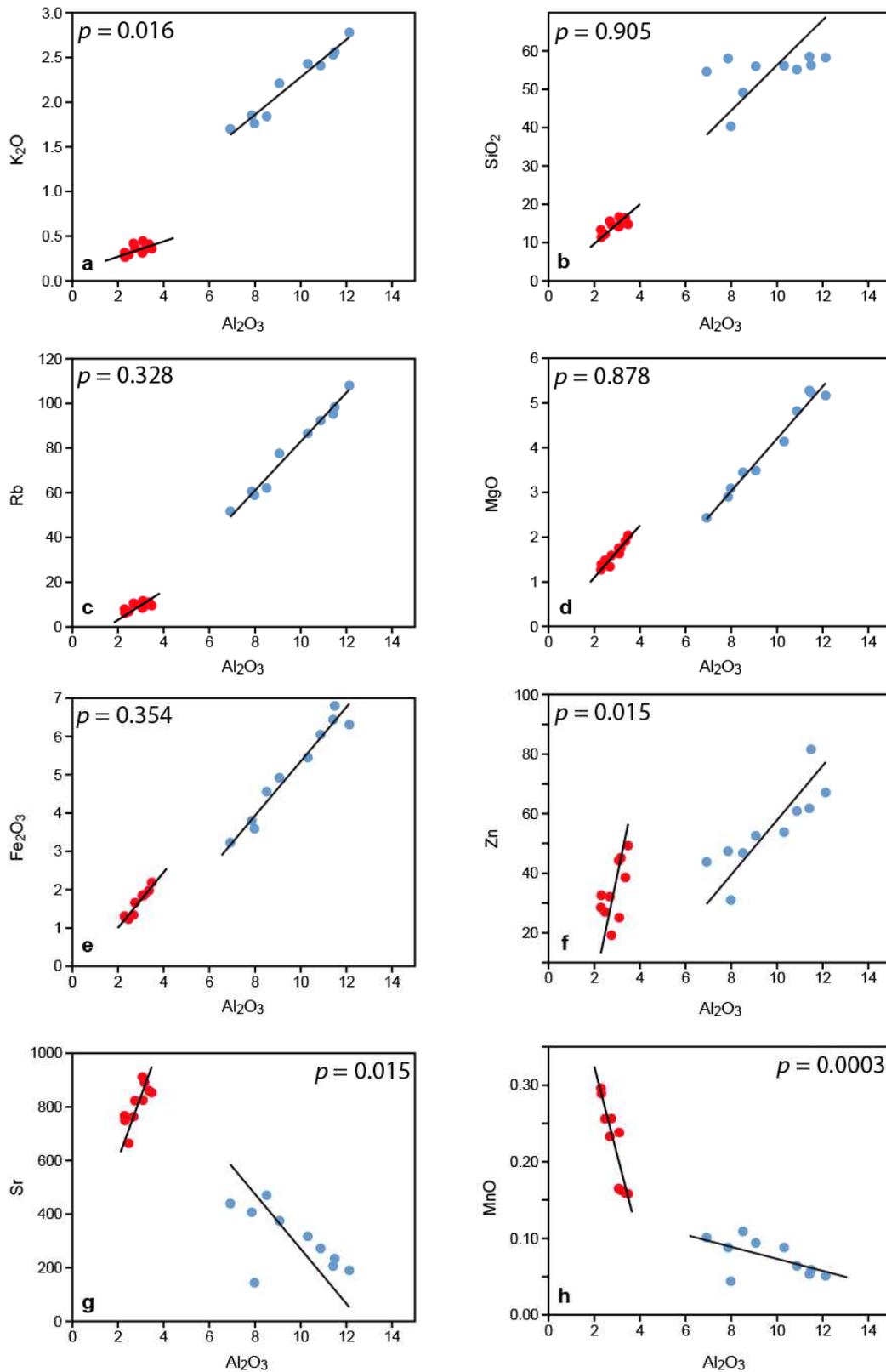
Supplementary Figure S5. Statistical analysis for the chitinozoan assemblage of the Solvang Formation. (a) Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at genus level. (b) Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at species level. (c) Detrended Correspondence Analysis (Bray-Curtis index) at genus level. (d) Detrended Correspondence Analysis (Bray-Curtis index) at species level. The statistical analyses indicate a similar composition of assemblages. Limestones are in red, marls in blue.



Supplementary Figure S6. XRF element ratios for the Solvang Formation. a-c: Elements preferentially bound to clay minerals. d-f: Elements preferentially bound to clay and calcite minerals. g-h: Elements bound to calcite minerals. Limestones are in red and marls in blue. P values < 0.05 indicate significant difference between the slopes.



Supplementary Figure S7. Statistical analysis for the Hovedøya Member of the Skogerholmen Formation. (a) Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at genus level. (b) Hierarchical Cluster Analysis (Bray-Curtis index and UPGMA linkage) at species level (c) Detrended Correspondence Analysis (Bray-Curtis index) at genus level. (d) Detrended Correspondence Analysis (Bray-Curtis index) at species level. The statistical analyses indicate a similar composition of assemblages. Limestones are in red, marls in blue.



Supplementary Figure S8. XRF element ratios for the Hovedøya Member of the Skogerholmen Formation. a-c: Elements preferentially bound to clay minerals. d-f: Elements preferentially bound to clay and calcite minerals. g-h: Elements bound to calcite minerals. Limestones are in red and marls in blue. P values < 0.05 indicate significant difference between the slopes

4. Chitinozoan biostratigraphy and carbon isotope stratigraphy from the Upper Ordovician Skogerholmen Formation in the Oslo Region. A new perspective for the Hirnantian lower boundary in Baltica.

Chitinozoan biostratigraphy and carbon isotope stratigraphy from the Upper Ordovician Skogerholmen Formation in the Oslo Region. A new perspective for the Hirnantian lower boundary in Baltica.

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Abstract

The end-Ordovician has received wide attention because it hosts major global events including mass extinctions, glaciations, significant sea-level fluctuations, and large-scale perturbations of the Earth's carbon cycle. Knowing the order and timing of these events and their components is crucial for establishing an understanding of the dynamics of these environmental changes. Integrated biostratigraphical and chemostratigraphical correlation augment stratigraphic resolution. Here, we use stable carbon isotope stratigraphy in combination with chitinozoan biostratigraphy to correlate the Upper Ordovician *Belonechitina gamachiana* chitinozoan Biozone. Its position has long been a matter of debate; some argue that it is of late Katian age and others that it is of early Hirnantian age. The Skogerholmen Formation from the Oslo-Asker District in Norway has been correlated with the lower-middle Pirgu Baltic Stage, hitherto believed corresponding to the upper Katian in international terms. Our study, however, reveals the presence of *B. gamachiana*, diagnostic of the eponymous biozone, in the descending limb of a modest carbon isotope excursion in the lower part of this formation. This pattern is strikingly similar to data from coeval end-Ordovician sections in North America, where the prevailing evidence suggests an early Hirnantian age for the *B. gamachiana* chitinozoan Biozone. This new correlation suggests that the lower Hirnantian boundary is positioned within the Pirgu Baltic Stage.

Keywords: End-Ordovician, Hirnantian, Baltica, chitinozoans, biostratigraphy, carbon isotopes

4.2 Introduction

The Late Ordovician was a period of profound environmental and biological change. Glacial events in the latest Ordovician were associated with the first of the “big five” mass extinctions of the Phanerozoic (Sheehan, 2001) and with a pronounced positive carbon isotope excursion (Brenchley *et al.*, 1994; Harper *et al.*, 2014). Originally thought to be a unique, short discrete glacial event in a period of prevailing greenhouse climatic conditions (Brenchley *et al.*, 1994), the Hirnantian glaciations are increasingly perceived as the glacial acme of prolonged Ordovician cooling (Saltzman & Young, 2005; Armstrong, 2007; Trotter *et al.*, 2008; Vandenbroucke *et al.*, 2009a, 2010a; Nardin *et al.*, 2011; Turner *et al.*, 2011, 2012; Rasmussen *et al.*, 2016), governed by Cenozoic-style tempos and mechanisms (Armstrong, 2007; Ghienne *et al.*, 2014; Pohl *et al.*, 2015). Nonetheless, a detailed understanding of the cause-and-effect relations between sea level falls, mass extinction events, C-cycle perturbations, and glaciations are hampered by uncertainties about the number, succession, order and correlation of the successive events, notably linked to the incompleteness of the stratigraphic record (Ghienne *et al.*, 2014; Sadler *et al.*, 2009; Mclaughlin *et al.*, 2008) as well as the limits of biostratigraphical resolution and bio-provincialism of stratigraphically useful groups (Vandenbroucke *et al.*, 2010b). Integrated HiRes biochemostratigraphical stratigraphy can help resolve some of these problems (Cramer *et al.*, 2015), although certain issues, such as the specific correlation problem around the base of the *B. gamachiana* chitinozoan Biozone addressed in this paper, require additional primary data (Fig. 1).

Graptolite biostratigraphy is the “gold” standard in the Upper Ordovician Series, defining the bases of the Upper Ordovician global stages (Sandbian, Katian, Hirnantian). The GSSP for the base of the Hirnantian was defined in the Wangjiawan North Section in China (Chen *et al.*, 2006) at the base of *Normalograptus extraordinarius* graptolite Biozone. This section also contains the second Hirnantian graptolite biozone, which is characterized by the presence of *Normalograptus persculptus*. The nearby Wangjiawan River Section contains a $\delta^{13}\text{C}_{\text{org}}$ excursion, identified as the HICE (Hirnantian Carbon Isotopic Excursion, Bergström *et al.*, 2006). It has two peaks, the lowest one in the *N. extraordinarius* graptolite Biozone, and the upper peak in the *N. persculptus* graptolite biozone (Chen *et al.*, 2006). The HICE, more frequently recorded in carbonate carbon ($\delta^{13}\text{C}_{\text{carb}}$) than in organic material, is considered a global isochronous event and a useful correlation tool for the Hirnantian (Brenchley *et al.*, 2003; Bergström *et al.*, 2006; Kaljo *et al.*, 2007), however, caution is required as to the completeness of sections and to their isotope record (Ghienne *et al.*, 2014).

Several $\delta^{13}\text{C}$ excursions have been recognized below the HICE in the Upper Ordovician in the Baltic region (Kaljo *et al.*, 2007, 2008; Schmitz and Bergström, 2007; Ainsaar *et al.*, 2010; Bergström *et al.*, 2010a&b, 2011, 2014, 2015) and North America (Long, 1993; Bergström *et al.*, 2006, 2010a&b; Desrochers *et al.*, 2010; Young *et al.*, 2010; Mclaughlin *et al.*, in press). Correlations between excursions in Baltica and Laurentia have been suggested as follows (Fig. 2): (1) the Paroveja Isotopic Excursion (Kaljo *et al.*, 2008; Ainsaar *et al.*, 2010) in the upper Pirgu Stage in Baltica and in the upper Richmondian North American stage in

Laurentia; (2) the Moe Excursion (Kaljo *et al.*, 2004, 2007; Ainsaar *et al.*, 2010) in the lower Pirgu Stage in Baltica that corresponds to the Whitewater Excursion (Bergström *et al.*, 2007) in the mid-Richmondian Stage in Laurentia; (3) the Saunja Excursion (Kaljo *et al.*, 2004, 2007; Ainsaar *et al.*, 2010) in the Nabala Stage in Baltica that approximately corresponds to the stratigraphic position of the Waynsville Excursion (Bergström *et al.*, 2007) in the lower Richmondian Stage in Laurentia; (4) the Rakvere Excursion in the Rakvere Stage in Baltica (Kaljo *et al.*, 2004, 2007) corresponds to the Kope Excursion (Bergström *et al.*, 2011) in the Chatfieldian-Edenian Stage in Laurentia, and (5) the GICE (Guttenberg Isotope Carbon Excursion, Bergström *et al.*, 2011) in the upper Keila Stage in Baltica and in the lower Chatfieldian Stage in Laurentia (Bergström *et al.*, 2009). These correspondences imply that positive carbon isotope excursions are useful for global correlations.

The Oslo-Asker District in Norway contains a series of limestone-marl rhythmites that are scrutinized as potentially recording glacio-eustatic sea level fluctuations (Nielsen 2004; Amberg *et al.*, 2016). Isotope excursions originally named in the US have been recognized in two of these rhythmites in the Oslo region, i.e., the GICE in the Mjøsa Formation (a local formation in the northern Lake Mjøsa region, situated at the Keila/Oandu baltic stages boundary) and the Kope in the Solvang Formation (Bergström *et al.*, 2011). This suggests that some of the other rhythmites from the Oslo-Asker District, if not all of them, may host $\delta^{13}\text{C}$ excursions (Fig. 2). As demonstrated further in this paper, the rhythmic Hovedøya Member of the Skogerholmen Formation also contains significant variation in its stable carbon isotopes. Although direct correlation to the US $\delta^{13}\text{C}$ stratigraphy of Bergström *et al.* (2007, 2009, 2011, 2014, 2015) is tempting, care should be taken not to introduce long-distance mismatches, especially as much more variation and many more (minor) excursions exist in the Upper Ordovician of the USA, than there are rhythmites in the Oslo Region (McLaughlin and Hurth, 2011; McLaughlin *et al.*, 2015).

Another reliable tool for correlation in the Upper Ordovician is chitinozoan biostratigraphy, which has been widely used in Laurentia (Achab, 1981, 1989; Soufiane & Achab, 1999, 2000; Achab *et al.*, 2011; Verniers and Vandenbroucke, 2006), Baltica (Nölvak, 1999, 2001; Nölvak *et al.*, 2006; Nölvak and Grahn, 1993; Grahn *et al.*, 1994), Avalonia (Davies *et al.*, 2013; Vandenbroucke 2008; Vandenbroucke *et al.*, 2005, 2008a&b, 2009b) and Gondwana (Paris, 1990, Paris *et al.*, 1995) to construct regional biostratigraphical frameworks. The local zonations, established for the Baltic, Laurentian and Northern Gondwanan areas (Paris 1996; Webby 2004), differ in many intervals, due to provincialism of the faunas (Vandenbroucke *et al.*, 2010 a&b). However, some species can be used to correlate between Laurentia and Baltica in the interval of interest (Brenchley *et al.*, 2003; Nölvak *et al.*, 2006). According to Nölvak (1999), in Baltica, the *Spinachitina taugourdeai* chitinozoan Biozone, which lies above the *Belonechitina gamachiana* chitinozoan Biozone, is considered a “relatively good criterion for the lower boundary of the Porkuni Stage”. The Baltic Porkuni Stage is regarded as the equivalent of the Hirnantian Global Stage (Bergström *et al.*, 2014). Brenchley *et al.* (2003) record the HICE and the *B. gamachiana* and *S. taugourdeai* biozones in core sections from Latvia and Estonia and considered the shape and amplitude of the carbon excursions from those core sections to be very similar to those in Nevada. Therefore they proposed to use

it as a chemostratigraphical “bench-mark” for long-distance correlations with North America. However, there are issues with this model as, for instance, in Anticosti Island, (Quebec, Canada) the base of the Hirnantian has been placed at different levels by different authors (Delabroye and Vecoli, 2010). The current consensus, based on graptolite biostratigraphy, places the base of the Hirnantian close to the base of the Ellis Bay Formation in Western Anticosti (Desrochers *et al.*, 2010, Achab *et al.*, 2011, 2013; Delabroye *et al.*, 2011; Melchin 2008; Melchin *et al.*, 2003, 2013) which means that the *B. gamachiana* chitinozoan Biozone is included in the lower Hirnantian and that the *S. taugourdeui* chitinozoan Biozone constitutes the upper Hirnantian (Fig. 1).

In Avalonia, Vandenbroucke *et al.* (2008a) did not recognize the *B. gamachiana* chitinozoan Biozone, but some specimens of *Hercochitina* cf. *gamachiana* co-occur with *S. taugourdeui* in the Hirnant Limestone Quarry in North Wales. This *S. taugourdeui* chitinozoan Biozone is of mid-late Hirnantian age. Challands *et al.* (2014) found specimens of *B. cf. gamachiana* in the southern part of the Welsh Basin associated with the *D. anceps* graptolite Biozone, and defined a *B. cf. gamachiana* chitinozoan Biozone of late Katian age. However, the relation between the Welsh *B. cf. gamachiana* and true *B. gamachiana* remains to be explored in detail.

In this paper we aim to present an integrated study of new carbon isotope data constrained by chitinozoan biostratigraphy from the two members of the Skogerholmen Formation in the Oslo Region in Norway (Fig. 3), described as part of the Baltic Pirgu Stage (Nölvak and Grahn, 1993; Grahn *et al.*, 1994; Nielsen, 2004). Containing *B. gamachiana* and a low-amplitude $\delta^{13}\text{C}$ drop, these rocks provide yet another piece of the puzzle that may eventually lead to a consolidated correlation between Estonia, Anticosti Island, and other places of the world, and they could potentially lead to new perspectives for the identification of the lower Hirnantian boundary in the Baltic Region.

4.3 Material and methods

We collected 68 samples in total from the Skogerholmen Formation in the south-west corner of the Hovedøya Island (N59°53'32.0" E10°43'38.2"). For the palynological study, 23 samples were collected bed-by-bed from the alternating limestone and marl layers, starting at approximately 6m below the top of the Hovedøya Member. A few samples were also collected in the lower and the uppermost Spanslokket Member. For the chemostratigraphical ($\delta^{13}\text{C}_{\text{carb}}$) study, another batch of 45 samples was collected only from limestones, starting in the lowest level accessible above the sea level in the lower Hovedøya Member, up to the top of the Spanslokket Member. The chitinozoan analyses were carried out in the University of Lille (France), for a complete description of the extraction method of the chitinozoans, see Amberg *et al.* (2016). The carbon isotope analyses were performed in the University of Erlangen-Nuremberg (Germany). The rock samples were cut with a saw, cleaned, and few mg of micritic carbonate was drilled with a dentist's drill. Carbonate powders were reacted with 100% phosphoric acid at 70°C using a Gasbench II connected to a ThermoFinnigan Five Plus

mass spectrometer. All values are reported in per mil relative to V-PDB by assigning a $\delta^{13}\text{C}$ value of +1.95‰ and a $\delta^{18}\text{O}$ value of -2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than ± 0.07 (1 σ). For chemostratigraphy only the $\delta^{13}\text{C}$ values are used.

4.4 Existing stratigraphic framework

The stratigraphy of the Oslo Region was fully described in Bruton *et al.* (2010). The studied section exposes the Skogerholmen Formation on Hovedøya Island in the Oslo Fjord, Norway. This formation was described by Owen *et al.* (1990) and comprises two members, the Hovedøya Member and the Spansløkket Member (for a summary of older names, see Owen *et al.*, 1990). The Skogerholmen Formation overlies the Skjerholmen Formation and is in turn overlain by the Husbergøya Formation. The Hovedøya Member consists of alternating siltstones, limestones and marls whereas the Spansløkket Member comprises two distinct parts: A lower unit consisting of 4-6m of grey shales and silts and an upper unit resembling the Hovedøya Member, i.e., alternating limestone, siltstone and marl. The limestone beds become more nodular near the top of the Spansløkket Member (Fig. 4). The fossil content is poor but some trilobites and brachiopods found in various horizons (Fig. 5), especially in the Spansløkket Member, indicate an Ashgill age (Owen *et al.*, 1990).

Rare specimens of trilobites identified as *?Tretaspis latilimbus* forma *typica* have been found in the Skjerholmen-Skogerholmen formations and *T. sortita broeggeri* occurs in the overlying Husbergøya Formation (Størmer 1945). Owen (1980) defined the species *T. latilimbus norvegicus* on Hovedøya Island, where it occurs in the Skjerholmen and Skogerholmen formations. Brenchley & Cocks (1982) described the “*Tretaspis* Association” from the entire Husbergøya Formation, where *T. latilimbus norvegicus* is very common, except for the topmost three meters, where the presence of *T. sortita broeggeri* could be correlated with the Lady Burn Starfish Beds in Scotland, suggesting that these levels are within the uppermost Rawtheyan Stage (Owen 1980; Harper 1982). A few specimens assigned to *Toxochasmops* sp. are also recorded in the Husbergøya Formation; they probably represent a new species of *Valdarios* (A. T. Nielsen, pers. comm.). Some brachiopods also occur in the middle and upper part of the section containing the “*Tretaspis* Association”, such as *Eoplectodonta oscitanda*. *Oniella kalvoya* is also recorded and is the reason why the upper part of the Husbergøya Formation is regarded as yielding the “*Tretaspis-Oniella* Association”. The “*Hirnantia* Association” appears in the few last centimeters of the Husbergøya Formation and becomes more common in the overlying Langøyene Formation. The association contains the brachiopods species *Hirnantia sagittifera* and *Dalmanella testudinaria*, a few specimens assigned to *Cliftonia* aff. *pistticina* and *Eostropheodonta hirnantensis* and the trilobite species *Mucronaspis mucronata*. Strand (1933) found the cephalopod *Beloitoceras heterocurvatum* in the Skogerholmen Formation on the Skjerholmen Island, south of Oslo. The species *Danoceras broeggeri* (South Skjerholmen Island, S. of Oslo) and *Diestoceras isotelorum* (Skjerholmen Island, S. of Oslo) are found in the upper part of the Spansløkket Member. Strand (1933) considered the species *Beloitoceras heterocurvatum* as being related to *B. percurvatum* found at Anticosti Island in zone 6 of the Ellis Bay Formation (White &

Skorina, 1999). Moreover, Spjeldnæs (1964) noted that the Skjerholmen Formation corresponds to the *Dicellograptus anceps* graptolite zone, and according to Brenchley & Cocks (1982) *Dicellograptus* sp. occurs in the first meter of the Husbergøya Formation. Nölvak & Grahn (1993) correlated the Skogerholmen Formation with the middle-upper part of the Pirgu Stage, but Grahn *et al.* (1994) subsequently equated this formation with the lower-middle part of the Pirgu Baltic Stage based on the presence of *Tanuchitina bergstroemi* in the overlying Husbergøya Formation. The *T. bergstroemi* chitinozoan Biozone in Baltica ranges from the lower Vormsi Baltic Stage to the lower Pirgu Baltic Stage (Nölvak *et al.*, 2006), but large *Tanuchitina* species such as *T. bergstroemi* range until high in the Upper Ordovician, above levels usually attributed to the *T. bergstroemi* chitinozoan Biozone (Vandenbroucke *et al.* 2005), which can explain its presence in the Husbergøya Formation. In addition, *T. bergstroemi* is suggested by Paris (1990) to be potentially a junior synonym of *T. elongata*, indicator of the eponymous biozone in Gondwana, ranging until the middle Hirnantian. Summarizing all the existing information, Nielsen (2004) assigned the Husbergøya Formation to the upper Pirgu Baltic Stage and, hence, the underlying Skogerholmen Formation was correlated with the middle part of the Pirgu Baltic Stage.

4.5 Results

4.5.1 Biostratigraphy

A relatively rich and diverse fauna is recovered from the 23 samples collected for the biostratigraphical analysis of the Skogerholmen Formation: 2451 specimens of chitinozoans were identified, and 13 species were encountered representing 10 genera. The section can be divided into three parts, based on the chitinozoan assemblages: The lowest part, from sample TVDB 12-160 to TVDB 12-169 in the Hovedøya Member, yielded *Belonechitina gamachiana* (Fig. 6, 1-7), *Cyathochitina campanulaeformis* and *kuckersiana* (group), *Conochitina* sp., *Desmochitina minor*, *D. ovulum*, *Bursachitina* sp., *Hercochitina florentini*? (Fig. 6, 8-10), *Rhabdochitina* sp., *Spinachitina* sp., *Ancyrochitina longispina*? (Fig. 6, 19) as well as some unidentifiable specimens. The second part, from sample TVDB 12-161 to TVDB 12-181, also in the Hovedøya Member, yielded *Spinachitina multiradiata*, *S. cf. taugourdeau* (Fig. 6, 11-17), *Belonechitina micracantha* (Fig. 6, 18), *Cyathochitina campanulaeformis* and *kuckersiana* (group), *Conochitina* sp., *Desmochitina minor*, *D. ovulum*, *Bursachitina* sp., *Rhabdochitina* sp. and some unidentifiable specimens. The third and topmost part is in the Spannslokket Member, from sample TVDB 12-181 to TVDB 12-184, and is almost barren, with only 3 specimens of *Belonechitina* sp., 2 specimens of *Spinachitina* sp., a *Tanuchitina* sp. specimen and 9 unidentified specimens. The preservation of the specimens is rather uneven, depending on whether they are extracted from limestones, which usually yielded three-dimensionally preserved specimens with fairly well-preserved ornamentation, or from mudstones, which yielded flattened specimens with indistinct ornamentation.

4.5.2 Description of selected species

The species *Belonechitina gamachiana* and *Spinachitina taugourdeoui* have been described earlier (Achab 1978, Eisenack, 1968), so only a few remarks are made herein on the biostratigraphically important species present in the Skogerholmen Formation. The morphological terminology and abbreviations are following Paris (1981): L = total length, Dp = chamber diameter and Dc = diameter of oral tube. Measurements were performed on both flattened and three dimensions specimens and no correction factors *sensu* Paris (1981) were employed.

4.5.2.1 *Belonechitina gamachiana*

Description: The specimens from the Hovedøya Member of the Skogerholmen Formation have a cylindrico-conical body with a flat to slightly convex base and a short neck measuring about one third of the total vesicle length and ending with a lacinated collaret. Several simple or forked spines with a thick base occur around the rounded margin and the wall is covered by simple, generally aligned spines with a thick base. These spines are well-developed on the chamber and becoming smaller on the neck (Fig. 6, 1-7).

Remarks: The specimens differ from the holotype by being larger, and having smaller and scarcer spines on their walls. However, the reduced ornamentation may be due to imperfect preservation.

Dimensions: As the specimens are preserved in 3D in the limestone samples and flattened in the mudstone samples, two sets of measurements were performed. Calculated from 12 complete 3D specimens selected from a population of 72 3D specimens, the average L = 183 μ m (147 μ m – 258 μ m); the average Dp = 84 μ m (79 μ m – 95 μ m); the average Dc = 57 μ m (44 μ m – 82 μ m). Calculated from 15 complete flattened specimens selected from a population of 91 specimens, the average L = 187 μ m (ranges from 148 μ m to 244 μ m); the average Dp = 97 μ m (ranges from 71 μ m to 116 μ m) and the average Dc = 61 μ m (ranges from 41 μ m to 84 μ m).

4.5.2.2 *Spinachitina cf. taugourdeoui*

Description: The specimens from the Hovedøya Member of the Skogerholmen Formation present a glabrous elongated conical to sub-cylindrical body. They have a flat base with complexly branched spines, and the aperture displays a lacinated/reticulated margin. The flexure is often not well defined, which makes it difficult to differentiate the chamber from the neck (Fig. 6, 11-16).

Remark: *S. cf. taugourdeoui* differs from *S. taugourdeoui* in having a relatively glabrous wall, and overall less complex basal spines, but the shape and dimensions are similar. This species is considered transitional between *S. multiradiata* and *S. taugourdeoui*, in a morphological lineage that displays an increasing complexity of the spines.

Dimensions: For this species, all the 11 complete specimens measured are flattened. The average L = 205 μ m (ranges from 143 μ m to 300 μ m); the average Dp = 75 μ m (ranges from 58 μ m to 89 μ m) and the average Dc = 44 μ m (ranges from 32 μ m to 51 μ m).

4.5.3 Carbon isotopes

The results of the C-isotope analysis (Table 1) provide a narrow range of values, which nonetheless aids in refining the age of the Skogerholmen Formation. The $\delta^{13}\text{C}$ results from the Hovedøya Member start with values just below 2‰ near the 2 m position and drop with minor oscillation to just below 1‰ through the overlying 11 meters to near the contact with the Spannslokket Member. No values are recorded for the shaly basal 4 meters of the member. The overlying 15 meters record a slow rise in values from near 0.5‰ to just above 1‰.

4.6 Discussion

Grahn *et al.* (1994) placed the Skogerholmen formation in the *Tanuchitina bergstroemi* chitinozoan Biozone. Baltic stratigraphic correlation schemes (e.g. Brenchley *et al.*, 2003, Nielsen, 2004; Nölvak *et al.*, 2006; Kaljo *et al.*, 2007, 2008; Bergström *et al.*, 2006, 2014) attribute a late Katian age to the Skogerholmen Formation and/or placed it in the mid-upper Pirgu Baltic Stage. However, our new biostratigraphical analysis of the Skogerholmen Formation reveals the presence of the species *Belonechitina gamachiana*, index fossil of the eponymous biozone. This result is at odds with the previous correlations of the Skogerholmen Formation outlined above. *Belonechitina gamachiana* usually occurs slightly higher than the levels the Skogerholmen Formation and has hitherto been equated in the Baltic area with the very top of the Pirgu Baltic Stage, just below the base of the Porkuni. In addition, based on correlation with new graptolites and carbon isotope data from the Dob's Linn Section in Scotland (the GSSP of the basal Silurian), Anticosti Island and Arctic Canada, the *B. gamachiana* chitinozoan Biozone in Laurentia has been re-assigned to the lower Hirnantian (Melchin *et al.*, 2003; Melchin and Holmden, 2006; Delabroye and Vecoli 2010), implying that the Skogerholmen Formation is of early Hirnantian age.

Our new combined biostratigraphical and chemostratigraphical data provide a strong correlation between the Skogerholmen Formation from the Oslo-Asker District with the lower part of the Ellis Bay Formation in western Anticosti (Fig. 7). The range of $\delta^{13}\text{C}$ values recorded by Desrochers *et al.* (2010) and Delabroye *et al.* (2011, 2012) in the lower Ellis Bay Formation has a very similar structure and magnitude to that observed in the Skogerholmen Formation and lies within the same biostratigraphical range (Fig. 8).

In a $\delta^{13}\text{C}$ curve from Mirny Creek in Siberia (Kaljo and Martma, 2011; Kaljo *et al.*, 2012), where the carbon isotopes are constrained with graptolite biostratigraphy, we can see a very similar trend to the $\delta^{13}\text{C}$ curve from the sections and subsurface drillcore in Anticosti (Long 1993; Desrochers *et al.*, 2010; Holmden *et al.*, 2013). In the Mirny Creek $\delta^{13}\text{C}$ curve, below the HICE, the rising limb of a first modest excursion starts close to the base of the *N. extraordinarius* graptolite Biozone, but no graptolites have been recovered from the exact interval where the rising limb of the excursion starts, situated close to the Katian/Hirnantian

boundary. This excursion is comparable, in shape and magnitude, to that in Anticosti in the *H. crickmayi* and *B. gamachiana* chitinozoan biozones at the base of the Ellis Bay Formation (Desrochers *et al.*, 2010; Delabroye and Vecoli, 2010). As the interval with the Mirny Creek $\delta^{13}\text{C}$ excursion contains graptolites indicative of the early Hirnantian just above the falling limb of the small excursion, the Siberian section lends support to *B. gamachiana* being of early Hirnantian age, as suggested on Anticosti Island (Melchin 2008; Desrochers *et al.*, 2010; Achab *et al.*, 2011; Delabroye *et al.*, 2011).

In Baltica, however, an excursion in the *B. gamachiana* Biozone is poorly recognized. Such a structure is visible neither in the $\delta^{13}\text{C}$ data from the Latvian Jurmala R-1 nor in the Estonian Valga-10 core sections, nor do these contain the *B. gamachiana* chitinozoan Biozone due to a stratigraphic gap, commonly observed in the upper Pirgu Baltic Stage in Latvia and Estonia (Ainsaar *et al.*, 2010). Only a few Estonian core sections such as Kaugatuma and Kardla comprise (a part of) the *B. gamachiana* chitinozoan Biozone. There, the $\delta^{13}\text{C}$ curves show a little “bump” in this biozone (Kaljo *et al.*, 2008), never identified as ‘an excursion’, but which may nevertheless correspond to the trend in carbon isotope signatures observed in the Skogerholmen Formation.

In earlier correlation schemes, summarized by Nielsen (2004), the lower part of the Spanslokket Member of the Skogerholmen Formation is an equivalent of the Paroveja Formation in South Estonia, which is known to contain a positive carbon isotope excursion, i.e., the Paroveja Excursion (Aisaar *et al.*, 2010), previously described as the Mid-Ashgill Excursion (Kaljo *et al.*, 2007, 2008). This excursion has been documented in Latvia and Estonia with data from drill core sections such as the Jurmala R-1 or Valga-10 (Kaljo *et al.*, 2007), the latter containing *Conochitina rugata*, assigning the Paroveja Formation to the eponymous chitinozoan Biozone situated in the upper Katian or mid Pirgu Baltic Stage in Estonia, i.e., well below the *B. gamachiana* chitinozoan Biozone (Nölvak *et al.*, 2006). These $\delta^{13}\text{C}$ trends are similar in terms of amplitude and structure to the $\delta^{13}\text{C}$ data from the Skogerholmen Formation, but the biostratigraphical ranges of the co-occurring chitinozoans do not match those of the Skogerholmen Formation.

A certain degree of confusion exists as to the usage of names for the uppermost Ordovician pre-HICE excursions. The Paroveja Excursion from the Jurmala R-1 drill section in Latvia has been correlated by Bergström *et al.* (2014), using the base of the HICE as a reference level, to the Elkhorn Excursion from the Monitor Range succession in Nevada, and to an unnamed excursion from the Western Anticosti succession in Canada, both situated in the mid Richmondian North American Stage, and respectively coinciding with the *Calpichitina scabiosa* - *B. tenuispinata* chitinozoan biozones (Nevada) and the middle-upper *Hercochitina crickmayi* chitinozoan Biozone (Canada). Subsequently, Bergström *et al.* (2015) reinterpreted this correlation based on the same $\delta^{13}\text{C}$ curve from the Jurmala R-1 drill section and a composite curve from the Cincinnati Region for the lower Katian and western Anticosti Island for the upper Katian. This later study actually differentiates two excursions, the Elkhorn Excursion in the Elkhorn Formation (mid-Katian) and the Paroveja Excursion in the Vauréal Formation (upper Katian).

In contrast, a correlation of several $\delta^{13}\text{C}$ curves from China, USA, Canada, Scotland, Scandinavia, Siberia and Bohemia (Holmden *et al.*, 2013; Melchin *et al.*, 2013) reverses this order, and suggests that the Paroveja Excursion is in the upper Katian and corresponds to the *C. rugata/T. anticostiensis* chitinozoan biozonal boundary, and that the Elkhorn Excursion is above it, occurring at the base of the Hirnantian and corresponding to the *B. gamachiana* chitinozoan Biozone. In summary, the Paroveja and Elkhorn excursions of Bergström *et al.* (2014, 2015) are well below the strata from the Skogerholmen Formation studied here, whereas the decreasing trend in our $\delta^{13}\text{C}$ curve from the Oslo region does correlate well with the decreasing limb of the Elkhorn excursion in the *B. gamachiana* chitinozoan Biozone at the base of the Ellis Bay Formation, as interpreted by Melchin *et al.* (2013) and Holmden *et al.* (2013). Given the complex labeling of the isotope excursions and the partial nature of our data, we prefer not to introduce a name for the $\delta^{13}\text{C}$ trend observed in the Skogerholmen Formation. Nevertheless, our data convincingly correlates the lower part of the Ellis Bay Formation from Western Anticosti with the Skogerholmen Formation.

4.7 Conclusion

Our new data contribute to the ongoing construction of a robust global biostratigraphical and chemostratigraphical framework that will enable us to correlate the timing of events around the base of the Hirnantian. Three conclusions can be drawn from the study of the combined biostratigraphical and geochemical data from the Skogerholmen Formation in the Oslo-Asker district:

1. Based on the presence of the species *Belonechitina gamachiana* in the chitinozoan assemblage, the Hovedøya Member of the Skogerholmen Formation is placed in the eponymous chitinozoan biozone. The carbon isotope data shows a modestly decreasing trend from 1.91‰ to 0.32‰ in the Hovedøya Member.
2. The combined bio- and chemostratigraphical ($\delta^{13}\text{C}_{\text{carb}}$) data from the Skogerholmen Formation provide a strong correlation with data from the lower part of the Ellis Bay Formation on Anticosti Island, where a modest $\delta^{13}\text{C}$ excursion also occurs within the *B. gamachiana* chitinozoan Biozone.
3. Following the interpretation of Melchin *et al.* (2013) and Holmden *et al.* (2013), who assigned an early Hirnantian age to the *B. gamachiana* chitinozoan Biozone on Anticosti Island, the upper part of the Pirgu Baltic Stage may also be of early Hirnantian age. The presence in our assemblage of *Spinachitina cf. taugourdeau*, interpreted as a precursor of true *S. taugourdeau*, also supports a Hirnantian age.

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Author contributions

TRAV, AM and ATN designed the research project, ATN, TRAV conducted field work, CEAA conducted the palynological analyses, AM conducted the carbon isotopes analyses, CEAA and PMcL correlated the data into the USA sections, TRAV supervised CEAA (PhD), all authors contributed to the writing.

Additional information

The authors declare no competing financial interests.

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4.9 Figures

Global & regional stages			Graptolite biozones	Chitinozoan biozones		Stratigraphy			
				Baltica <i>Nölvak et al., 2006</i>	Laurentia <i>Melchin, 2008</i>	Oslo <i>Bruton, 2010</i>	Anticosti <i>Brenchley et al., 2003</i>	Anticosti <i>Melchin, 2008</i>	
Upper Ordovician	Hirnantian	Porkuni	<i>N. persculptus</i>	<i>C. scabra</i>	<i>A. ellisbayensis</i>	Langøyene Formation	Upper Ellis Bay Formation	Ellis Bay Formation	
			-----	<i>S. taugourdeai</i>	<i>S. taugourdeai</i>				
	Katian	Pirgu	<i>D. anceps</i>	<i>B. gamachiana</i>	<i>H. crickmayi</i>				Husbergøya Formation
				<i>T. anticostiensis</i>					Skogerholmen Formation

Figure 1: Different correlation schemes of Ordovician chitinozoan biozones and local stratigraphy in the Oslo Region and Anticosti Island. The grey boxes represent the fauna and the formation discussed in the present study and their correlation as proposed by previous authors.

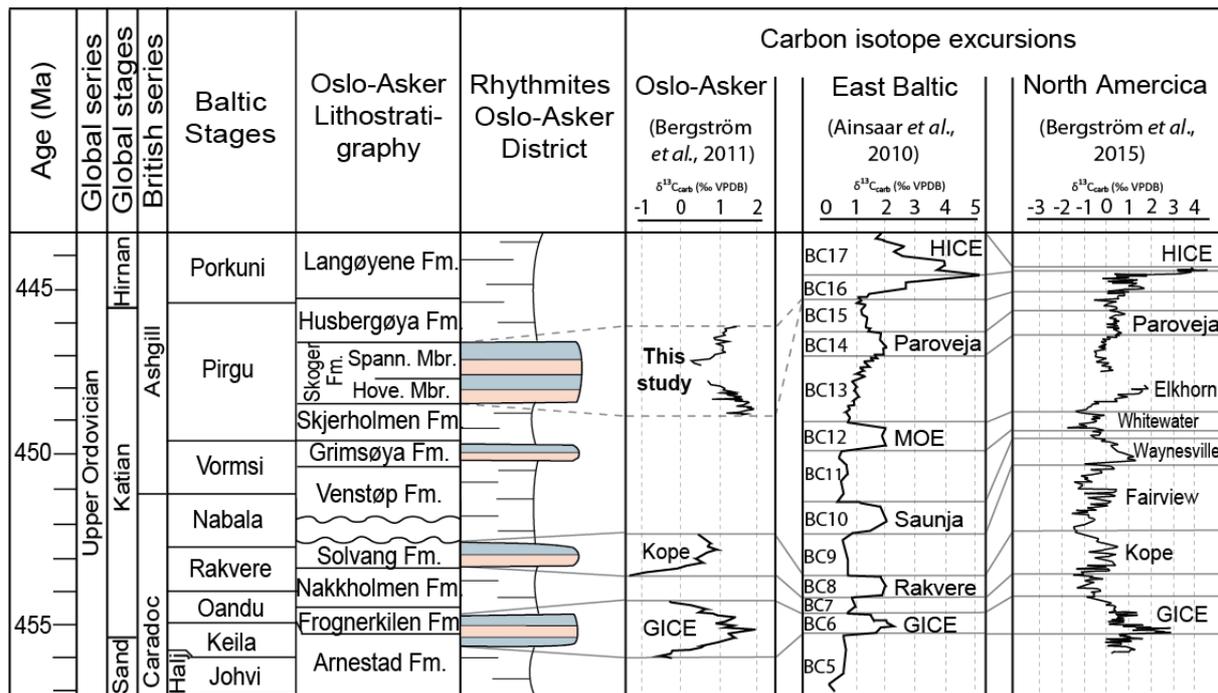


Figure 2: Traditional correlation of the rhythmites found in the Oslo Asker District, the $\delta^{13}\text{C}$ positive excursions in the Oslo Region, the recognized $\delta^{13}\text{C}$ positive excursions in the Baltic Region (Jurmala R-1 core section in Latvia), and their equivalent in North America (composite section from the Cincinnati Region -lower part- and western Anticosti -upper part-). The continuous grey lines represent the correlation from Bergström *et al.* (2011 for Oslo-Asker; 2015 for East Baltic and North America). BC stands for Baltic Carbon, chemostratigraphic units. The dotted grey lines are additional correlations suggested based on our data. For a revised correlation, see Figure 8.

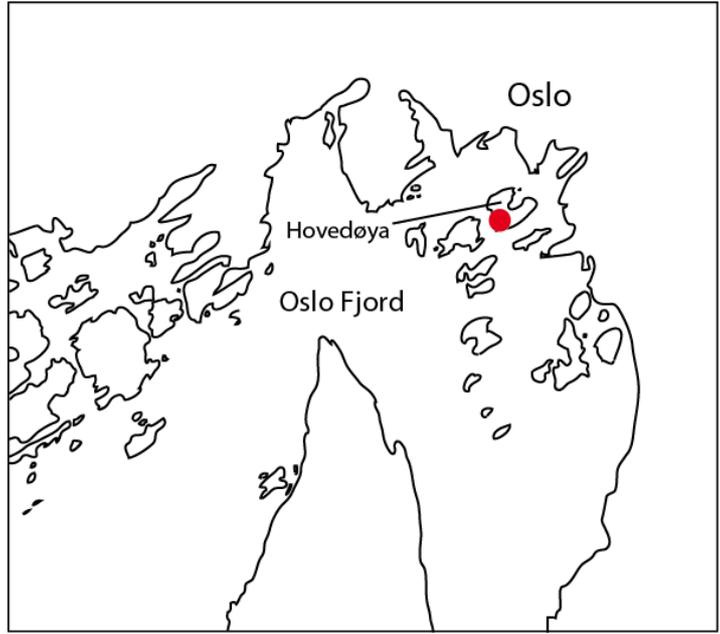


Figure 3: Map of the Oslo region with the Hovedøya Island situated in the Oslo Fjord (Modified from Google Map <https://www.google.fr/maps/@59.8915139,10.70346,12z>).

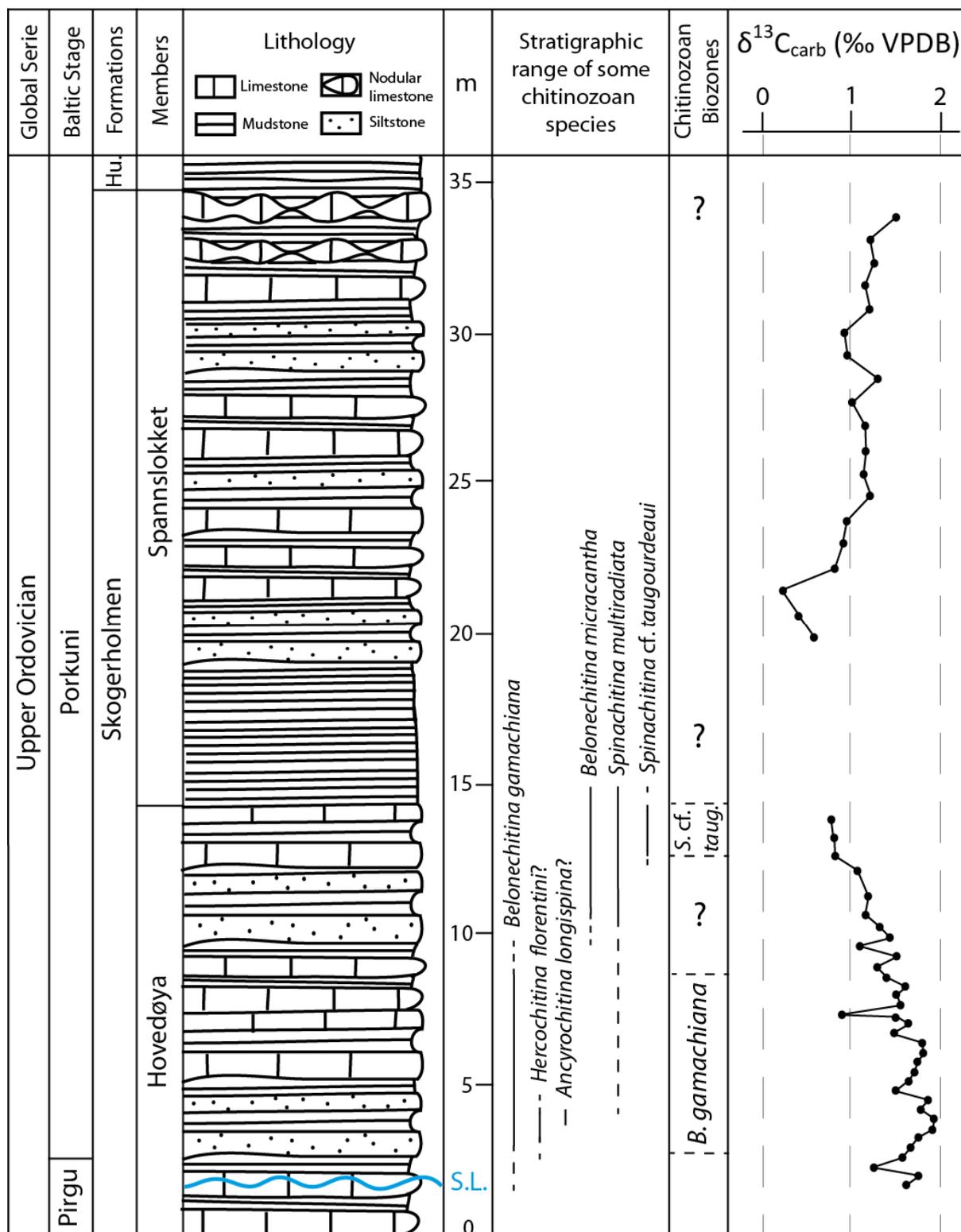


Figure 4: Stratigraphic section from the Skogerholmen Formation at Hovedøya Island in the Oslo Fjord with some selected chitinozoan stratigraphic ranges, chitinozoan biozones and $\delta^{13}\text{C}$ chemostratigraphy. Hu. = Husbergøya. SL = Oslo fjord sea level.

Formations, members	Strand, 1933			Størmer, 1945	Owen, 1980	Brenchley & Cocks, 1982										
	<i>Beloitoceras heterocurvatum</i>	<i>Diestoceras isotelorum</i>	<i>Danoceras broeggeri</i>	<i>Tretaspis sortita broeggeri</i>	<i>T. latilimbus forma typica</i>	<i>T. latilimbus norvegicus</i>	<i>Tretaspis</i> (- <i>Oniella</i>) Association:					<i>Hirnantia</i> Association:				
						<i>T. latilimbus norvegicus</i>	<i>T. sortita broeggeri</i>	<i>Toxachasmops</i> sp.	<i>Eoplectodonta oscitanda</i>	<i>Oniella kalvoya</i>	<i>Hirnantia sagittifera</i>	<i>Cliftonia aff. pisttacinia</i>	<i>Mucronaspis mucronata</i>	<i>Dalmanella testudinaria</i>	<i>Eostropheodonta hirnantensis</i>	
Langøyene Fm.																
Husbergøya Fm.																
Skogerholmen Fm.																
Skjerholmen Fm.																

Figure 5: Macrofauna found in the Skogerholmen Formation and in the underlying and overlying formations. The fauna indicate a general Ashgill age, but the presence of *T. sortita broeggeri* could be correlated with the uppermost Rawtheyan Lady Burn Starfish Beds in Scotland (Owen 1980; Harper 1982).

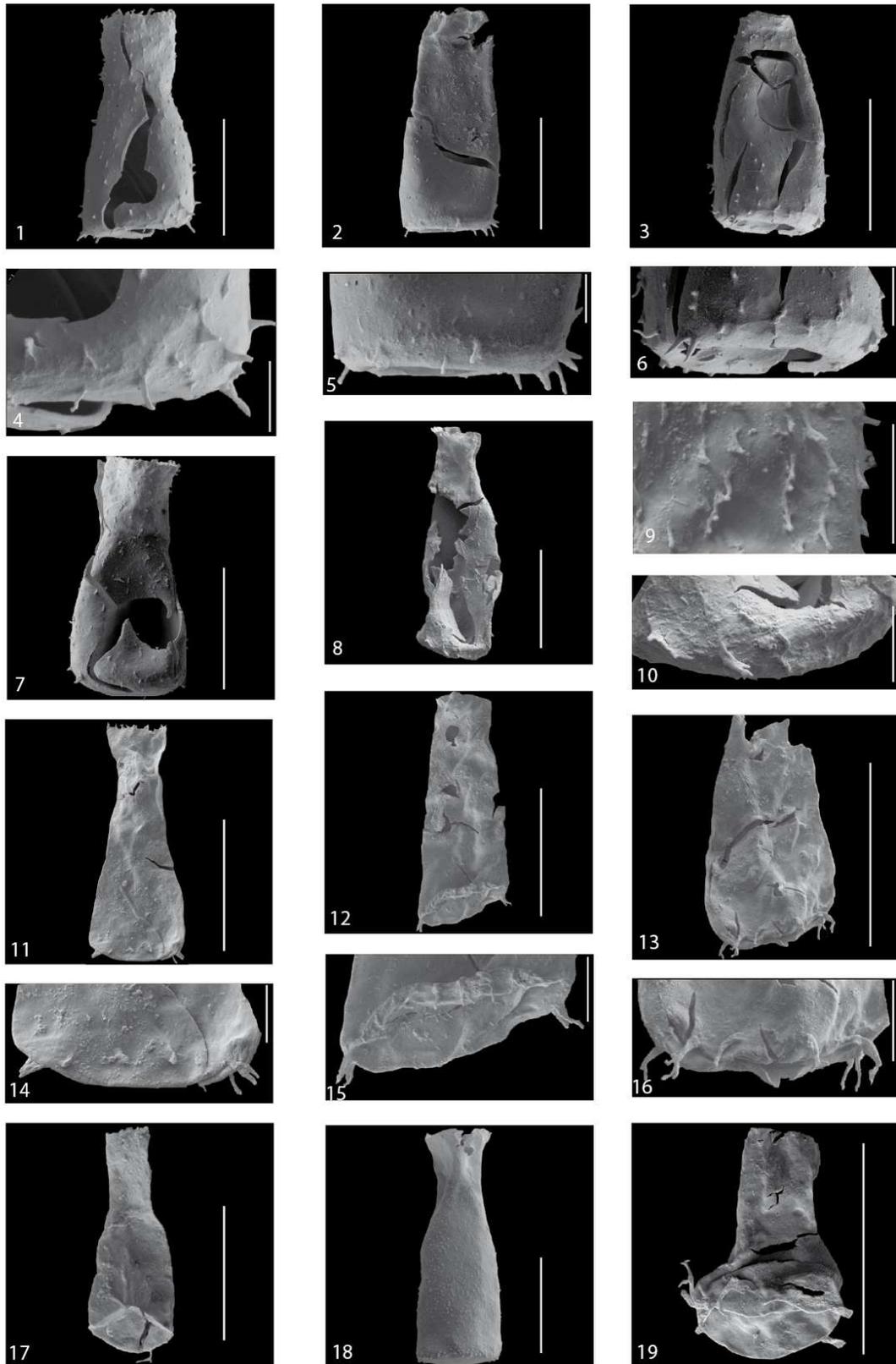


Figure 6: SEM pictures of selected chitinozoans from the Skogerholmen Formation. 1-7: *Belonechitina gamachiana*; 8-10: *Hercochitina florentini*?; 11-17: *Spinachitina* cf. *taugourdeau*; 18: *B. micracantha*; 19: *Ancyrochitina longispina*? All scale bars = 100 μ m, except 4-6, 9-10 and 13-15 = 20 μ m.

Samples	$\delta^{13}\text{C}$ ‰ VPDB		Samples	$\delta^{13}\text{C}$ ‰ VPDB	
TVDB 12-170	1,16	Hovedøya Member	TVDB 12-231	1,47	Spannslokket Member
TVDB 12-172	1,20		TVDB 12-232	1,20	
TVDB 12-174	1,07		TVDB 12-233	1,21	
TVDB 12-176	0,83		TVDB 12-234	1,11	
TVDB 12-178	0,80		TVDB 12-235	1,19	
TVDB 12-180	0,79		TVDB 12-236	0,88	
TVDB 12-202	1,32		TVDB 12-236 (II)	0,92	
TVDB 12-203	1,42		TVDB 12-237	1,29	
TVDB 12-205	1,05		TVDB 12-238	1,01	
TVDB 12-206	1,48		TVDB 12-239	1,15	
TVDB 12-207	1,27		TVDB 12-240	1,15	
TVDB 12-208	1,37		TVDB 12-241	1,11	
TVDB 12-209	1,58		TVDB 12-242	1,19	
TVDB 12-210	1,50		TVDB 12-243	0,93	
TVDB 12-211	1,52		TVDB 12-244	0,88	
TVDB 12-212	0,86		TVDB 12-244 (II)	0,88	
TVDB 12-213	1,64		TVDB 12-245	0,79	
TVDB 12-214	1,45		TVDB 12-246	0,32	
TVDB 12-215	1,78		TVDB 12-247	0,40	
TVDB 12-216	1,79		TVDB 12-248	0,57	
TVDB 12-217	1,73				
TVDB 12-218	1,66				
TVDB 12-219	1,60				
TVDB 12-220	1,51				
TVDB 12-221	1,86				
TVDB 12-222	1,79				
TVDB 12-223	1,91				
TVDB 12-224	1,88				
TVDB 12-225	1,71				
TVDB 12-226	1,62				
TVDB 12-227	1,54				
TVDB 12-228	1,26				
TVDB 12-229	1,74				
TVDB 12-230	1,59				

Table 1: Table with $\delta^{13}\text{C}$ values for the Hovedøya Member and the Spannslokket Member of the Skogerholmen Formation.

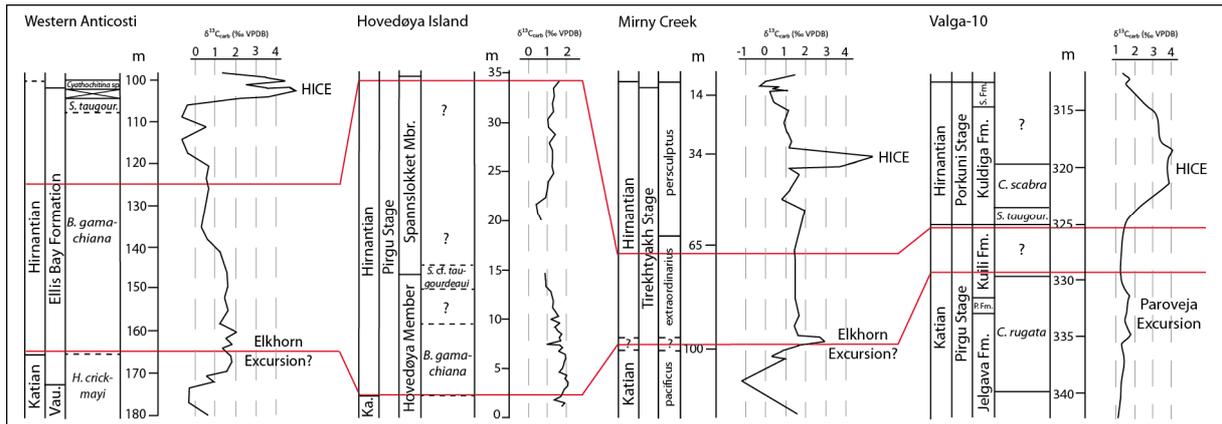


Figure 7: Revised correlation of the $\delta^{13}\text{C}$ curve and the chitinozoan biozones from Hovedøya Island in the Oslo-Asker area. $\delta^{13}\text{C}$ curve from western Anticosti, Canada modified from Desrochers *et al.* (2010), the siberian Mirny Creek $\delta^{13}\text{C}$ curve modified from Kaljo *et al.*, 2012 and the estonian Valga-10 drill core $\delta^{13}\text{C}$ curve modified from Kaljo *et al.* (2007).

5. Chitinozoan biostratigraphy of the historical Arenig series in Wales (Lower-Middle Ordovician).

Chitinozoan biostratigraphy of the historical Arenig series in Wales (Lower-Middle Ordovician).

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Abstract

The Lower to Middle Ordovician strata in North Wales (the Arenig Fawr area) and in South Wales (the Carmarthen and Whitland areas) constitute the historical type area for the British Arenig series. Six sections are sampled in the upper Tremadoc, the Arenig and the lowermost Llanvirn in order to establish a new chitinozoan biostratigraphy. Chitinozoans are recorded in all of these sections, although there is significant variation in their preservation and abundance. Thirty species are identified and four distinct assemblages are differentiated: the first assemblage principally consists of *Lagenochitinae* species, including *L. destombesi* and *L. brevicollis*, diagnostic of the eponymous Tremadoc biozones in Gondwana and Baltica. In the second assemblage, no index species were identified but their associated ones, such as *Conochitina queddichensis*, *Lagenochitina esthonica* and *Laufeldochitina cf. baculiformis*, which are present in assemblages from Gondwana. Several name-bearing species for Gondwana biozones were identified in the third assemblage such as *D. ornensis* and *B. henryi*, as well as most of their co-occurring species. The last assemblage does not contain index species, but some typical forms, such as *Tanuchitina achabae* and *Belonechitina micracantha typica*, indicating that this assemblage straddles the Arenig-Llanvirn boundary, a feature that is poorly expressed in the sedimentological record. Several of these taxa and assemblages are comparable to the fauna from Gondwana but also with Baltica for the Tremadoc, indicating faunal affinities between those palaeoprovinces, and reflecting the palaeogeographic history of Avalonia.

Key word: Arenig, South Wales, chitinozoan biozones,

5.1 Introduction

The Ordovician system was established by Lapworth (1879) in the Anglo-Welsh basin and has been used for international correlation for more than a century. The first correlation chart of the British and Irish Ordovician rocks by Williams *et al.*, (1972) remains the reference for British stratigraphy. Following the redefinition of the base of the Ordovician from the base of the Arenig Series in the British Isles (Williams *et al.*, 1972), to the base of the Tremadoc (originally in the Upper Cambrian in many other parts of the world, such as Scandinavia; Henningsmoen, 1973, Norford, 1988), there has been much effort to revise and refine the stratigraphy for international correlation of the six British Ordovician series (Whittington *et al.*, 1984): the Tremadoc, the Arenig, the Llanvirn, the Caradoc, the Ashgill and the Hirnantian. Due to issues revolving around the lack of continuous sections and fossil records, and the presence of several unconformities, e.g., at the base of the Arenig and the Caradoc series, and despite efforts to re-define the series in more appropriate sections (Fortey *et al.*, 1995, 2000) the stratigraphic community moved away from most of the British series and revised the Ordovician into 3 international series and 7 international stages (e. g. Bergström *et al.*, 2009). Nevertheless, the Anglo-Welsh area, where the Ordovician series were originally distinguished, remains the historic type area of the regional Tremadoc and Arenig thus a key reference area in Ordovician stratigraphy.

The term “Arenig” (sometimes spelled “Arennig”) was first used by Sedgwick (1855) for the rocks cropping out at Arenig Fawr District in North Wales, and the base of the Arenig was initially defined at the base of the Garth Grit Member in the type area of Arenig in North Wales (Williams *et al.*, 1972, Zalasiewicz 1984). However, this section is incomplete and presumed equivalent and more complete sections were described in South Wales in the Carmarthen area, where the lower Arenig is best developed (Fortey & Owens, 1978) and in the Whitland area, where the upper Arenig is best developed (Fortey & Owens, 1987). These formations have a relatively rich and diverse fossil content, but international correlations are obscured by the provincialism of many Arenig species (Cocks & Fortey, 1982). Nevertheless, Fortey & Owens (1987) proposed a subdivision of three stages of the Arenig based on the stratigraphy of the series in south Wales: the Moridunian, the Whitlandian and the Fennian, although only the Fennian yielded useful graptolites for international correlations. Molyneux (1987) described the acritarchs and a few chitinozoans of the same samples. However, the base of the Arenig series has not been defined by Fortey and Owens (1978, 1987), mostly because of the regional character of the fauna, making international correlations difficult (Fortey *et al.*, 1995).

A section exposing the Skiddaw Group nearby Trusmadoor in the English Lake District was also recognized as potential stratotype for the base of the Arenig (Fortey *et al.*, 1995). It is relatively continuous, exposes the Tremadoc-Arenig boundary and contains several graptolite species, but no *Tetragraptus approximatus*, then defining the base of the Arenig (Berry 1992). Instead, a graptolite assemblage similar to the lowest Arenig *T. phyllograptoides* graptolite Biozone of Baltica was recorded (Maletz *et al.*, 1991) alongside the *messaoudii-trifidum* acritarch assemblage. This assemblage was first described in the Watch Hill Formation of the

Lake District (Molyneux & Rushton, 1988) and has been subdivided into five sub-assemblages by Cooper *et al.*, (1995), the base of the Arenig located between the subdivisions 3 and 5 together with the graptolites similar to *T. phyllograptoides* assemblage. The acritarch assemblage now called *messaoudensis-trifidum* (Servais and Molyneux, 1997) is considered to be indicative of the upper Tremadoc to the lower-middle Arenig and can be correlated around the margin in Gondwana, as well as into Baltica (Servais *et al.*, 2003; Nowak *et al.*, 2015, 2016). The *T. phyllograptoides* graptolite Biozone has been accepted as defining the base of the Floian Stage in Avalonia, corresponding to the base of the Arenig Series (Fortey *et al.*, 1995, 2000; Zalasiewicz *et al.* 2009).

Graptolites are the quintessential tool for international correlations in the Ordovician, together with conodonts. Trilobites and other shelly fossils have also been used by Fortey & Cocks (1987). The full biostratigraphic potential of chitinozoans, which are widely used in Baltica (i.e. Nölvak, 1999; Nölvak *et al.*, 2006), Gondwana (i.e. Paris, 1990; Paris *et al.*, 1995, 2007), and Laurentia (Achab, 1989, Vandenbroucke *et al.* 2003), is still to be realized in Avalonia (Molyneux, 1990). Efforts were made in the upper Middle and Upper Ordovician in England and Wales (e.g., Jenkyns 1967, Vandenbroucke *et al.*, 2005, 2008a,b, 2009; Vandenbroucke, 2008; Challands *et al.*, 2014), but the Lower and most of the Middle Ordovician remained to be studied.

The scope of this paper is to describe chitinozoan assemblages from the upper Tremadoc, the Arenig and the lowermost Llanvirn series in the historical type area for these strata in Wales, to establish a biostratigraphical framework and to correlate the fauna with the established zonations in Gondwana and Baltica. The new data will help tracking the drift of Avalonia from Gondwana toward Baltica across the Iapetus Ocean (i.e. Cocks & Fortey, 1982; Torsvik & Rehnström, 2001; Torsvik and Cocks, 2013), and help constrain the stratigraphy of a time interval increasingly considered pivotal in the climatic evolution of the Ordovician Period (e.g. Trotter *et al.*, 2008; Turner *et al.*, 2011, 2012; Rasmussen *et al.*, 2016).

5.2 Geological overview

The Ordovician rocks in their historical type area were deposited in the Anglo-Welsh Basin, at the southern margin of the closing Iapetus Ocean (Fortey *et al.*, 1995). In south Wales, the Ordovician system tract extends over 160 km from the St Davis area to central Wales, following the Tywi lineament (Fortey, 2000). The Arenig Series are at the centre of this Ordovician tract and extend from Ramsey Island, off the most western point of the Pembrokeshire coast, towards Llandeilo in Carmarthenshire, along the Towy anticline. According to Fortey and Cocks (1986), the Carmarthen Whitland (Fig. 1) area holds the most complete Ordovician succession in the British Isles. In North Wales, the Ordovician system surrounds the Cambrian Harlech Dome, extending from Llŷn Peninsula in the west to the Bala area in the east and the Arenig Mountains in central Wales (Fig. 1). The Arenig Series in north Wales are much less complete than in south Wales. Here, we summarize the lithostratigraphy and biostratigraphy of the different areas sampled.

5.2.1 Carmarthen area

5.2.1.1 Lithology and sampling

Fortey & Owens (1978) described the geology and stratigraphy of the Carmarthen area (Fig. 2), where the Moridunian is best exposed. The exact contact with the underlying Tremadoc is not visible, but the “Login Beds” (Molyneux & Dorning, 1989), consisting of siltstones, shales and sandstones expose part of the upper Tremadoc. Ten subsamples (MPA 26829 to MPA 26838, Fig. 3, red dot) were taken from the British Geological Survey collections in the “Login Beds”, originally collected from Heol Login (“Login road”), about 2 km SE of Carmarthen on the old road A48 (SN 4352 1873-SN 4364 1870). The “Login Beds” are overlain by the lower Moridunian Ogof Hên Formation, comprising the Allt Cystanog Member made of conglomerates, sandstones and siltstones, and the Bolahau Member, made of micaceous mudstones and shales. The Ogof Hên Formation was not sampled because it is very poorly exposed. This formation is overlain by the Carmarthen Formation, comprising the black mudstones of the Pibwr Member, the turbidites and shales of the Cwmffrŵd Member and the grey mudstones of the Cwm yr Abbey Member. The Whitlandian series start with the Afon Ffynnant Formation, consisting of turbidites, and considered equivalent to the Blaencediw Formation of the Whitland area. The Carmarthen and Blaencediw formations were sampled in two different locations: at Allt Pen-y-Coed River (SN 4425 1823-SN 4446 1803), the samples CA 13-006 to CA 13-013 (Cwmffrŵd Member), CA 13-042 to CA 13-050 and TVDB 11-025 (Pibwr Member) were collected (Fig. 3 A) upstream from the point 51°50'28.1"N 4°15'45.1"W under the road A48, about 7 km SE of Carmarthen. At Cwm Yr Abbey River (SN 5002 1988-SN 5013 1943), the samples TVDB 11-001 to TVDB 11-009 (Fig. 3 B, the top of Cwmffrŵd Member, the Cwm yr Abbey Member and the base of the Afon Ffynnant Formation) have been collected upstream and downstream from the bridge on the B4300 road, about 10 km East of Carmarthen.

5.2.1.2 Fauna and age

In the Carmarthen area, Molyneux and Dorning (1989) revised the acritarch assemblage from the Login Beds and identified an assemblage similar to that of the Watch Hill Formation in the Lake District, where the *messaoudensis-trifidum* acritarchs assemblage was first described (Molyneux and Rushton, 1988). They conclude that the assemblage is younger than the Tremadoc *Angelina sedgwickii* Biozone but older than the early Arenig *Dydimograptus deflexus* Biozone, i.e., it might be of the same age as the *T. approximatus* biozone. Molyneux (1987) described four acritarch assemblages of Moridunian age: the lowest one in the Allt Cystanog Member of the Ogof Hen Formation including among others the species *Acanthodiacrodium* aff. *spinum* Rasul and ?*Coryphidium minutum* Cramer & Diez, the second one in the lower Cwmffrwd Member of the Carmarthen Formation dominated by *Acanthodiacrodium* aff. *angustum* Combaz, the third one in the upper Cwmffrwd Member of the Carmarthen Formation containing i. a. *Acanthodiacrodium* sp. A and *Barakella* sp. A and

the highest one in the Cwm Yr Abbey Member of the Carmarthen Formation distinguished by *Micrhystridium* aff. *henryi* Paris & Deunff, *M. cf. inconspicuum armoricanum* Paris & Deunff and *M. aff. nannacanthum* Deflandre.

The Carmarthen Formation yielded the graptolites *Phyllograptus* cf. *densus* and *Pseudophyllograptus* aff. *angustifolius* in the Pibwr Member, the Cwm Yr Abbey Member contains the graptolite *Callograptus* cf. *tenuis*, and the Afon Ffynnant Formation the graptolite *Azygograptus hicksii* (Rushton *et al.*, 2000).

5.2.2 Whitland area

5.2.2.1 Lithology and sampling

The Whitland area (Fig. 4), where the Whitlandian and the Fennian are best exposed, was fully described by Fortey & Cocks (1987). The lower Whitlandian Blaencediw Formation, which was not sampled as no remaining outcrop was found exposing this formation, consists of turbidites, shales and siltstones. The overlying Colomendy Formation is divided into the sandy shales of the Rhyd Henllan Member, the grey shales of the Castelldraenog Member and the black shales of the Whitland Abbey Member. The upper Cwmfelin Boeth Formation consists of turbidites and black shales. Both formations were sampled at Cwm Banau, NE of Whitland Abbey (SN 2123 1862), where the boundary between the Cwmfelin Boeth and the Colomendy formations is exposed (Fortey & Owens, 1987), although it is hardly expressed lithologically in the field (Fig. 4, red dot, CA 13-040, CA 13-041, CA 13-051, CA 13-052, TVDB 11-019, TVDB 11-020). The Colomendy Formation was also sampled (Fig. 4 C CA 13-053 to CA 13-059) in the area of Castelldraenog (51°51'43.9"N 4°36'15.3"W). The overlying Pontyfenni Formation made of black to dark grey shales and mudstones Formation was sampled (CA 13-036 to CA 13-039 and TVDB 11-021 to TVDB 11-024; Fig. 4 D) in the type location at the old quarry at Pontyfenni old quarry (SN 2379 1690-SN 2381 1693) and the light grey mudstones and shales of the overlying Llanfallteg Formation, exposing the boundary between the Arenig and the Llanvirn series, were sampled at the Llanfallteg old railway cutting (SN 1575 2020-SN1571 2013) (CA 13-001 to CA 13-005 and CA 13-014 to CA 13-035; Fig. 4 E).

5.2.2.2 Fauna and age

In the Whitland area, Molyneux (1987) described one acritarch assemblage of Whitlandian age in the Whitland Abbey Member of the Colomendy Formation including the species *Micrhystridium* spp. A-D, and two acritarch assemblages of Fennian age in the Pontyfenni Formation distinguished among others by *Coryphidium bohemicum* and ?*Frankea hamata* in the lowermost part of the Formation and by *Coryphidium bohemicum* Vavrdova and *Dasydorus cirritus?* in the upper part. The Whitlandian Blaencediw Formation yielded the

graptolites *Callograptus* and *Dendrograptus*, and the trilobite *Ogyginus hybridus*, characteristic of the middle Whitlandian (Rushton *et al.*, 2000). The Rhyd Henllan Member of Colomendy Formation contains the typical Whitlandian trilobite *Bohemopyge scutarix*, as also observed in the Castelldraenog Member and Whitland Abbey Member (Rushton *et al.*, 2000), the latter also contains the graptolite *Didymograptus simulans*, which is present throughout the Whitlandian (Fortey *et al.*, 2000). According to Rushton *et al.*, (2000), the most common fossils in the Pontyfenni Formation are the graptolites *Didymograptus (Expansograptus?) uniformis*, *Lepidus*, *D. (E.?) hirundo* and *Undulograptus cumbrensis*, the latter typical from the late Arenig (Fennian), and the trilobites *Pricyclopyge binodosa eurycephalathe*, *Placoparia cambriensis* and *Selenopeltis buchii macrophtalma*, the last two species being typical for the Fennian (Fortey and Owens 1987). The Llanfallteg Formation yielded the trilobites *Dionide levigena*, indicating the uppermost Arenig, and *Ectillaenus perovalis*, *Barrandia homfrayi*, *Stapeleyella inconstans*, *Amphyx linleyensis* and *P. cambriensis*, which all range into the Llanvirn (Fortey & Owens 1987). There are also the graptolites *U. cumbrensis*, only found in the uppermost Arenig, and *Acrograptus acutidens* and *U. austrodentatus*, ranging into the Llanvirn.

5.2.3 Arenig Fawr area

5.2.3.1 Lithology and sampling

This is the historical type area for the Arenig series, although they are less complete here than in South Wales, and an unconformity may be present at the top of the Carnedd Iago Formation. The entire Arenig is comprised in the Carnedd Iago Formation, divided into three members: the Garth Grit Member, consisting of quartz and feldspar sandstone, the Llyfnant Member, consisting of laminated dark siltstones and light sandstones and the Henllan Ash Member, made of feldspathic sandstones or sandy mudstones. Seven samples (TVDB 12-050 to TVDB 12-056; Fig. 5) were collected between the Mount Arenig Fawr, along a little stream from Hafotty Ffilltirgerig (52°55'53.3"N 3°45'33.8"W), from the Llyfnant and Henllan Ash members of the Carnedd Iago Formation.

5.2.3.2 Fauna and age

In the Arenig Fawr area, the Llyfnant Member contains abundant *Didymograptus* aff. *simulans*, which suggests a connection with the *D. nitidus* subzone of the *D. extensus* Zone in the Lake District (Zalasiewicz 1984). The species *D. aff. deflexus* and *Azygograptus* cf. *eivionicus* are also found, although the *D. aff. deflexus* differs from the type material, so the *deflexus* subzone cannot be inferred with certainty. The Henllan Ash Member contains an abundant trilobite fauna which has been described by Fortey and Owens (1978) and interpreted as early Moridunian. Some graptolite data were also re-examined by Zalasiewicz

(1984) and referred to *Dydimograptus* cf. *praenuntius* and *Tetragraptus reclinatus* in the uppermost Henllan Ash Member.

5.3 Results

5.3.1 Carmarthen area (Fig. 6)

The samples from the Tremadoc “Login Beds” revealed a modestly diverse fauna: five of the ten samples yielded chitinozoans and five species were encountered. They are not very abundant, but relatively well preserved although all are flattened. We found the species *Lagenochitina destombesi* (Plate 4.1-3), *L. brevicollis* (Plate 2,14-15), *L. obeligis*, *L. ?esthonica*, a few *Conochitina* sp. *?brevis* (Plate 2.16) and *Euconochitina* sp.

The samples from the Allt Pen-y-Coed river section exposing the Carmarthen Formation yielded a diverse chitinozoan fauna with ten species. Both 3D and flattened specimen are found, some are pyritised, and they are generally complete specimens, except for the largest ones. The species encountered are *Conochitina queddichensis* (Plate 1.1-4), *C. decipiens* (Plate 4.6-7), *C. clavaherculi* (Plate 4.10), *C. ?plicatura*, *C. hichami*, short and slender forms of *L. esthonica* (Plate 2.12-13), *L. obeligis*, *Laufeldochitina* cf. *lardeuxi* (Plate 2. 4,6), *Lau. ?baculiformis* (Plate 2.1-3) rare specimens of *Rhabdochitina* gr. *magna*, and some *Belonechitina* sp. and *Lau. ?protolardeuxi* (Plate 3.5), which is only found in the upper Cwmffrwd Member. The samples CA 13-007, 009, 010, 043 and 049 were barren.

The samples from the Cwm yr Abbey section revealed a relatively low diversity fauna, with seven species, all relatively poorly preserved, as the majority of the specimens are flattened, except for a few specimens of *Conochitina* that are preserved in 3D. The Cwm yr Abbey Member yielded the species *C. decipiens*, *C. clavaherculi* (Plate 4.10), *L. esthonica*, *L. obeligis*, *Lau. ?baculiformis* and *R. sp. gr. magna*. The sample CA-13 006 was barren.

5.3.2 Whitland area (Fig. 7)

The samples from the Cwm Banau section were almost barren, although large rock samples were dissolved (about 100 g). Only a few specimen of *Conochitina* sp. poorly preserved were recovered.

The samples collected at the old quarry in Pontyfenni yielded a diverse and abundant fauna with sixteen species. The specimens are well preserved although they are often flattened. The assemblage is characterized by numerous specimens of *Cyathochitina* aff. *calix* (Plate 1.12) and some *Cy. cf. giraffa* (Plate 1.9-11), *L. obeligis* (Plate 3.9) and a few rounded forms of *Lagenochitina esthonica* (which are bigger than the Whitlandian forms, plate 2.9-11), *L. grandis*, *L. maxima* (Plate 4.14), *Conochitina redouani* (Plate 4.3), *Belonechitina micracantha typica* (Plate 1.7-8), a few *B. henryi* (Plate 1.5-6), *Tanuchitina achabae* (Plate 4.13), *T.*

granbyensis (Plate 4.4-5), *Bursachitina ?laminaris* (Plate 2.1-4), *Desmochitina ornensis* (Plate 2.5), *D. minor*, *D. urceolata*, and a few *Rhabdochitina* sp. gr. *magna* and *Eremochitina* aff. *baculata* (Plate 3.11-12).

The Llanfallteg section revealed a rather diverse assemblage with twelve species although in rather low abundances. The specimens are often pyritised or broken, and both 3D and flattened specimens are found. The assemblage from the upper Arenig part of the succession yielded *Desmochitina* aff. *bullata* (Plate 2.6-8), *D.* sp. gr. *minor*, *D. urceolata*, *Bursachitina ?laminaris*, rare *D. ornensis*, *Euconochitina primitiva*, *Belonechitina micracantha typica*, *Tanuchitina ?domfrontensis* (Plate 4.11-12), *Cyathochitina ?protocalix* (Plate 4.8-9) and a few *T. ?achabae*, *Rhabdochitina* sp. gr. *magna*. The assemblage of the overlying lower Llanvirn contains *D.* sp. gr. *minor*, *T. achabae*, *T. domfrontensis*, *R.* sp. gr. *magna*, *B. micracantha*, that range upwards from below the series boundary, but also some specimens of *Cy. ?protocalix* that have their local FAD in the Llanvirn. A lot of samples were barren (CA 13-020 to 023 and 027 to 030) although some samples were processed up to three times in the lab (totaling up to about 150 g of dissolved rock for these samples) to enhance recovery.

5.3.3 Arenig Fawr area (Fig. 8)

The samples from the Arenig Fawr section yielded a rather poor assemblage with low abundance, almost all of the specimen are broken, and thus only about five species were identifiable as: *Lagenochitina obelgis* (Plate 3.10), *Desmochitina* sp. gr. *minor*, *Tanuchitina* sp. (Plate 3.7-8) and *R.* sp. gr. *magna*, all contained in two of the seven samples recovered.

5.4 Chitinozoan assemblages and their correlation

Five chitinozoan assemblages have been defined, regardless of the sections the samples came from. The first and oldest assemblage is recorded in the upper Tremadoc Login bed in the Carmarthen area, the second one occurs in two sections, i.e., at Allt Pen y Coed (Moridunian) and at Cwm Yr Abbey (Whitlandian-Moridunian) in the Carmarthen area. The third assemblage is recorded in the Fennian Pontyfenni section near Whitland, and the youngest assemblage is from the Llanfallteg section, straddling the Arenig-Llanvirn boundary. The species found in the Fennian samples from the Arenig Fawr area were all considered part of the Lower Fennian 'assemblage 3'. The composition of the assemblages and their constituent species are described and compared to existing assemblages and biostratigraphy from other parts of Avalonia, Gondwana and peripheral terranes (Morocco, Algeria, Argentina, Bolivia, China Bohemia) but also from Baltica (Estonia and Sweden). Figure 9 displays the ranges of key species in these areas, compared to those in the type Arenig, based on the original chronostratigraphic assignments in these various studies. Figure 9 re-correlates key assemblages from other areas into the type area using similarities between chitinozoan

assemblages (de facto making suggestions for revisions of the chronostratigraphy of sections outside of the type area)

5.4.1 Assemblage 1

The oldest assemblage is defined in the Tremadocian “Login Beds” from the samples MPA 26829 to MPA 26832. This assemblage is defined by the total range of *Lagenochitina destombesi*. Associated chitinozoans are *L. brevicollis*, *L. obeligis*, *L. ?esthonica*, *Euconochitina* sp. and *Conochitina* sp. In the original biostratigraphy of Gondwana, Paris (1990, p. 188) defined the *L. destombesi* chitinozoan Biozone in the Lower Fezouata Formation (Morocco) as having an “upper early Tremadoc-lower late Tremadoc age”. This biozone is followed by the *L. conifundus* chitinozoan Biozone (previously known as *Amphorachitina conifundus*), from the upper Tremadoc to the lower Arenig EL Gassi Formation in Algeria. In a more recent revision by Videt *et al.*, (2010), the *L. destombesi* chitinozoan Biozone is followed by the upper Tremadoc *L. brevicollis* Biozone instead of the *conifundus* zone. This better fits the first assemblage in Wales, which has both *L. destombesi* and *L. brevicollis*, (but does not contain *Lagenochitina conifundus*) if we can assume that *L. destombesi* can extend beyond the top of its biozone as defined in Paris (1990). Recent finds of the species alongside younger chitinozoans (Nowak *et al.*, 2016, where *L. cf. destombesi* co-occurs with the *Euconochitina paschaensis-symmetrica* group) suggest this may be a valid assumption. Also, in the original description from Elaouad-Debbaj (1988), *L. destombesi* was thought to be an upper Tremadoc species, which is consistent with its position here.

In South China, Wang *et al.*, (2013) defined a middle Tremadocian *L. destombesi* chitinozoan Biozone in the Yinzhubu Formation in Yiyang, also containing *L. brevicollis* and *L. obeligis*. However, this biozone is followed by the *L. esthonica* and the *Euconochitina symmetrica* biozones in the middle-upper Tremadocian; the latter is not observed in Wales and the presence of *L. esthonica* is uncertain in our first assemblage (some specimens might be present in our assemblage but these have a broken neck, which hampers identification). In North Argentina, De la Puente & Rubinstein (2009) observed *D. sp. cf. L. brevicollis* in the Tremadocian Parcha Formation together with *L. cf. longiformis*, *L. conifundus* and *Euconochitina paschaensis*. Wang *et al.*, (2013) suggested that the Argentinean *L. longiformis* might be equivalent to *L. destombesi*, which seems reasonable regarding their respective specimens in comparison to those from the present study.

In Estonia, in the upper Tremadocian assemblage from the Leetse Formation, Hints & Nõlvak (2006) described a single assemblage composed of *Euconochitina primitiva*, *E. symmetrica*, *E. sp. A aff. baculata* and *L. longiformis*. Again, their *L. longiformis* are rather similar to what we call *L. destombesi* in our first assemblage, and we propose these are conspecific. The Tremadocian biostratigraphy in Baltica also contains a *L. destombesi* chitinozoan Biozone with associated species *L. esthonica* (Nõlvak 1999; Nõlvak *et al.*, 2006), but in Baltica this biozone is restricted to the middle Tremadoc. *L. esthonica* ranges up into the upper Arenig

(together with index species *Cyathochitina primitiva* that has a FAD in the middle Tremadoc ; Nölvak & Grahn, 1993, Nölvak *et al.*, 2006).

In summary, Assemblage one from Wales presents similarities with Tremadoc assemblages in Gondwana and Baltica although, *L. destombesi* does not seem to occupy the exact same chronostratigraphical position in various places, when taking these positions at face value (Fig. 9). Certain taxonomic problem with these large Lagenochitid species are hampering exact biostratigraphical correlations because similar specimens were identified under different names.

5.4.2 Assemblage 2

The second assemblage is found from the sample CA 13-042 in the lower Pibwr Member of the Carmarthen Formation (middle Moridunian), to the sample TVDB 11-001 in the Afon Ffynnant Formation (lower Whitlandian). It corresponds to an interval range zone between the FAD of *Conochitina gueddichensis* and the LAD of *C. decipiens* and comprises the associated species *C. ?plicatura*, *C. hichami*, *C. clavaherculi*, *Lagenochitina esthonica*, *L. obeligis*, *Desmochitina* sp. gr. *minor*, *Laufeldochitina ?baculiformis*, *Lau.* cf. *?protoladeuxi*, *Lau. protolareuxi*, *Rhabdochitina* sp. gr. *magna* and rare *Belonechitina* sp.

The species *L. protolardeuxi* was observed in the Arenig by Soufiane and Achab (1993) in core sections from Morocco. It resembles *Tanuchitina achabae*, but it is much smaller. Paris (1990) noted that the stratigraphically lowest specimens of *Laufeldochitina* coexist with the middle Arenig species *E. brevis* in the Western Sahara. The species *C. gueddichensis* (Oulebsir & Paris, 1993) is indicative of the *E. brevis* Biozone and its holotype has been described from this biozone in the Hassi Touareg Formation in Algeria (Paris 1990), as is *C. plicatura*, which is morphologically similar but slightly smaller. As we find a wide range of sizes, both species probably are present in our assemblage. *C. hichami* is also found in the second assemblage and is also associated to *E. brevis*. *L. obeligis* has its FAD in the *E. brevis* but is a long ranging species. *C. decipiens* has its FAD in the *Conochitina symmetrica* chitinozoan Biozone (Paris 1990) but it ranges upwards.

In summary, the associated species allow us suggest a correlation with the *E. brevis* zone in Morocco/Algeria, although the index species has not been recovered in Wales. In addition, we have not observed the index species of the underlying biozones, i.e., the *Conochitina symmetrica* chitinozoan Biozone (Paris 1990; early Moridunian) and the upper Moridunian-lower Whitlandian *Eremochitina baculata* chitinozoan Biozone (described in the El Arich El Megta Formation in Algeria; Paris 1990). None of the associated species mentioned in the original description of the *baculata* biozone (*L. lata*, *Velatachitina pelucida* and *R. magna*) occur in Wales. A complication, however, emerges from the recent finds in the Fezouata Formation (Morocco) by Nowak *et al.*, (2016), who documented chitinozoans from the *E. brevis* biozone (including the index fossil) together with acritarchs of the *messaoudensis-trifidum* acritarch assemblage (sub assemblages 1-2) and graptolites of the *A. murrayi* biozone, indicating a late Tremadocian age. This led Nowak *et al.*, (2016), to suggest that the

chronostratigraphic assignment of the *E. brevis* zone may be in need of revision. This is not immediately supported by our data from the type Arenig, although we cannot be sure as we do not have the biozone's index species.

Samuelsson & Verniers (2000) observed a few specimens of *E. brevis* associated mostly with *L. obeligis* and *C. spp.* in the lower Whitlandian Abbaye de Villiers Formation in Belgium. This formation can thus be correlated the basal Whitlandian Afon Ffynnant Formation overlying the Carmarthen Formation in Wales. In Bolivia, Grahn (2006) defined the *C. decipiens* chitinozoan Biozone associated with *C. havliceki* and ranging from the lower to the upper Arenig in the Agua y Toro Formation. The former is present in our second assemblage of Wales but the latter has not been identified. In Argentina, De La Puente (2000) observed *Eremochitina* sp., *E. sp. cf. baculata*, *E. brevis* and *E. baculata brevis* in the upper Floian Acoite Formation.

5.4.3 Assemblage 3

The third assemblage occurs in the middle Fennian, from the samples CA 13-036 in the Pontyfenni Formation to the sample CA 13-019 in the Llanfallteg Formation. However, as the four following samples (CA 13-020 to CA 13-023) are barren, the boundary with the fourth assemblage is not well constrained. It is defined as interval from the FAD of *Bursachitina ?laminaris* at its base to the LAD of *Desmochitina aff. bulla* at its top. The assemblage comprises *Desmochitina ornensis*, *D. urceolata*, *D. sp. gr. minor*, *Lagenochitina esthonica*, *L. obeligis*, *L. grandis*, *L. maxima*, *Tanuchitina granbyensis*, *Rhabdochitina sp. gr. magna*, *Belonechitina micracantha typica*, *B. henryi*, *B. sp.*, *Cyathochitina aff. calix*, *Cy. cf. giraffa*, *?Eremochitina aff. baculata* and *Conochitina redouani*.

Several of the species identified in this assemblage feature prominently in the biostratigraphy from Gondwana, Paris (1990), i.e., in the *Desmochitina ornensis* and *Belonechitina henryi* chitinozoan biozones in lower-middle Fennian series. Next to the biozonal (name-bearing) index species, the following associate species are the same between the two areas: *L. obeligis*, *L. esthonica*, for the *D. ornensis* Biozone and *B. micracantha*, *L. obeligis*, *L. esthonica*, for the *B. henryi* Biozone. The combination of species observed in Wales can be best correlated to the Gonwanan *henryi* biozone, which has a mid Fennian age according to the latest revision of Videt *et al.*, (2010). Certain forms in this third assemblage such as *Desmochitina urceolata* and *D. aff. bulla* are similar to *D. bulla*, the index species of the upper Fennian biozone overlying the *henryi* zone, but this identification cannot be confirmed. *Desmochitina aff. bulla* differs from the type material by its wider opening, and a less sub-spherical shape. *Desmochitina urceolata* (described in the upper Arenig in the Sahara by Benoit and Taugourdeau, 1961) is much smaller and has a more ovoid shape. Therefore, these occurrences do justify correlating our third assemblage to the *bulla* zone instead of the *henryi* zone, although they may indicate we are not far below the FAD of true *D. bulla*. *Desmochitina ornensis*, ranging upwards from the lower Fennian, also has an ovoid shape and does not have copula, unlike the two others Desmochitiniids.

Another species with high biostratigraphic potential is *Tanuchitina granbyensis*. It has been reported in the upper Arenig of Sweden, from a level considered to be within the Baltic *cucumis* Biozone. *Tanuchitina granbyensis* is probably also present in the uppermost Arenig lowermost Pissot Formation in France (Grahn, Nölvak and Paris, 1996). We do not have complete specimens in our assemblage, but the largest one measures more than 600µm and our specimens have the typical ovoid apex with a carina, which corresponds to the description of Grahn, Nölvak and Paris (1996). However, it needs to be noted that other, and much older species, are morphologically rather similar to *T. granbyensis*. For instance, these include *Eremochitina* sp. A aff. *baculata* in the Leetse Formation (Hints and Nölvak, 2006) and *Er.* aff. *baculata* in the Fezouata Formation (Nowak *et al.*, 2016).

In our assemblage 3 some forms could belong to ?*Eremochitina* aff. *baculata sensu* Benoit and Taugourdeau (1961) or *Velatachitina veligera* (Poumot 1968) which are typical of the middle-upper Arenig, but their identification is not confirmed yet, as no specimen with all the characteristics has been found. As discussed by Paris (1981) these forms are variable in size, and appear to be bigger in North Africa. *Velatachitina veligera* has also been recovered in the lowermost Pissot Formation in France and in the Huy Formation in Belgium (Vanmeirhaeghe 2007, unpub.).

A different form of *Lagenochitina esthonica*, a long ranging species, is found in the Fennian of Wales. It has a larger and more slender test and a less conspicuous shoulder than the forms recovered from the Tremadoc and Whitlandian. Some of the largest *Lagenochitinae* forms found in the third assemblage are attributed to *L. maxima*, a very large form with a claviform vesicle and *L. grandis*, which has a flat bottom and is a little smaller. Both species have been described by Taugourdeau and de Jekhowsky (1960) in Algeria, where *L. maxima* appears slightly before *L. grandis*. Grahn, Nölvak and Paris, (1996) described a species in the upper Arenig they named *Clavachitina poumoti*, which is very similar to our *Lagenochitina maxima*. *Conochitina redouani* is another similar claviform species commonly found in assemblage 3, but is much smaller again than *L. grandis*. *Conochitina redouani* is, following the original description from Oulebsir and Paris (1993) in Algeria, of middle Arenig age. *Belonechitina micracantha typica* (Eisenack 1965) are also widely present in the third assemblage in Wales. Paris (1981) observed both *B. micracantha* and *B. micracantha typica* (which is similar to *B. henyi* but has larger spines on the basal margin and is overall larger) in the lower Pissot Formation (middle Arenig to Llanvirn) in France, and he noticed the latter becomes more abundant in the upper Arenig series. We see a similar pattern in the upper Pontyfenni Formation.

The species *Cyathochitina calix* defined by Eisenack (1931) presents stratigraphical and taxonomical issues and is in need of revision (Paris 1981). It has, e.g., been observed in the upper Fennian and lower Llanvirn in Gondwana (Paris, 1990) and in the Llanvirn Hope Shale in Avalonia (Shropshire; Jenkins, 1967). We choose to name our specimens *Cy.* aff. *calix* as their dimensions differ from the holotype and the constriction above the carina is clearly demarcated. The largest specimens of *Cyathochitina* that also have the longest neck (more than the half of the total length) are named *Cy.* cf. *giraffa*, originally described by Grahn and Nölvak (2010) as a middle Sandbian species.

In summary, our third assemblage, has good correlation potential with the North Gondwanan Fennian *Belonechitina henryi* biozone defined by Paris (1990), and to some extent with the *D. bulla* zone. For instance, our assemblages are very similar with the upper Arenig lower Pissot Formation in France, which can be correlated to the upper Pontyfenni and lower Llanfallteg formations in Wales. In addition, *Tanuchitina granbyensis* enable us to correlate these levels to the upper Arenig of Sweden.

5.4.4 Assemblage 4

The youngest assemblage occurs in the upper Fennian and lowermost Llanvirn boundary, in the lower part of the Llanfallteg Formation from the sample CA 13-019 to CA 13-005. It is defined by the range of *Tanuchitina domfrontensis*, associated with *Conochitina primitiva*, *Rhabdochitina* sp. gr. *magna*, *Belonechitina* sp., *Siphonochitina* sp., *Tanuchitina ?achabae*, *T. ?domfrontensis* and rare *Cyathochitina campanulaeformis*, *Cy. ?protocalix* and *Desmochitina* sp. gr. *minor*.

Tanuchitina achabae has been described in the lowermost Pissot Formation in France by Paris (1981) corresponding to the uppermost Arenig. *T. domfrontensis* also occurs in the Pissot Formation but only in the Llanvirn portion of the unit; this has been applied elsewhere to identify the Arenig-Llanvirn boundary, for instance, in the Cacemes Formation in Portugal (Paris 1981). However, *T. achabae* is rather similar to *T. domfrontensis* and only differs from it by its bigger size. Unfortunately, very few complete specimens were recovered in Wales, so it is hard to differentiate between these two species based on our material. In Llanfallteg, *T. domfrontensis* occurs from a few m below Arenig-Llanvirn boundary, suggesting it straddles the boundary, rather than pinpoints it.

Given the vagaries of preservation in the section, *Cy. ?protocalix* may also be present in this assemblage, although it is very difficult to separate it from the specimens identified as *Tanuchitinae*. Nevertheless, some specimens do seem to display the required restriction (Plate 4.8-9) that typifies *Cy. protocalix*. *Cy. protocalix* also occurs in the lower Pissot Formation and it defines the eponymous biozone straddling the uppermost Arenig-lowermost Llanvirn in the Gondwana biostratigraphic framework (Webby *et al.*, 2004; Videt *et al.*, 2010). Species characteristic of the underlying upper Fennian *D. bulla* biozone, known from the upper Klabava Formation in Bohemia (Paris and Mergl 1984) and the Tachilla Formation in Morocco (Videt *et al.*, 2010) are not recorded from Llanfallteg.

In Baltica, the chronostratigraphical equivalents should be within the upper *C. cucumis*/lower *Cy. regnelli* chitinozoan biozones (Nölvak & Grahn, 1993, Nölvak 1999; Nölvak *et al.*, 2006), yielding assemblages that differ completely from assemblage 4 in Wales.

Our fourth assemblage correlates well with the Gondwanan assemblages, although some of the key species are not easily differentiated from one another, such as *Tanuchitina domfrontensis* or *Cyathochitina protocalix*. But nevertheless, we can confirm that this

assemblage traces the Arenig-Llanvirn boundary although the exact limit is difficult to identify.

5.5 Discussion and palaeogeography

Four chitinozoan assemblages are recognized in the upper Tremadoc, the Arenig and the lowermost Llanvirn that are mostly comparable with the fauna from Gondwana, but also show some resemblance to Baltica. The species found in Wales are most of the time comparable to the ones described by Paris (1990) in his biozonation for the Tremadoc and the Arenig in the Northern Gondwana domain, although they at times are chronostratigraphically slightly misaligned when correlated in the Arenig type area in Avalonia.

The first assemblage in the Tremadoc is mostly composed of *Lagenochitiniid* species, thus presenting the lowest diversity amongst our assemblages. It is comparable to the fauna described in Gondwana as the *L. brevicollis* chitinozoan Biozone (Paris 1990; Videt *et al.*, 2010; Fig 10), the *L. destombesi* chitinozoan Biozone (Wang *et al.*, 2013), and the assemblages from the Parcha Formation (De la Puente *et al.*, 2009). This solid link is not a surprise given the close palaeogeographic position of Avalonia in the peri-gondwana realm at this time. The fauna is also similar to that of Baltica, at least correlating to the Leetse Formation (Nölvak 1999; Nölvak *et al.*, 2006).

The second middle Moridunian assemblage is more diverse and contains principally Conochitiniid, Laufeldochitiniid, Lagenochitiniid a few Desmochitiniid species. This assemblage is very similar to the fauna from Gondwana although the index species such as *Eremochitina baculata* or *E. brevis* are absent in Wales. The absence of Eremochitiniids in Wales is remarkable, given that has been widely found elsewhere, i.e., in Morocco and Algeria (Paris 1990; Videt *et al.*, 2010), in the Brabant Massif by Samuelsson and Verniers (2000), in Estonia (Nölvak & Grahn, 1993, Nölvak 1999) and in Argentina (De La Puente 2000). There are several explanations for the absence of *E. brevis* in Wales, including incompleteness of section, issues with the assumed chronostratigraphic position of the biozone as suggested by Nowak *et al.*, (2016), palaeogeographic and palaeo-ecological factors. The co-occurrences between *brevis* biozone chitinozoans and Tremadocian graptolites and acritarchs are peculiar indeed and require further study, but our finds of *brevis* biozone chitinozoans (*C. queddichensis* and *C. decipiens*) in the Moridunian-Whitlandian suggest that re-assigning the *brevis* biozone to the Tremadoc might be a bit premature. Increased faunal provincialism of the Avalonian fauna due to the drifting of Avalonia paleocontinent away from Gondwana is unlikely to be cause either, given its onwards trajectory only increases the distance with Gondwana during the Whitlandian and the Fennian, while the faunas become more similar to Gondwana again. Local palaeogeography, governed by species-specific tolerances to oceanic or climatic conditions are a more plausible explanation.

The third assemblage is the one with the greatest diversity, containing several species of Desmochitiniids, Belonechitiniids, Lagenochitiniids and some Cyathochitiniids. It is also very similar to the Gondwanan fauna, yielding eponymous species of the biozones described in

Gondwana such as *B. henryi* and *D. ornensis* (Paris 1990; Webby *et al.*, 2004, Videt *et al.*, 2010). It is rather different from the assemblage in Baltica, which suggests again different environmental conditions or palaeogeography (or a combination of both), with the notable exception of the presence of *Tanuchitina granbyensis*, known from the upper Arenig assemblage of the Granby crater in Sweden (Grahn, Nölvak and Paris, 1996).

The last assemblage has a regular to low diversity and is mostly compound of *Tanuchitinid* and *Belonechitinid* species. It is similar to Gondwana although some of the key species are absent, but *Cyathochitina ?protocalix*, *Tanuchitina ?achabae* and *T. domfrontensis* cement the Gondwanan affinities of this assemblage

From our study of the type Arenig sections, in Wales, it is clear that its chitinozoans faunas, for all of the stratigraphy studied, are an integral part of the Gondwanan province, unaffected by the initial closure of the Iapetus Ocean and onset of the northwards drift of Avalonia during the Arenig-Llanvirn (Torsvik and Rehnström, 2003; Torsvik and Cocks, 2013). While the Tremadocian assemblages can be correlated across to faunas on various palaeocontinents and palaeolatitudes (in modern Baltica, China, Arentina), this is much less the case for the Arenig assemblages from Wales and polar Gondwana (Morocco, Algeria, France; Fig. 8). We hypothesize that this could reflect changing palaeo-environmental conditions. In this context, it is interesting to note that several studies using proxy data, sequence stratigraphy and Global Circulation Models have suggested important global cooling during the Early-Middle Ordovician (Trotter *et al.*, 2008), with ice caps being present from the Darriwilian if not earlier (Turner *et al.*, 2011, 2012; Dabard *et al.*, 2015; Rasmussen *et al.*, 2016; Pohl *et al.*, in subm.). Chitinozoan distribution patterns have been shown earlier to respond to global cooling (Vandenbroucke *et al.*, 2010 a, b). The emergent chitinozoan biostratigraphy at Avalonian mid-palaeolatitudes, pioneered in this paper, has the potential to help better understand chitinozoans migrations during this pivotal period of the time in the Earth's climate system.

5.6 Conclusion

Our biostratigraphical study from Wales reveals relatively well preserved and abundant chitinozoans assigned to 8 genera and 30 species and grouped into four distinct assemblages. These assemblages can be linked to a series of Gondwanan biozones (Fig. 10), i.e., the *brevicollis/destombesi*, the *brevis*, the *henryi* and the *protocalix* biozone, as well as a few levels in Baltica.

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5.8 Figures

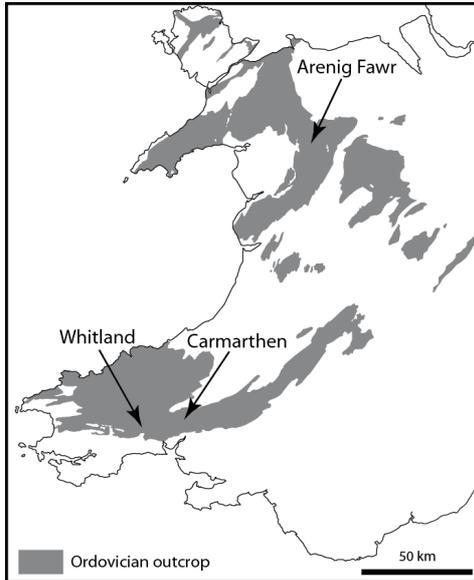


Figure 1. Sampling locations: The Arenig Fawr area, the Whitland area and the Carmarthen area.

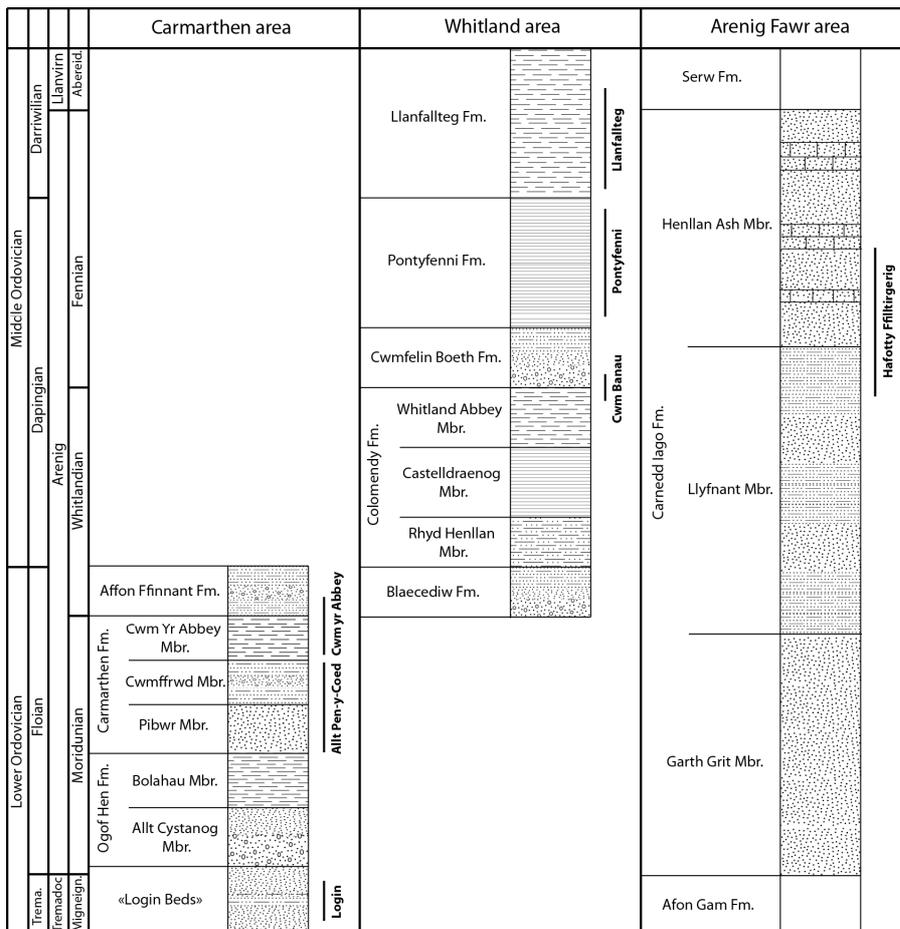


Figure 2. Lithostratigraphical log with the sampled sections in the Carmarthen, Whitland and Arenig Fawr areas.

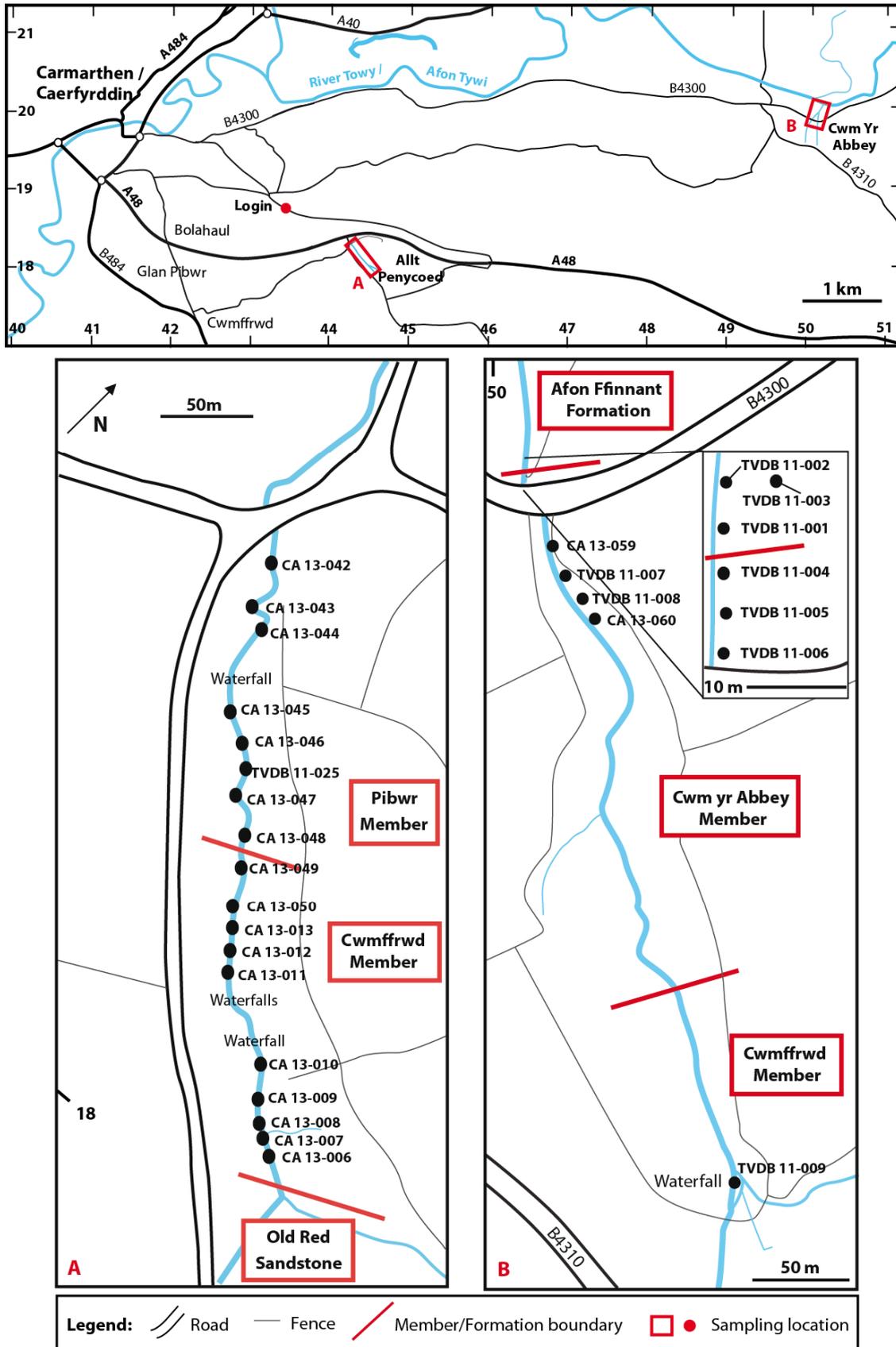


Figure 3. Sampling in the Carmarthen area. A: Allt Pen y Coed section, B: Cwm Yr Abbey section.

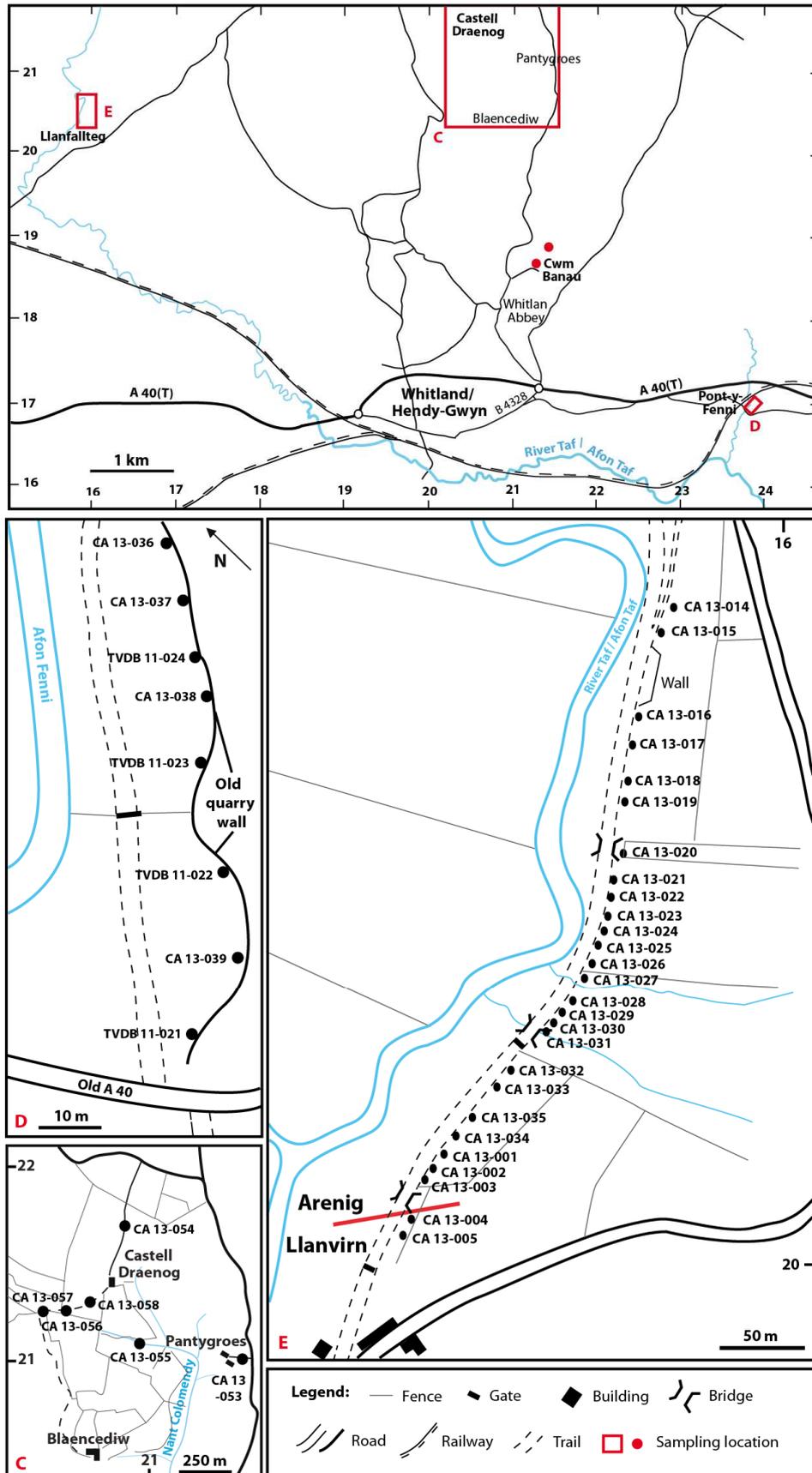


Figure 4. Sampling in the Whitland area. C: Castell Draenog, D: Old quarry at Pontyfenni, E: Old railway at Llanfallteg

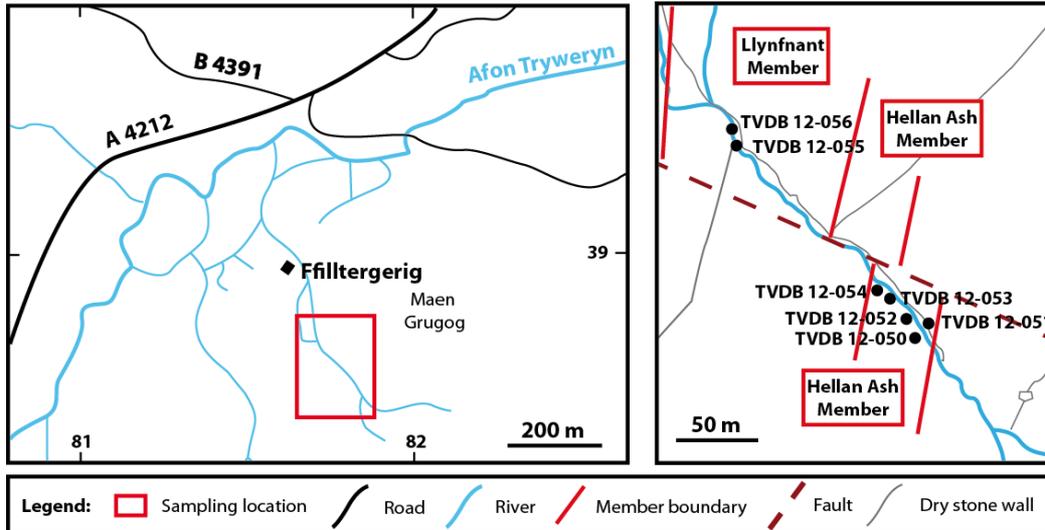


Figure 5: Sampling in the Arenig Fawr area.

		Carmarthen area			
		Formations/ Members	Chitinozoan biostratigraphy	Assemblages	
Lower Ordovician	Floian	Whitlandian	Blaecediw Fm.		?
			Affon Ffynnant Fm.		Assemblage 3
	Arenig	Moridunian	Cwm Yr Abbey Mbr.		Assemblage 2
			Cwmffrwd Mbr.		
			Pibwr Mbr.		
	Ogof Hen Fm.	Bolahau Mbr.		?	
		Allt Cystanog Mbr.			
	Tremadoc		«Login Beds»		Assemblage 1

Chitinozoan species ranges (indicated by vertical lines):

- Lagenochitina obeligitis*
- Lagenochitina esthonica*
- Lagenochitina destombesi*
- Conochitina* sp.
- Lagenochitina brevicollis*
- Euconochitina* sp.
- Conochitina queddichensis*
- Conochitina* ?*plicatura*
- Conochitina hichami*
- Conochitina decipiens*
- Rhabdochitina gracilis*
- Conochitina clavaherculi*
- ?*Laufeldochitina* cf. *baculiformis*
- ?*Laufeldochitina* cf. *lardeuxi*
- Desmochitina urceolata*
- Desmochitina* sp. *gr. minor*
- Laufeldochitina* cf. *protolardeuxi*
- Belonechitina* sp.

Figure 6. Chitinozoan ranges and biozones in the Carmarthen area

		Middle Ordovician		Whitland area		
				Formations/ Members	Chitinozoans ranges	Assemblages
Lower Ordovician	Floian	Dapingian		Fennian	Llanfallteg Fm.	?
		Arenig				
		Whitlandian		Pontyfenni Fm.	<i>Lagenochitina obelgis</i> <i>Conochitina clavaherculi</i> <i>D. sp. gr. minor</i> <i>Lagenochitina esthonica</i> <i>R. sp. gr. magna</i> <i>Desmochitina ornensis</i> <i>?Bursachitina laminaris</i> <i>Cyathochitina aff. calix</i> <i>Eremochitina cf. baculata</i> <i>Tanuchitina granbyensis</i> <i>Belonechitina henryi</i> <i>Belonechitina micracantha typica</i> <i>Lagenochitina maxima</i> <i>Lagenochitina grandis</i> <i>Desmochitina urceolata</i> <i>Conochitina ?primitiva</i> <i>Desmochitina aff. bulla</i> <i>Tanuchitina achabae</i> <i>Cyathochitina ?protocalix</i> <i>Tanuchitina domfrontensis</i>	Assemblage 3
		Colomendy Fm.				
		Rhyd Henllan Mbr.		?		
		Castelldraenog Mbr.			?	
		Whitland Abbey Mbr.		?		
		Blaecediw Fm.			?	

Figure 7. Chitinozoan ranges and biozones in the Whitland area

		Arenig Fawr area	
		Formations/ Members	Chitinozoans ranges
L. O.	Middle Ordovician		
Floian	Dapingian		
	Arenig		
	Whitlandian		
	Fennian		
		Henllan Ash Mbr.	
		Carnedd Iago Fm.	
		Llyfnant Mbr.	<div style="display: flex; flex-direction: column; align-items: center;"> <div style="width: 10px; height: 15px; background-color: black; margin-bottom: 5px;"></div> <div style="width: 10px; height: 15px; background-color: black; margin-bottom: 5px;"></div> <div style="width: 10px; height: 15px; background-color: black; margin-bottom: 5px;"></div> <div style="width: 10px; height: 15px; background-color: black;"></div> </div> <p style="text-align: center; margin-top: 5px;"><i>Lagenochitina obeligijs</i></p> <p style="text-align: center; margin-top: 5px;"><i>D. sp. gr. minor</i></p> <p style="text-align: center; margin-top: 5px;"><i>Tanuchitina sp.</i></p> <p style="text-align: center; margin-top: 5px;"><i>Rhabdochitina sp. gr. magna</i></p>

Figure 8. Chitinozoan ranges and biozones in the Arenig Fawr area

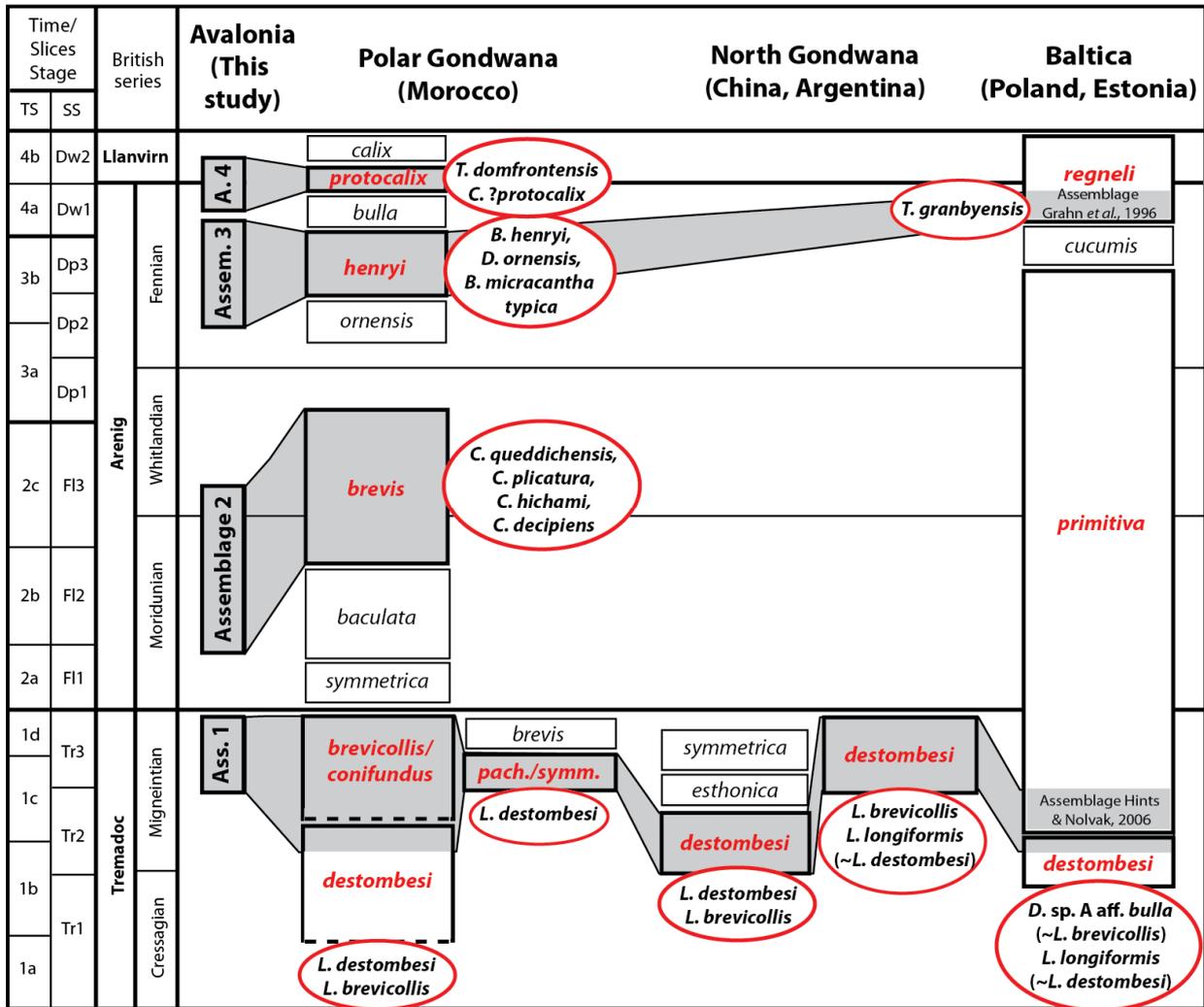


Figure 10: Correlation of the assemblage from Wales with biozonation from Gondwana and Baltica. The species in the red circles are the ones driving the correlations in grey. The biozonation for the polar Gondwana is from Webby *et al.* (2004) for the left column (*destombesi* to *calix*), except for the *brevicollis* biozone (Videt *et al.*, 2010) and from Nowak *et al.* (2016) for the right column (*pach./symm.* = *pachaensis/symmetrica* to *brevis*). The biozonation for the Northern Gondwana is from Wang *et al.* (2012) for left column (*destombesi* to *symmetrica*) and from De la Puente and Rubinstein (2009) for the right column (*destombesi*). The biozonation from Baltica is from Nölvak *et al.* (2006).

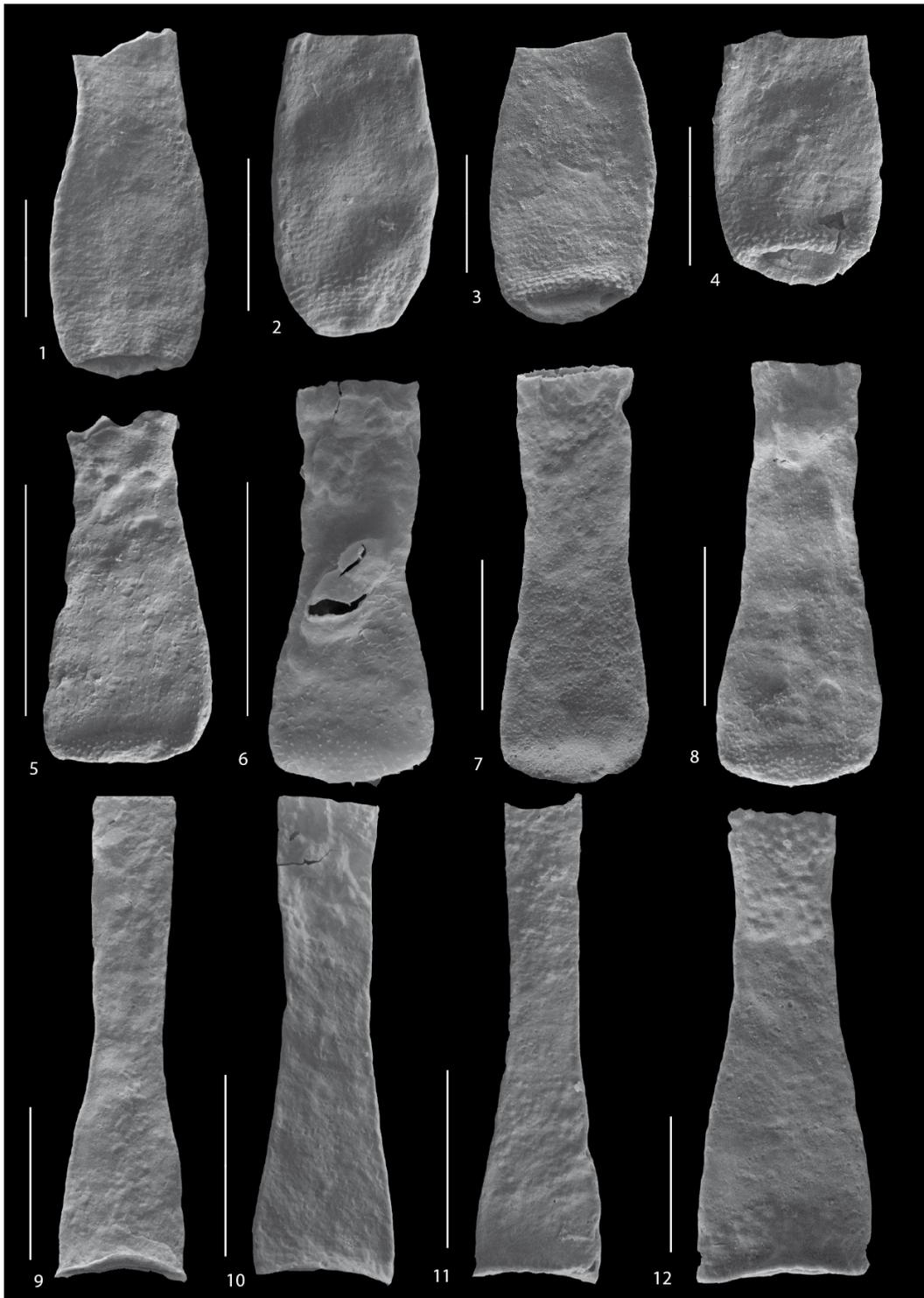


Plate 1: SEM pictures of selected chitinozoans. 1-4: *Conochitina gueddichensis*, Pibwr Member of the Carmarthen Formation exposed in the Allt Pen-y-Coed Section, middle Moridunian. 5-6: *Belonechitina henryi*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 7-8: *B. micracantha typica*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 9-11: *Cyathochitina cf. giraffa*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 12: *Cyathochitina cf. calix*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. Scale bars = 100 μ m except 9-11 = 200 μ m.

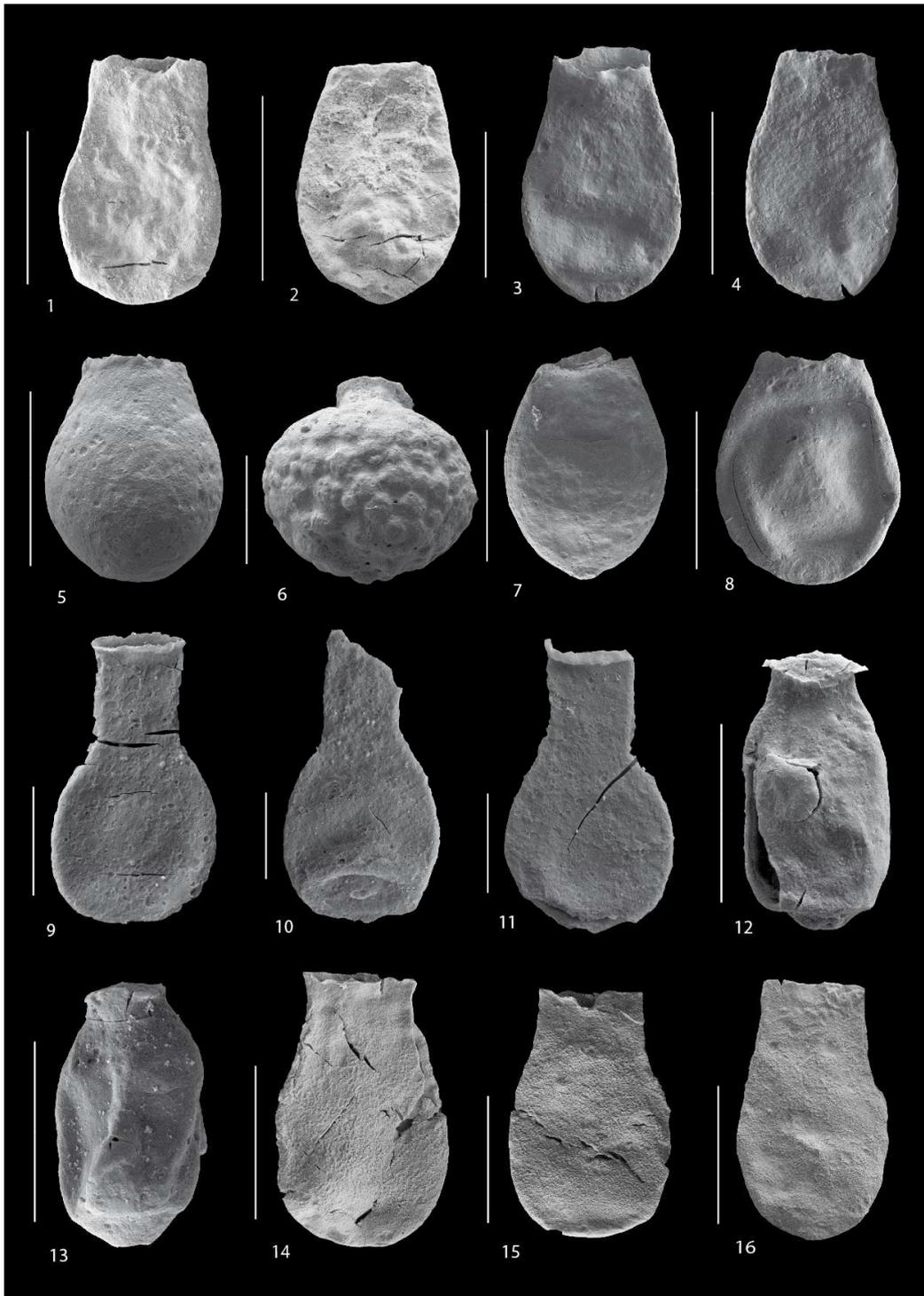


Plate 2: SEM pictures of selected chitinozoans: 1-4: *Bursachitina ?laminaris* Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 5: *Desmochitina ?ornensis*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 6-8: *Desmochitina* aff. *bullata*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 9-11: *Lagenochitina esthonica*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 12-13: Short forms of *L. esthonica*, Pibwr Member of the Carmarthen Formation exposed in the Allt Pen-y-Coed Section, middle Moridunian. 14-15: *L. brevicollis*, “Login Beds” exposed in Login Section, upper Tremadoc. 16: *Conochitina ?brevis*, “Login Beds” exposed in Login Section, upper Tremadoc. Scale bars = 100µm.

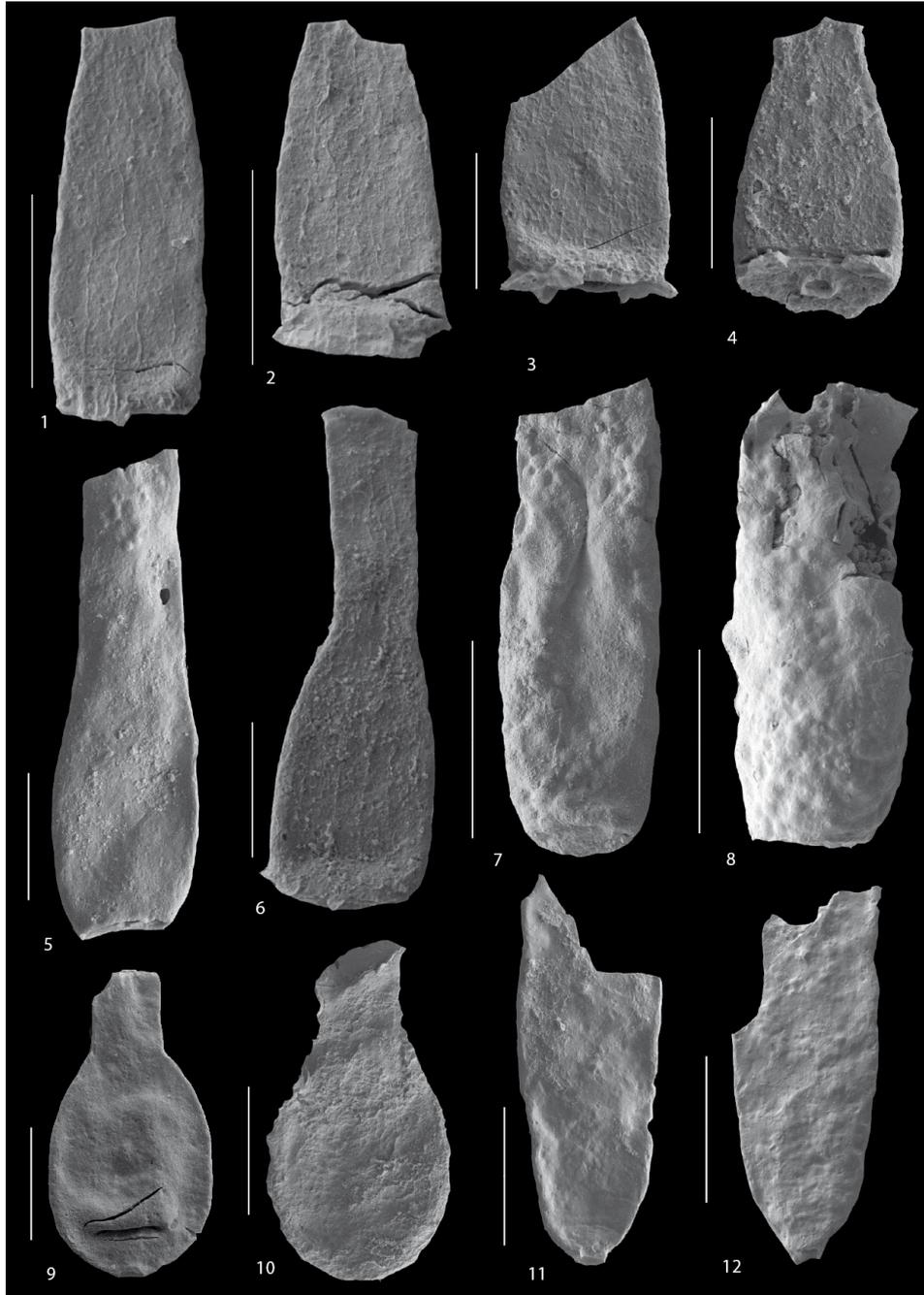


Plate 3: SEM pictures of selected chitinozoans: 1-3: *Laufeldochitna ?baculiformis*, Cwm Yr Abbey Member of the Carmarthen Formation exposed in the Cwm Yr Abbey Section, upper Moridunian. 4, 6,: *Laufeldochitina cf. lardeuxi*. A, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 5: *Laufeldochitina ?protolardeuxi*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 7-8: *Tanuchitina* sp., Henllan Ash Member of the Carned Iago Formation exposed at Arenig Fawr, Fennian. 9-10: *Lagenochitina obelgis*, respectively from the Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian and Henllan Ash Member of the Carned Iago Formation exposed at Arenig Fawr, Fennian and the Henllan Ash Member of the Carned Iago Formation exposed at Arenig Fawr, Fennian. 11-12: *?Eremochitina baculata brevis*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. Scale bars = 100 μ except 1-2 = 200 μ m.

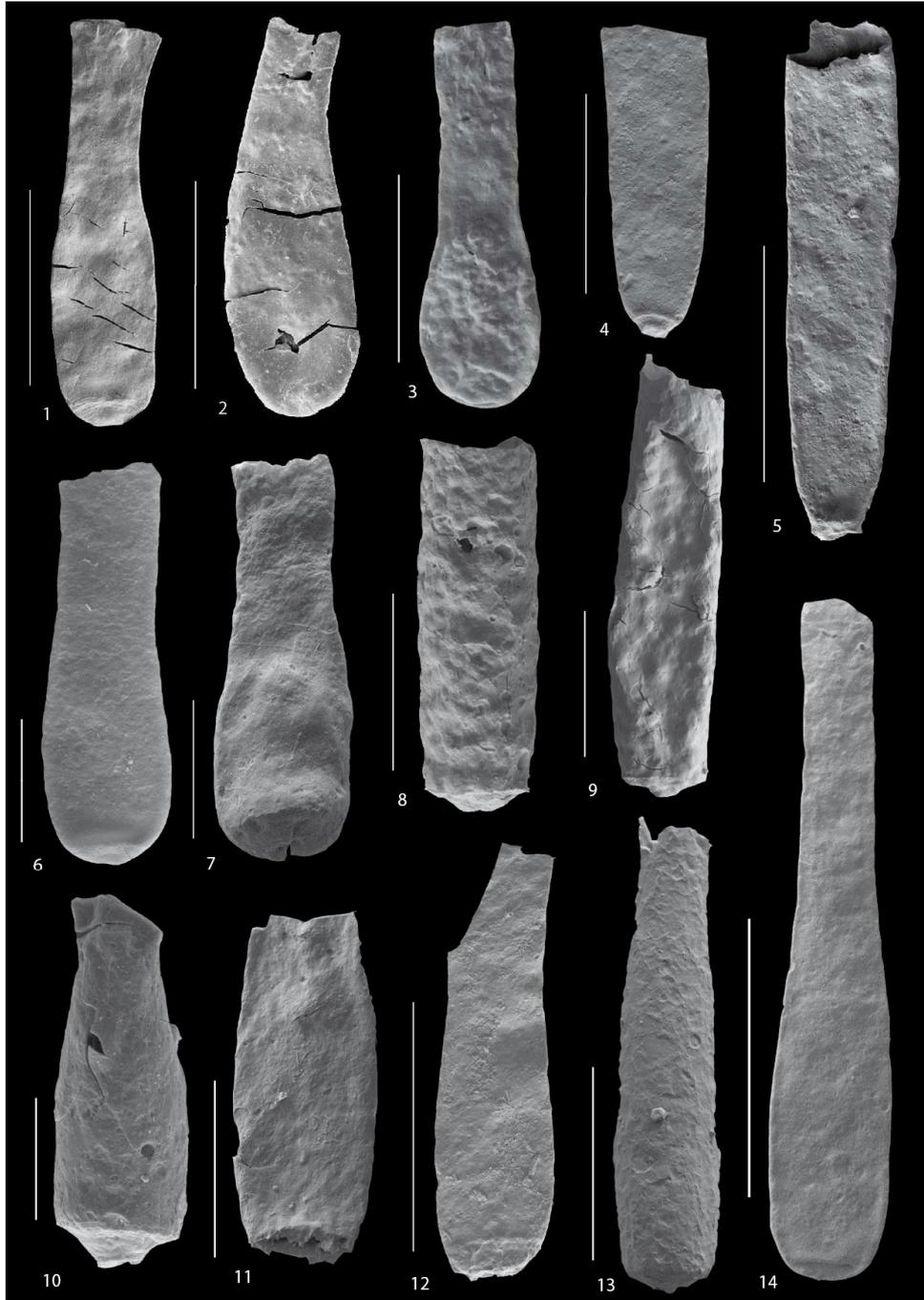


Plate 4: SEM picture of selected chitinozoans: 1-2: *Lagenochitina destombesi*, “Login Beds” exposed in Login Section, upper Tremadoc. 3: *Conochitina hichami*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 4-5: *Tanuchitina granbyensis*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. 6-7: *Conochitina decipiens*, Afont Ffynnant Formation exposed in the Cwm Yr Abbey Section, lower Whitlandian. 8-9: *Cyathochitina ?protocolix*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 10: *Conochitina clavaherculi*, Cwmffrwd Member of the Carmarthen Formation exposed in the Allt Pen y Coed Section, upper Moridunian. 11-12: *Tanuchitina domfrontensis*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 13: *Tanuchitina achabae*, Llanfallteg Formation exposed in the Llanfallteg old cuttings Section, upper Fennian. 14: *Lagenochitina maxima*, Pontyfenni Formation exposed in the Pontyfenni old quarry, middle Fennian. Scale bars = 200 μ , except 3, 6-7, 10-11 = 100 μ m.

**6. Chitinozoans from the
Tremadocian/Floian boundary
(Lower Ordovician) of the Watch
Hill Formation, Lake District
(Northern England)**

Chitinozoans from the Tremadocian/Floian boundary (Lower Ordovician) of the Watch Hill Formation, Lake District (Northern England)

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Abstract

The Global Stratotype Section and Point (GSSP) for the Floian Stage (Lower Ordovician) is defined by the first appearance datum (FAD) of the graptolite *Tetragraptus approximatus*. Sedimentological successions displaying the Tremadocian-Floian that do not contain a graptolite fauna can be correlated with the help of palynomorphs, organic-walled microfossils, such as acritarchs and chitinozoans. The distinctive *Cymatiogalea messaoudensis* - *Stelliferidium trifidum* acritarch assemblage spans the Tremadocian/Floian boundary and is commonly used to correlate successions of the southern margin of Gondwana. This assemblage was first described from the Watch Hill and Hope Beck formations of the Skiddaw Group in the Lake District, Northern England. Here we describe a chitinozoan assemblage from the uppermost Tremadocian Watch Hill Formation. The assemblage contains the species *Euconochitina symmetrica*, a taxon that is known to straddle the Tremadocian/Floian boundary, based on reports from various sites along the margin of Gondwana, and other palaeocontinents (Taugourdeau and de Jekhowsky, 1960; Benoit and Taugourdeau, 1961; Achab 1980, de la Puente and Rubinstein, 2009; Wang *et al.*, 2013a).

6.1 Introduction

The Global Stratotype Section and Point (GSSP) for the Floian Stage (Lower Ordovician) is defined in the Diabasbrottet Section at Hunneberg Mountain in southwestern Sweden. The GSSP is marked by the first appearance (FAD) of the graptolite *Tetragraptus approximatus* that also correlates with the base of the *phyllograptoides* graptolite Biozone. Conodonts and trilobites are also present in the stratotype section and are useful for international correlation (Bergström *et al.*, 2004).

Many sedimentary successions, however, do not display macrofossils, and in particular when the two groups used for the definition of the Ordovician GSSP's, graptolites and conodonts, are absent, microfossils are very useful for stratigraphical correlations. In a biostratigraphical

calibration charts from Webby *et al.* (2004), they showed the classical graptolite and conodont biozones alongside a biozonation of the chitinozoans, based on detailed studies of chitinozoan biostratigraphy from different palaeocontinents (i.e., Achab 1989; Paris, 1990; Nölvak, 1999). One of these detailed studies was that of Paris (1990), who described a chitinozoan biozonation of the 'Northern Gondwana domain' of the peri-Gondwanan margin in high southern latitudes that became the standard for international correlations, including the Lower Ordovician.

These chitinozoan biozones, however, are in need for calibration, against the British chronostratigraphical scheme, historically used in many parts of the world as well as against the new international chronostratigraphy for the Ordovician, recently revised by the International Commission on Stratigraphy (Bergström *et al.*, 2009). This has been partly done for the Upper Ordovician, with studies focussing both on the chitinozoan biostratigraphy of the historic type are in the Anglo-Welsh Basin (Vandenbroucke 2008; Vandenbroucke *et al.*, 2005, 2008 a, b, 2009; Challands *et al.*, 2014) as well as on the chitinozoans of the new GSSPs (Vandenbroucke, 2004; Goldman *et al.*, 2007; Tessitore *et al.*, in prep). Such a calibration currently does not exist for the Lower and Middle Ordovician.

For the Tremadocian-Floian boundary, Molyneux *et al.* (2007) proposed a correlation based on the distinctive *Cymatiogalea messaoudensis* - *Stelliferidium trifidum* acritarch assemblage. This assemblage was originally described from upper Tremadoc to lower Arenig rocks of the English Lake District (Molyneux and Rushton, 1988), and first called the "Watch Hill assemblage." Subsequently, the assemblage was subdivided into five subzones by Cooper *et al.* (1995). The *messaoudensis* - *trifidum* acritarch assemblage has been correlated with the *Araneograptus murrayi* and *Tetragraptus phyllograptoides* graptolite biozones (Molyneux *et al.*, 2007). Additionally, the five different sub-assemblages of the *messaoudensis* - *trifidum* acritarch assemblage allow a precise correlation along the southern margin of Gondwana of successions from Ireland, Wales, the Isle of Man, Belgium, Germany, Spain, Turkey, and other areas (Molyneux *et al.*, 2007).

The objective of the present paper is to analyze the chitinozoan assemblages in the Watch Hill Formation of the English Lake District, from where the *Cymatiogalea messaoudensis* - *Stelliferidium trifidum* acritarch assemblage was first described. A major aim of the study is to test if the chitinozoan taxa appear in a successive order that may allow biostratigraphical correlations, and if the recovered assemblages allow calibrating better chitinozoan biostratigraphy against the Tremadocian/Floian boundary in a classic section for this interval.

6.2 Material and methods

The Watch Hill Formation is part of the Skiddaw Group in the Lake District, Northern England (Fig. 1), which is divided into two distinct stratigraphical units: the Northern Fells Belt and the Central Fells Belts. The Northern Fells Belt comprises the upper Tremadoc Bitter Beck and Watch Hill formations, overlain by the lower Arenig Hope Beck, Loweswater and Kirk Stile formations (Fig. 2, Cooper *et al.*, 1995). The Skiddaw Group is made of clastic

turbidites (sand, silt and mud) deposited before Avalonia started drifting towards Baltica and thus represents a sedimentary succession within the realm of the 'Northern Gondwana' margin during the Early Ordovician (Cooper *et al.*, 2004). The Watch Hill Formation consists of brown sandstones, siltstones and mudstones where volcanic fragments are common (Cooper *et al.*, 1995, 2004). Bouma T_{abcd} cycles are very common, indicating turbidity currents. The formation is equivalent to the Watch Hill Grits and Grits Group of the previous authors (i.e., Eastwood *et al.*, 1968).

The Watch Hill Formation is considered to be of latest Tremadoc or earliest Arenig age, on the basis of graptolites and the presence of the *messaoudensis-trifidum* acritarch assemblage (Molyneux and Rushton, 1988).

Eight samples (MPA 28677, 28680 to 26682, 28685, 28704, 28706 and 28707, Fig. 3) were subsampled in the collections at the British Geological Survey (BGS). These samples were collected for the detailed lithostratigraphical, biostratigraphical and structural study of the Skiddaw Group of the English Lake District, published in the BGS Memoir of Cooper *et al.* (2004). The samples were collected at the type area of the Watch Hill Formation, about three km E-NE of Cockermouth in the Lake District, from the north, south and the crest of the Watch Hill. The samples were processed and analyzed in the Evo-Eco-Paleo research department at the University of Lille. For the complete extraction methods of the chitinozoans, see Amberg *et al.* (2016). The residues are filtered at 51 μ m and the upper fraction is handpicked and examined using a Scanning Electron Microscopy for specific identification. All figures specimens are housed in the collections of the Evo-Eco-Paleo research department at the University of Lille.

6.3 Results

All eight samples, except the uppermost one (MA 28706) were productive (Fig. 3). The diversity is low, as is commonly the case in Lower Ordovician chitinozoan assemblages, where usually only a few species are present. Nevertheless, in total three genera and four chitinozoan species are identified in the Watch Hill Formation. The chitinozoans recovered in the samples MPA 28677 to MPA 28682 were abundant and relatively well preserved whereas the chitinozoans from the samples MPA 28704 and MPA 28707 were much altered and the sample MPA 28706 is considered barren as only very few unidentified fragments were recovered.

The species identified are (Fig. 3): *Euconochitnia symmetrica*, *Euconochitina paschaensis*, *Lagenochitina destombesi*, *L. cf. obeligis*, *L. ?esthonica*, and *Conochitina* sp. aff. *decipiens*.

L. destombesi, *L. cf. obeligis*, and *E. symmetrica* are present in all samples including the lowermost part of the section (corresponding to levels where the sub-assemblage 2 of the *messaoudensis-trifidum* acritarch assemblage has been recorded), i.e., corresponding to the lowermost and middle part of the *A. murrayi* graptolite Biozone (Fig. 3). *L. ?esthonica* is present slightly higher with a first occurrence in sample MPA 28680 (i.e., still in levels

where the sub-assembly 2 of the *messaoudensis-trifidum* acritarch assemblage has been documented). The two species *Conochitina* sp. aff. *decipiens* and *Euconochitina paschaensis* appear higher in the succession, in levels where the sub-assembly 3 of the *messaoudensis-trifidum* acritarch assemblage has been recorded. All six taxa are present in the uppermost part of the investigated succession in levels co-occurring with sub-assembly 4 of the *messaoudensis-trifidum* acritarch assemblage. Molyneux *et al.* (2007) correlated the sub-assemblies 1-4 of the *messaoudensis-trifidum* acritarch assemblage with the uppermost Tremadocian *A. murrayi* graptolite Biozone, while sub-assembly 5 can be correlated with the lowermost Floian *T. phyllograptoides* graptolite Biozone (Fig 3)

6.4 Taxonomic notes

The holotype of *Conochitina symmetrica* was described in the Floian by Taugourdeau and de Jekhowsky (1960) in Algeria. It is 250 μm long and presents a membranous collaret at the end of the neck, but Paris and Mergl (1984) noted that smaller specimens are much more common. In the Czech Republic, *Conochitina symmetrica* has been described in the lower part of the Arenig Klabava Formation (Paris and Mergl, 1984). Subsequently, Paris (1999) emended the genus *Euconochitina* to represent a conical form of Conochitinidae without a mucron. In the upper Tremadoc Leetse Formation in Estonia, Hints and Nölvak (2006) described *Euconochitina symmetrica* with morphologies between 130 and 230 μm in length, together with *Euconochitina primitiva*, which has body lengths between 218 and 359 μm and a very similar shape to *C. symmetrica*. Hints and Nölvak (2006) discussed the difficulty to differentiate those species, which is not unimportant, as in Baltica, *E. primitiva* is diagnostic of the eponymous chitinozoan biozone straddling the Tremadoc-Arenig boundary (Nölvak *et al.*, 1999; 2006). De la Puente and Rubinstein (2009) created a new species with a similar shape and length (from 134 μm to 209 μm) but without a collaret and a poor widening, which they named *Euconochitina paschaensis*. Nowak *et al.* (2016) grouped together *E. paschaensis* and *E. symmetrica* as the *E. paschaensis-symmetrica* group in the Moroccan material, with morphologies that are about 150 μm long. Only a single specimen identified as *E. symmetrica* has a wide collaret (Nowak *et al.*, 2016).

In the present study, the specimens from the English Lake District are ranging from 130 μm to 250 μm in length, with a more or less pronounced flexured shape. Some specimens display a wide open collaret whereas other forms present a narrow opening (Plate 1). Therefore, the two taxa *E. symmetrica* and *E. paschaensis* are identified in the investigated assemblage, but not *E. primitiva*.

6.5 Stratigraphic discussion

All chitinozoan taxa reported in this study are found in levels that are attributed to the upper Tremadocian on the basis of acritarchs and graptolites. Molyneux and Rushton (1988) defined

the *messaoudensis-trifidum* acritarch assemblage in the Watch Hill Formation and based on its co-occurrence with the *A. murrayi* graptolite Biozone, it was thought to be of late Tremadocian age (Cooper *et al.*, 1995). Molyneux and Dorning (1989) considered the Watch Hill Formation to be a stratigraphical equivalent of the latest Tremadoc Login Bed from the Carmarthen Area in South Wales. The chitinozoan assemblage of this latter unit is currently under investigation by the authors (Amberg *et al.*, in prep.) and contains a different assemblage, with both *Lagenochitina destombesi* and *L. brevicollis*, i.e., diagnostic of the eponymous Tremadoc chitinozoan biozones from Gondwana (Paris, 1990; Webby *et al.*, 2004; Videt *et al.*, 2010). This suggests the Login Beds occupy a slightly different stratigraphic level than the Watch Hill Formation, containing *Euconochitina symmetrica*, diagnostic of the eponymous chitinozoan biozone overlying the *L. brevicollis* zone in Gondwana (Paris 1990, Webby *et al.*, 2004).

In the seminal study of Paris (1990) on the biostratigraphical application of (Early) Ordovician chitinozoans, the species *Euconochitina symmetrica* was originally considered the index fossil of the eponymous chitinozoan Biozone, diagnostic of an early Arenig age, while *L. destombesi* is indicative of the eponymous Tremadocian biozone (Paris, 1990; Webby *et al.*, 2004). Paris (1990, p. 190) immediately noted, however, that the stratigraphic control in the type locality of *Euconochitina symmetrica* is poor, the type strata (in Algeria) only tentatively referred to the lower Arenig by Legrand (1985). Since this original work, *Euconochitina symmetrica* has been reported from the upper Tremadoc of China, co-occurring with *A. murrayi* graptolites and *messaoudensis - trifidum* acritarch assemblages (Wang *et al.*, 2013 a, b). Achab (1980) also mentioned occurrences of *E. symmetrica* (then *Conochitina symmertica*) both from the upper Tremadoc and lower Arenig in Québec (Canada). In addition, *E. paschaensis*, co-occurring with *E. symmetrica* in our section, is considered to be indicative for the late Tremadocian in Argentina (de la Puente and Rubinstein, 2009). Our new finds from the Lake District confirm *E. symmetrica* straddling the Tremadocian-Arenig boundary.

The co-occurrence of *L. destombesi* with *E. symmetrica* is less frequently observed, however. Nowak *et al.* (2016) already noted *Lagenochitina cf. destombesi* occurring rather high in the Fezouata Formation, together with chitinozoans of the *Euconochitina symmetrica* biozone, the graptolite *Araneograptus murrayi* and the acritarch assemblage *messaoudensis-trifidum* (subzones 1 and 2,) indicating the upper Tremadocian. In addition, they found *Euconochitina paschaensis* in their assemblage, which was described by de la Puente and Rubinstein (2009) in Argentina (Western Gondwana) as corresponding to the Tremadocian *Lagenochitina conifundus* chitinozoan Biozone from Northern Gondwana. Nowak *et al.* (2016) also found chitinozoan species that are typically considered to be of Floian age just above these levels. They suggested a redefinition of the respective chitinozoan biozones from total-range zones to partial-range zones to remediate some of these issues, as well as chronostratigraphic recalibration of some of these zones. Amberg *et al.* (in prep.) also noted that *L. destombesi* occurs later than previously recorded (i.e. in the upper Tremadoc “Login Beds”) in the Type Arenig sections in South Wales.

As a final remark, it appears that *E. symmetrica* is found both in the upper Tremadoc in Gondwana and the lowermost Arenig, as observed in Canada (Achab 1980).

6.6 Conclusions

- The new description of the chitinozoan assemblage in the Watch Hill Formation revealed the presence of *E. symmetrica*.
- There are very similar co-occurrences in China, with *A. murrayi* graptolites, *messoudensis* - *trifidum* acritarch assemblage and *E. symmetrica*.
- This co-occurrence allows to tie chitinozoan biostratigraphy for this level into the classic Tremadoc-Arenig stratigraphy of the UK type area.
- *E. symmetrica* is then considered as late Tremadocian indicator, likely to straddle the Tremadoc-Arenig boundary.

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6.8 Figures

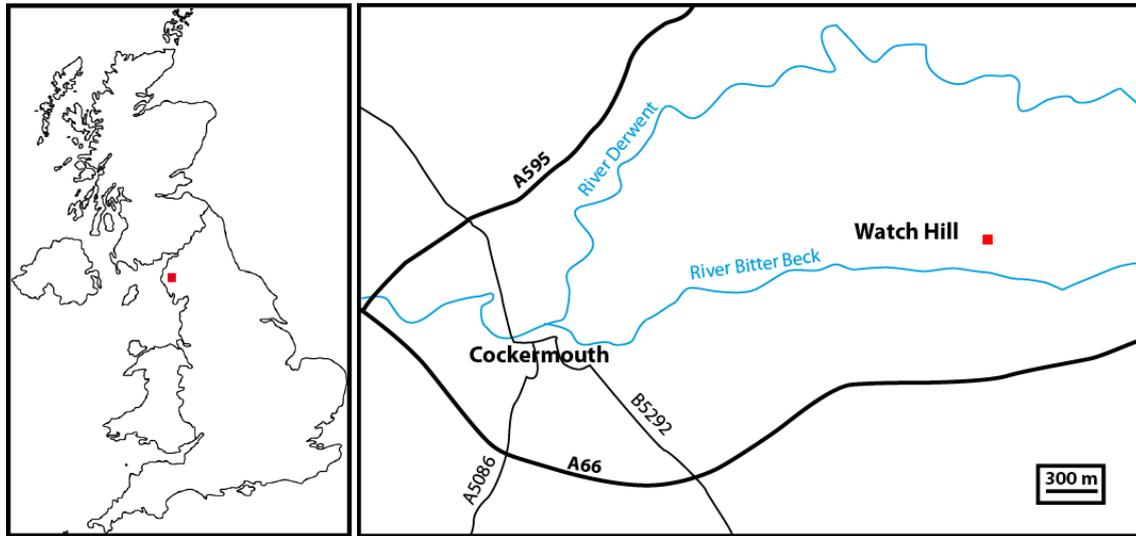


Figure 1: Location of Watch Hill in the English Lake district (red square).

	Formations	Graptolite biozones	Acritarch biozones	Chitinozoan biozones
Lower Arenig	Hope Beck	<i>D. varicosus</i>	<i>C. bohemicum</i>	<i>C. symmetrica</i>
		<i>T. phyllograptoides</i>	<i>S. trifidum</i> - <i>C. bohemicum</i>	
Upper Tremadoc	Watch Hill		<i>A. murrayi</i>	5
		4		
	3			
	2			
Bitter Beck		1		

Figure 2: Correlation of the lithostratigraphy in Lake District with acritarch and graptolite biozones from Molyneux *et al.* (2007).

Lithostratigraphy	Samples	Acritarch zones	Graptolite zones	Chitinozoans							
				<i>Lagenochitina desombesi</i>	<i>Lagenochitina testhonica</i>	<i>Lagenochitina cf. obeligit</i>	<i>Canochitina</i> sp. aff. <i>decipiens</i>	<i>Euconochitina symmetrica</i>	<i>Euconochitina paschaensis</i>		
H. B. Fm.			5 -?- <i>T. phyllogra.</i>								
Watch Hill Formation	MPA 28706 MPA 28704	<i>C. messaoudensis</i> - <i>S. trifidum</i>	4 <i>A. murrayi</i>			x	x	x	x		
	MPA 28707			x	x		x				
H. B. Fm.			5 -?- <i>T. phyllogra.</i>								
Watch Hill Formation	MPA 28685	<i>C. messaoudensis</i> - <i>S. trifidum</i>	4		x	x	x	x	x	x	
	MPA 28682 MPA 28681		3 <i>A. murrayi</i>				x	x	x		
	MPA 28680		2		x	x	x		x		
	MPA 28677		1		x	x		x			
B. B. Fm.			1								

Figure 3: Position of the samples in the Watch Hill Formation with acritarch and graptolite biozones from Cooper *et al* (2004) with the ranges of chitinozoans from this study. In red: the fault that repeats the section.



Plate 1: SEM pictures of selected chitinozoans from the Watch Hill Formation. 1, 2, 4, 6: *Euconochitina symmetrica*. 3, 5: *Euconochitina paschaensis*. 8: *Conochitina* sp. aff *decepiens*. 9: *Lagenochitina destombesi*.

7. Description of chitinozoan assemblages from Arenig formations in the Anti-Atlas, Morocco

Description of chitinozoan assemblages from Arenig formations in the Anti-Atlas, Morocco

The end Ordovician glaciation has been well documented in the near field sections close to the South Pole ice sheet in the Western Sahara and Arabian Peninsula (Beuf *et al.*, 1971; Ghienne, 2003) and also in the Anti Atlas in Morocco (Destombes, 1968, 1985; Le Heron, 2007; Loi *et al.*, 2010; Clerc *et al.*, 2013; Ghienne *et al.*, 2014) based on glacial erosion surfaces and sedimentological evidence. The maximum extension of the ice sheet was mapped; it covered most of the Western Gondwana (Ghienne *et al.*, 2007; Le Heron and Craig, 2009).

There are many incisions in the Ordovician succession of the Anti-Atlas in southern Morocco (Fig. 7.1), most of them from the Hirnantian and related to erosion during phases of the ice sheet development. Recently, an emerging revised sedimentary framework suggests that some incisions may also be significantly older, and may even date back to the Floian. If such incisions may be ascribed to pre-Hirnantian glacial lowstands, it would be in agreement with the emerging theory that a global cooling started earlier in the Ordovician (i.e., Trotter *et al.*, 2008).

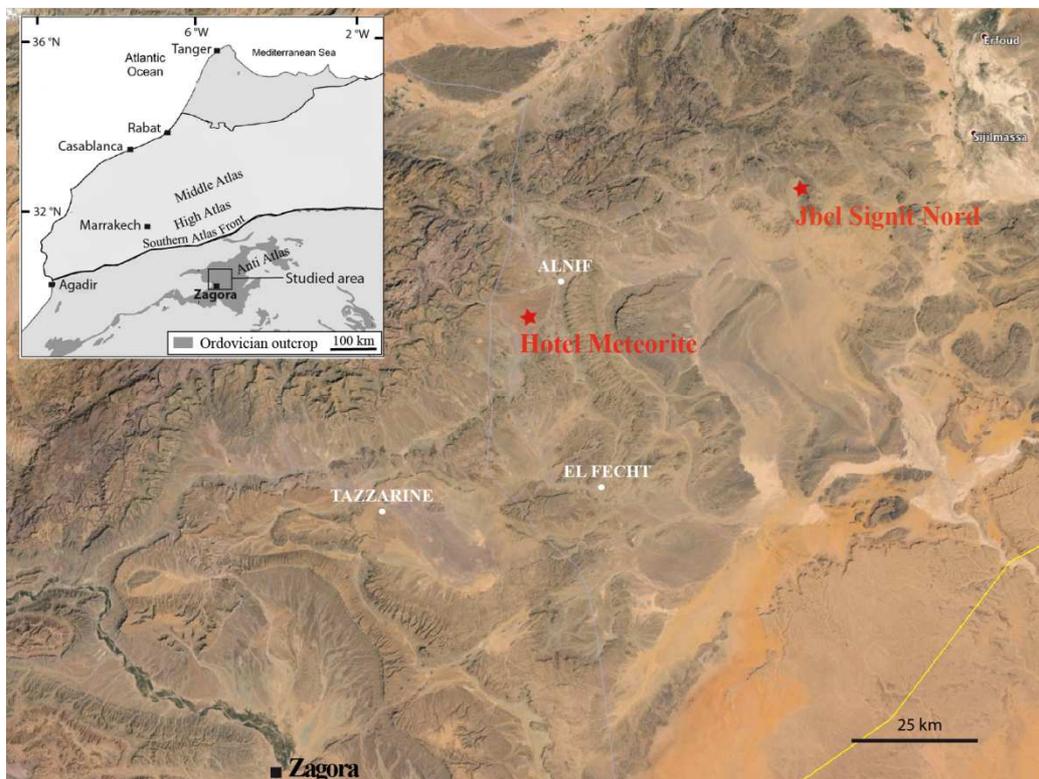


Figure 7.1: Location of the studied areas, Jbel Signit and Hotel Meteorite, in the Anti-Atlas, Morocco.

Here we use chitinozoan assemblages from samples collected in a succession presenting incisions of unknown age to constrain the duration of those events and potentially to correlate them with far field sections, such as in Avalonia, if those incisions appear to be the expression of glacio-eustatic sea-level fluctuations.

The chitinozoans are used in the ‘northern Gondwana’ domain for comparison and correlation with international stratotypes, because graptolites, the standard tool for correlations in the Ordovician, are essentially found in the Lower Ordovician (Tremadoc, Arenig and Llanvirn), but are rare above these levels (Destombes 2004). The chitinozoan biozonation of the ‘northern Gondwana’ domain is well established for the entire Ordovician (Paris 1990). This ‘northern Gondwana’ biozonation has been correlated with other biozonations worldwide in Webby *et al.*, (2004) and was revised in Videt *et al.*, (2010) as shown in figure 7.2.

Global series and stages		British series	Chitinozoan biozones		Lithostratigraphy in Anti-Atlas
			Paris, 1990	Videt <i>et al.</i> 2010	
Middle Ordovician	Darrivillian	Llanvirn	<i>Cy. calix</i>		Tachilla Formation
			<i>Cy. protocolix</i>	<i>Cy. calix</i>	
				<i>Cy. protocolix</i>	
	Dapingian	Arenig	<i>D. bulla</i>	<i>D. bulla</i>	?
			?	<i>B. henryi</i>	
			<i>B. henryi</i>	?	
Lower Ordovician	Floian	Arenig	<i>D. ornensis</i>	<i>E. brevis</i>	Upper Fezouata Formation
			<i>E. brevis</i>		
			<i>E. baculata</i>	<i>E. baculata</i>	Lower Fezouata Formation
	<i>C. symmetrica</i>	<i>C. symmetrica</i>			
	<i>L. confundus</i>	<i>L. brevicollis</i>			
	?				
	Tremadocian	Tremadoc	<i>L. destombesi</i>	<i>L. destombesi</i>	

Figure 7.2: Chitinozoan biozonation from Paris (1990), the recalibration after Webby *et al.* (2004) from Videt *et al.* (2010) and the lithostratigraphy of the Anti-atlas modified after Destombes (2004) from Videt *et al.* (2010).

7.1 Geological setting

The structure of the Anti-Atlas is a large antiform extending from SE to NW created in front of the Variscan Orogen by the Late Carboniferous Permian compression (Burkhard *et al.*, 2006; Michard *et al.*, 2010). Its basement includes the Panafrican suture (Anti Atlas Major Fault or Major Anti Atlas Suture), which resulted from the collision between the West African craton and the Reguibat Shield during the Panafrican compressive phase in the Precambrian (Black and Fabre, 1980; Ennih and Liégeois, 2001; Coward and Ries, 2003). During the early Palaeozoic, the area was tectonically relatively stable, enduring continuous subsidence. However, an extensive phase from the late Cambrian to the Ordovician led to the creation of graben and semi graben structures (Clerc *et al.*, 2013). The Hercynian compressive phase in the upper Palaeozoic led to the deformation, uplift and partial erosion of the lower Paleozoic cover, which is unconformably overlain by Mesozoic and Cenozoic series.

Destombes (2004) described a first-order transgression starting during the early Tremadoc with large epicontinental sea deposits represented by the thick (up to 100m) argillaceous succession of most of the Lower Fezouata Formation. Then, a regressive event is observed in the upper Lower Fezouata Formation and the Upper Fezouata Formation (upper Tremadoc-lower Arenig) and again a transgression is registered in the upper Arenig *D. bulla* chitinozoan Biozone (Benoit and Taugourdeau, 1961; Ghienne *et al.*, 2007), part of the large deposits of shales and siltstone from the Upper Fezouata Formation. The latter formation is truncated by the sandstones of the Zini Formation, which is locally divided into two members, separated by argillaceous levels in the Folded Bani (“Bani Plissé”). The sandstones of the Zini Formation are ascribed to shoals in the region of the High Occidental Atlas and tentatively interpreted as the result from the erosion after the uplift of the basement (Destombes, 2004).

In the Middle Ordovician, there is a gap in the lithostratigraphy in the middle and upper Arenig succession (Dapingian and lowermost Darriwilian, Videt *et al.*, 2010, Dabard *et al.*, 2015) before the occurrence of the Tachilla Formation straddling the Arenig/Llanvirn boundary. The latter is made up of transgressive siltstones spreading in the Anti Atlas with subordinate sandstone beds at the base of the formation.

The litho- and biostratigraphical framework of the Central Anti Atlas has been described by Destombes (1968, 1985, 2004), but the Lower and Middle Ordovician in the Anti Atlas lack of detailed sedimentological studies (Videt *et al.*, 2010). Elahouad-Debbaj (1984) described the chitinozoan assemblage of the Arenig and the Llanvirn from the Anti Atlas in Morocco and in her PhD thesis in 1987 she described the biostratigraphy of the Ordovician in Morocco and proposed a series of correlations using chitinozoans.

7.2 Studied areas and sampling

Samples were collected at the transition between the Central and the Eastern Anti-Atlas, where the Zini Formation has not been formally recognized, yet the Fezouata/Tachilla formational boundary has been mapped on paleontological grounds by Destombes (2004).

The first studied area is located on the northern slope of the Jebel Signit, (Fig. 7.1), where a large, up to 20 m deep, NNW/SSE-oriented incision of poorly constrained age with is observed (N31°13'37'' W004°38'33''). It is included in the Fezouata Fm. according to the geological map. Its infill shows patent onlap relationships on the incision margin. Metre-thick sandstone beds show horizontal laminae, current ripples and load structures. Six samples were recovered from this area, amongst them two samples (JFG 2013-116-117) were recovered from the underlying strata (green micaceous siltstones), two samples (JFG 2013-118-119) were recovered from fine-grained interbeds infill (i.e., above the unconformity), and two samples (JFG 2013-120-121) were recovered from siltstones strata above, and thus postdating, the incision infill.

The second studied area is near the Meteorite Hotel and is situated to the West of Alnif (Fig. 7.1). Here, an erosional coarse-grained sandstone bed with conglomeratic intervals (flat channels?) may be reminiscent of the uppermost Lower Ordovician Zini Formation described in the Western and Central Anti-Atlas. Six samples were recovered from this area, amongst them three (TVDB 14-044 to TVDB 14-046) were collected from outcrops below the sandstone bed in shales/siltstones. Two samples (TVDB 14-047 and TVDB 14-049) were recovered from wells on the top of the sandstone bed, one (TVDB 14-047) assumed to be representative of strata on top of the sandstone bed and therefore assumed to be the Tachilla Formation; another one (TVDB 14-049) of uncertain level as the deep well may well have pierced the 'Zini' sandstone layer. A last sample (TVDB 14-050) from a small outcrop directly on the top of the sandstones and assumed to be as well the Tachilla Formation.

7.3 Description of the assemblages and correlation

1.2.5 Jbel Signit Nord

The palynological study from the samples collected around the incision at Jbel Signit (Fig. 7.3) indicates a middle Arenig age, with the presence of *Eremochitina brevis* (plate 1.1-7) in every sample, characterizing the eponymous middle Arenig chitinozoan Biozone. The associated species found in the assemblage are: *Conochitina decipiens* (plate 2.6-9), *Conochitina brevis* (plate 2.1-4-5), *Conochitina brevis conica* (plate 2.10), *Bursachitina ?laminaris* (plate 2.2-3), *Eremochitina baculata* (plate 1.9-10), *Eremochitina baculata brevis* (plate 1.11-12), *Lagenochitina obeligitis* (plate 2.11-13), *Rhabdochitina magna* (plate 2.14) and *Tanuchitina achabae* (plate 1.13-15).

Tanuchitina achabae has been described in the middle Arenig, in the lower part of the Pissot Formation (Paris 1981) and in the chitinozoan assemblages 3 and 4 in South Wales found in the middle Arenig Pontyfenni and Llanfallteg formations (Amberg et al. in prep.). It is also found in the middle Arenig in the Klabava Formation in Bohemia (Paris and Mergl 1984). *Lagenochitina obelgis* and *Conochitina brevis* are stratigraphically long-ranging species found in the Arenig and the Llanvirn (Chen et al., 2008). They are also found in the middle-upper Arenig assemblage 2 and 3 in South Wales (Amberg et al. in prep).

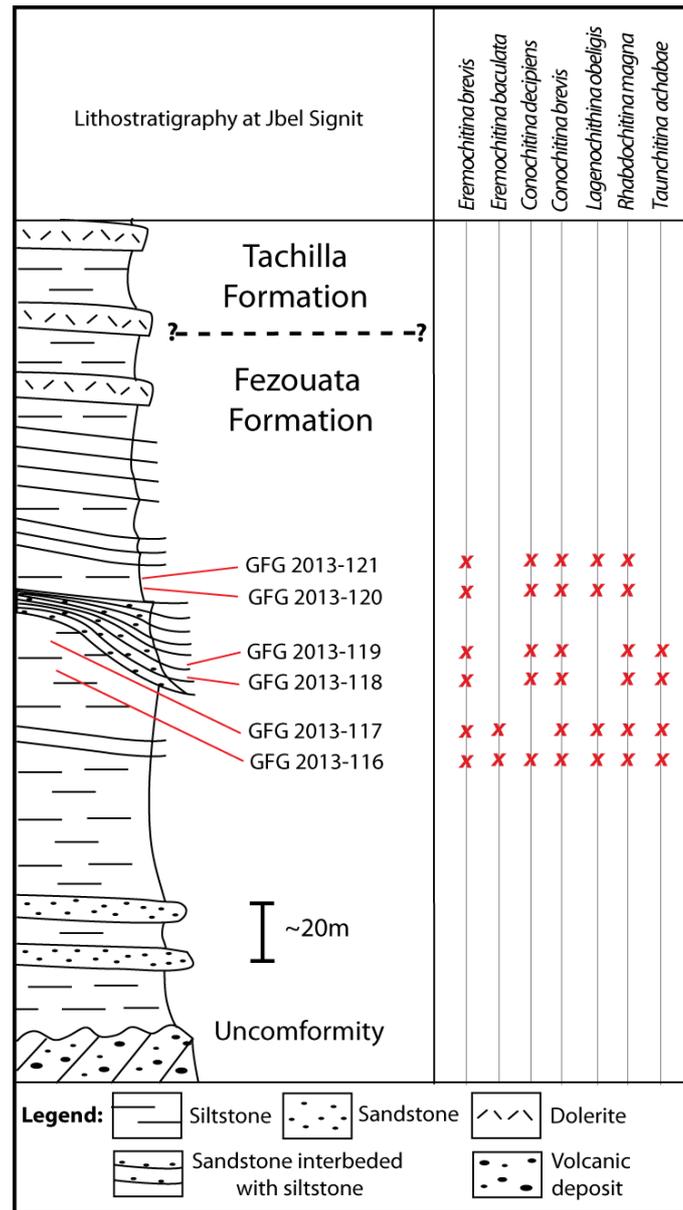


Figure 7.3: Lithostratigraphical log of Jbel Signit with the position of the samples and their chitinozoan assemblage (after Ghienne, unpub. field draft).

Euconochitina vulgaris was first described by Jenkins (1967) as *Sphaerochitina vulgaris* in the lower Llanvirn Hope Shales Formation in Shropshire and Paris (1981) observed it in the middle Arenig Gres Armorica Formation and in the lower part of the Pissot Formation, straddling the Arenig-Llanvirn boundary in France. *Bursachitina laminaris* has been described by Tang *et al.* (2007) in China from the middle Arenig (upper Dapingian and lower Darriwilian). It has also been found in the middle-upper Arenig assemblage 3 in South Wales (Amberg *et al.*, in prep). However, the specimens from Morocco and Wales are slightly larger than the holotype and have thick walls, whereas the original description from Tang *et al.* (2007) described thin walls, therefore we attribute this specimens to *Conochitina brevis*, a widespread morphologically similar species during the Arenig.

However, in the region of Zagora, Nowak *et al.* (2016) investigated the Lower Fezouata Formation, dated to the late Tremadoc with the graptolite *A. murrayi*, associated with the sub-assemblage 1-2 of the *messaoudensis-trifidum* acritarch assemblage, and they recovered an unusually mixed fauna, with *Eremochitina brevis* and specimens of the *Euconochitina paschaensi-symmetrica* group, the latter normally indicating the Tremadoc-Arenig boundary. This led Nowak *et al.* (2016), to suggest that the chronostratigraphic assignment of the *E. brevis* zone may be in need of revision, slightly older than previously thought. However, this was not supported by our data from the type Arenig (cf. chapter 5), although we cannot be sure as the biozone's index species was not found in the assemblages from Wales.

1.2.6 Meteorite Hotel

The samples TVDB 14-044 to TVDB 14-046 that were collected under the coarse-grained sandstone (three from the outcrop) as well as the sample TVDB 14-047 from an unknown level in the well piercing the sandstone level revealed a typical assemblage from the middle Arenig *Eremochitina brevis* (plate 3.1-8) chitinozoan Biozone, with the associated *Conochitina decipiens*, *Conochitina brevis*, *Lagenochitina obelgis*, *Rhabdochitina magna*, and *Tanuchitina achabae*.

The samples recovered on the top of sandstone (TVDB 14-049 from the well and TVDB 14-050 from the small outcrop) revealed an assemblage diagnostic of the upper Arenig *Desmochitina bulla* (plate 4.9-14) chitinozoan Biozone, associated with *Sagenachitina oblonga* (plate 5.1-8), *Lagenochitina obelgis* (plate 3.9-12), *Conochitina decipiens*, *Conochitina brevis* (plate 4.1-2), *Euconochitina vulgaris* (plate 4.3-8) and *Rhabdochitina magna*.

Desmochitina bulla is a widespread species in Morocco and has also been recovered in the upper Arenig of the Klabava Formation in Bohemia (Paris and Mergl, 1984). Paris (1981) described *Sagenachitina oblonga* as a common species in the *D. bulla* biozone. It presents a varying shape from conical to campanuliform and the collarete is varying from a net starting directly from the basal margin (plate 5.2-3,5-3) to perforations in a kind of carina (plate 5.1,7-8). Chen *et al.* (2009) described *Sagenachitina dapingiensis* in the upper Dapingian-upper Darriwilian Dawan Formation in China with a larger size than *S. oblonga* and a perforated

carina, therefore some specimens of *S. dapingiensis* can be present within the *S. oblonga* population.

In summary, the level investigated at the Hotel Meteorite near Alnif can be within the *E. brevis* chitinozoan Biozone (if sample TVDB 14-047 is from above the sandstone level in the well) or it can be in between the *E. brevis* and *D. bulla* biozones (if sample TVDB 14-047 is from below the sandstone level in the well). The latter option is considered to be more likely (given the absence of *E. brevis* from outcrops above the well, although the section has not been sampled exhaustively).

7.4 Conclusions

The palynological content of the Jbel Signit section demonstrates that the sediments beneath, within and above the incision belong to the same middle Arenig *Eremochitina brevis* chitinozoan Biozone. Therefore, erosion and infill are thought to represent a short term lowstand event and ensuing transgression within the Fezouata Fm.

Near the meteorite Hotel in Alnif, at about 50 km away from Jbel Signit, the same middle Arenig chitinozoan *E. brevis* biozone is found in samples from under the sandstone bed, but the lowest sampled strata overlying the sandstone bed belong to the *D. bulla* biozone, suggesting a correlation with the Tachilla Formation, which is a fundamental difference with the Jbel Signit area. The sandstone bed and associated erosion surface are thus associated to a relatively long hiatus, essentially covering the Dapingian. The correlation with the Jbel Signit, though possible, cannot be demonstrated. Sandstones of the Meteorite Hotel are tentatively correlated with the Zini Fm.

The hiatus of the Dapingian is a usual feature in north Gondwana stratigraphy (Dabard *et al.*, 2015; Gutiérrez-Marco *et al.*, 2014), possibly linked either to condensation during the Late Arenig transgression or to platform-wide but localized tectonic uplifts of Arenigian age (Galeazzi *et al.*, 2010; Ghienne *et al.*, 2013). In contrast, the short-term lowstand event evidenced by the incision within the Upper Fezouata Fm., and the return to offshore condensation with no fundamental change in the overall depositional environment, may suggest that a glacio-eustatic lowstand occurred in the Early Ordovician. Formal relationships with other Arenig regressive successions (the Zini Formation to the west; the Khneg el Aatène succession in northern Algeria, Ghienne *et al.*, 2007) remain to be elucidated. If of glacial origin, comparable incisions might have a worldwide extent, which would however not be associated to a patent hiatus, at least on palaeontological grounds, owing to its short term development.

We did not come across the same issues as suggested by Nowak *et al.* (2016), however, *Eremochitina brevis* has not been found in the middle Arenig assemblages 2 and 3 in the type area in Wales, (Amberg *et al.* in prep.), which hampers correlation with the type area. Nevertheless, assemblage 2 and 3 in Wales contains similar assemblages to the upper

Fezouata Formation, and notably also to the upper Gres Armoricaïn and lower Pissot formations in France.

If both those incisions are confirmed to be glacio-related, they could be found also in peri Gondwana areas, such as Avalonia (Amberg *et al.*, in prep), Armorica (Paris 1990) and Bohemia (Paris and Mergl 1984).

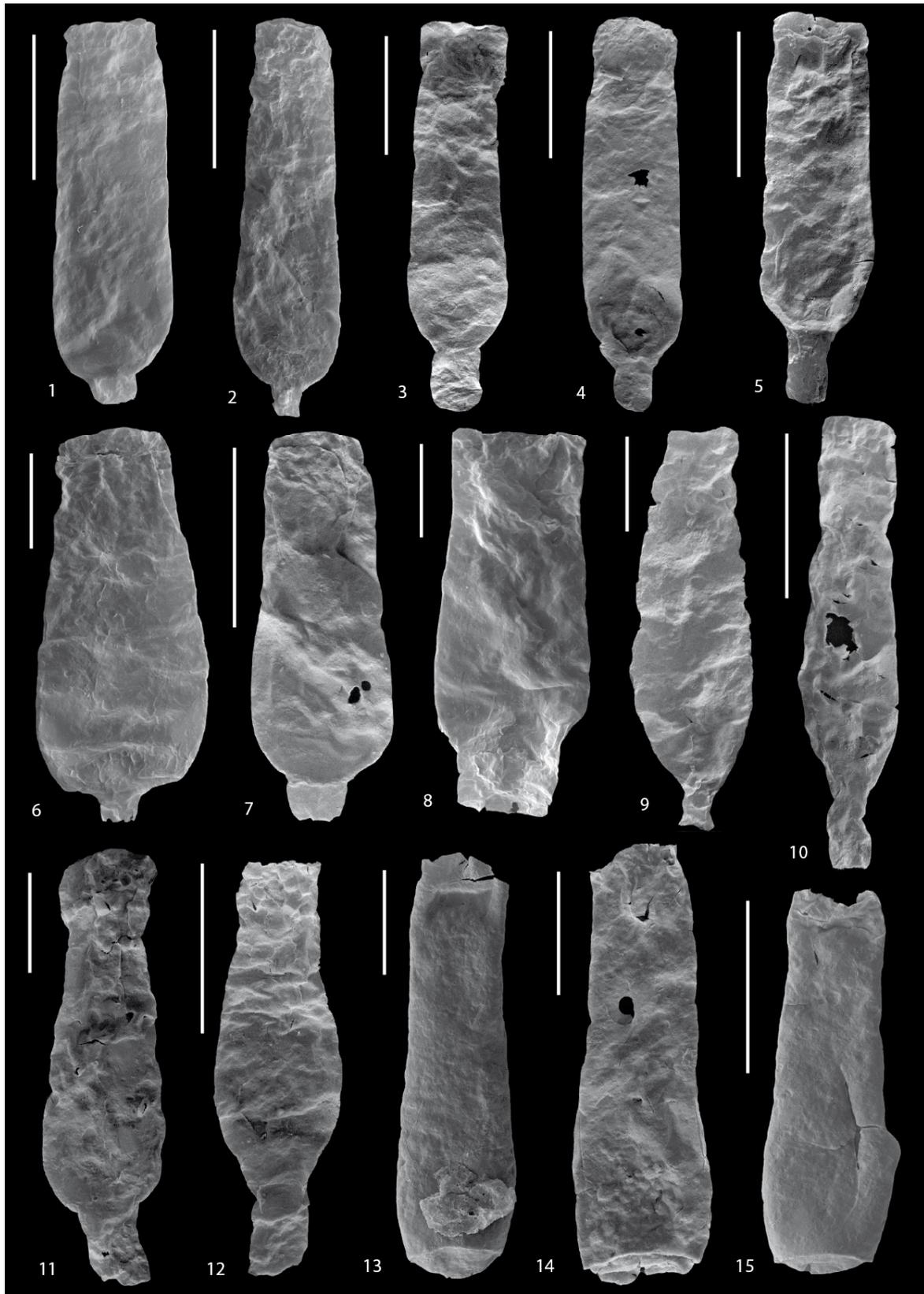


Plate 1: SEM Picture of selected chitinozoans from Jbel Signit. 1-7 *Eremochitina brevis* (1, 3, 5: JFG 2013-119; 2, 6: JFG 2013-120; 4, 7: JFG 2013-118); 8: *Eremochitina* sp. (JFG 2013-118); 9-10: *Eremochitina baculata* (JFG 2013-117); 11-12: *Eremochitina baculata brevis* (JFG 2013-117); 13-15: *Tanuchitina achabae* (JFG 2013-117). Scale bars = 100 μ m

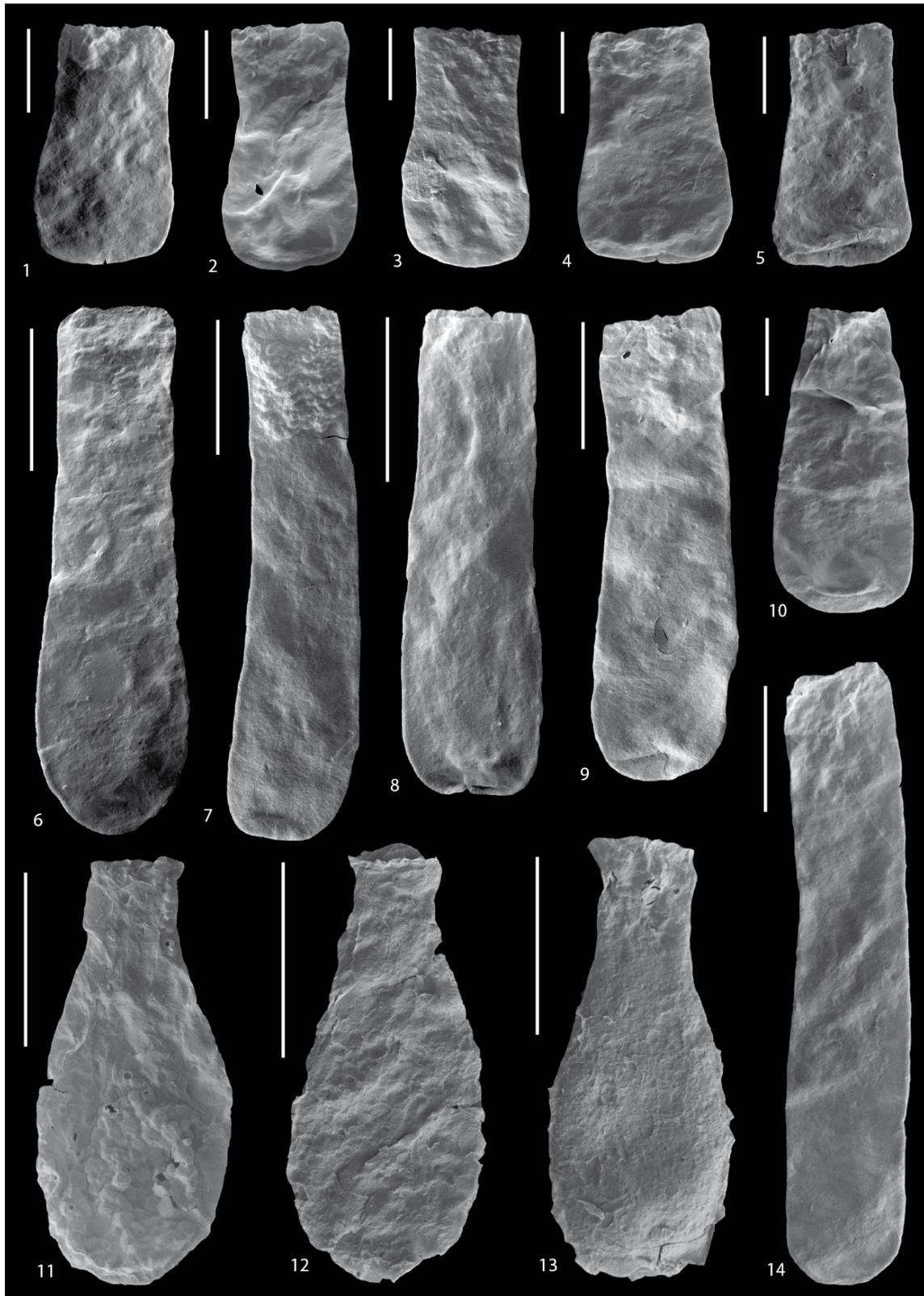


Plate 2: SEM Picture of selected chitinozoans from Jbel Signit. 1, 4, 5: *Conochitina brevis* (1: JFG 2013-119; 4-5: JFG 2013-120); 2-3: *Bursachitina ?laminaris* (JFG 2013-118, JFG 2013-119); 6-9: *Conochitina decipiens* (6,8 JFG 2013-119; 7,9: JFG 2013-118); 10: *Conochitina brevis conica* (JFG 2013-118); 11-13: *Lagenochitina obeligit* (JFG 2013-117); 14 *Rhabdochitina magna* (JFG 2013-118). Scale bars = 100 μ m

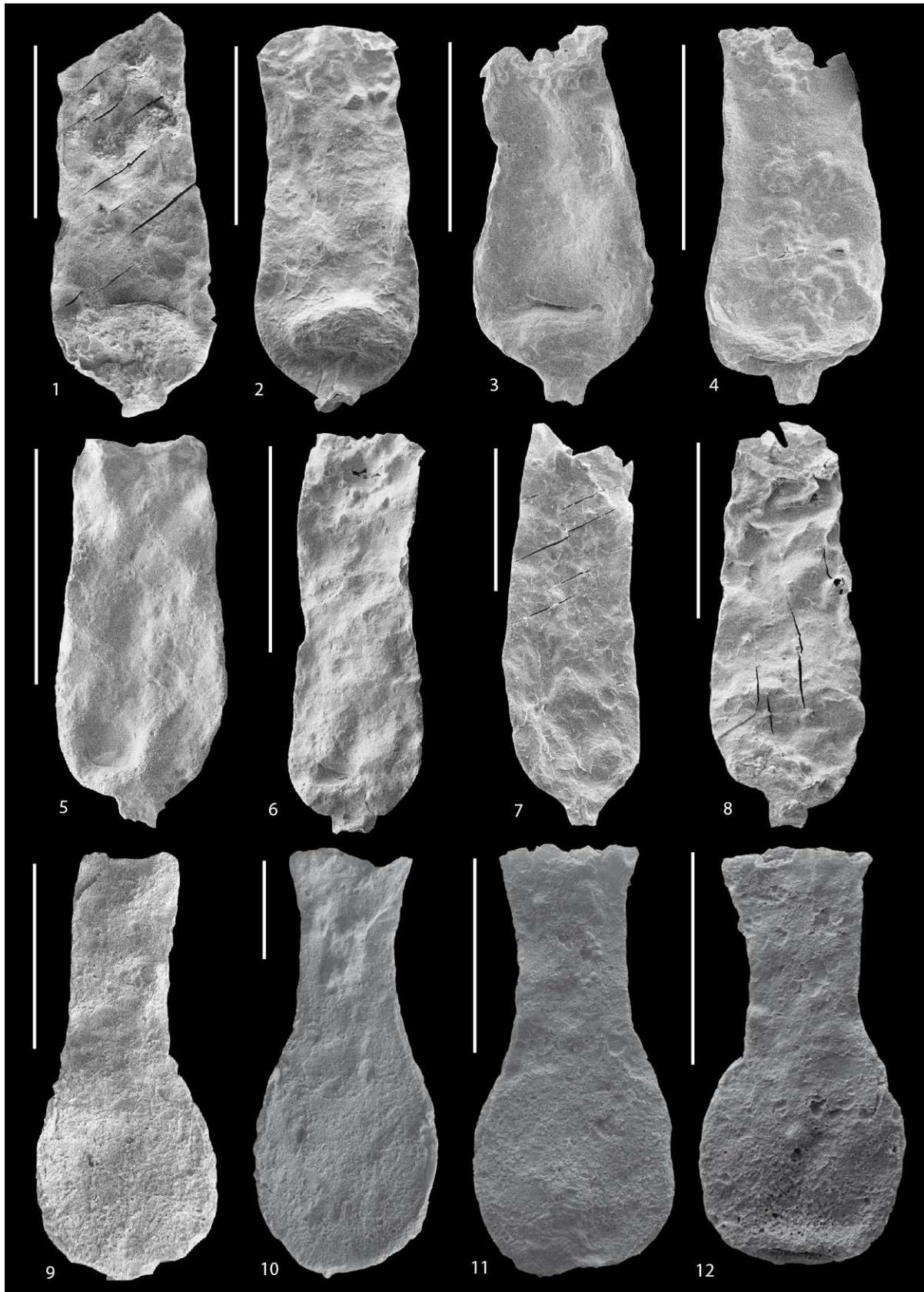


Plate 3: SEM Picture of selected chitinozoans from Meteorite Hotel (Alnif). 1-8: *Eremochitina brevis* (1, 7, 8: TVDB 14-047; 2-5: TVDB 14-044; 6: TVDB 14-045); 9-12: *Lagenochitina obeligi* (9-11: TVDB 14-050; 12: TVDB 14-049). Scale bars = 100 μ m.

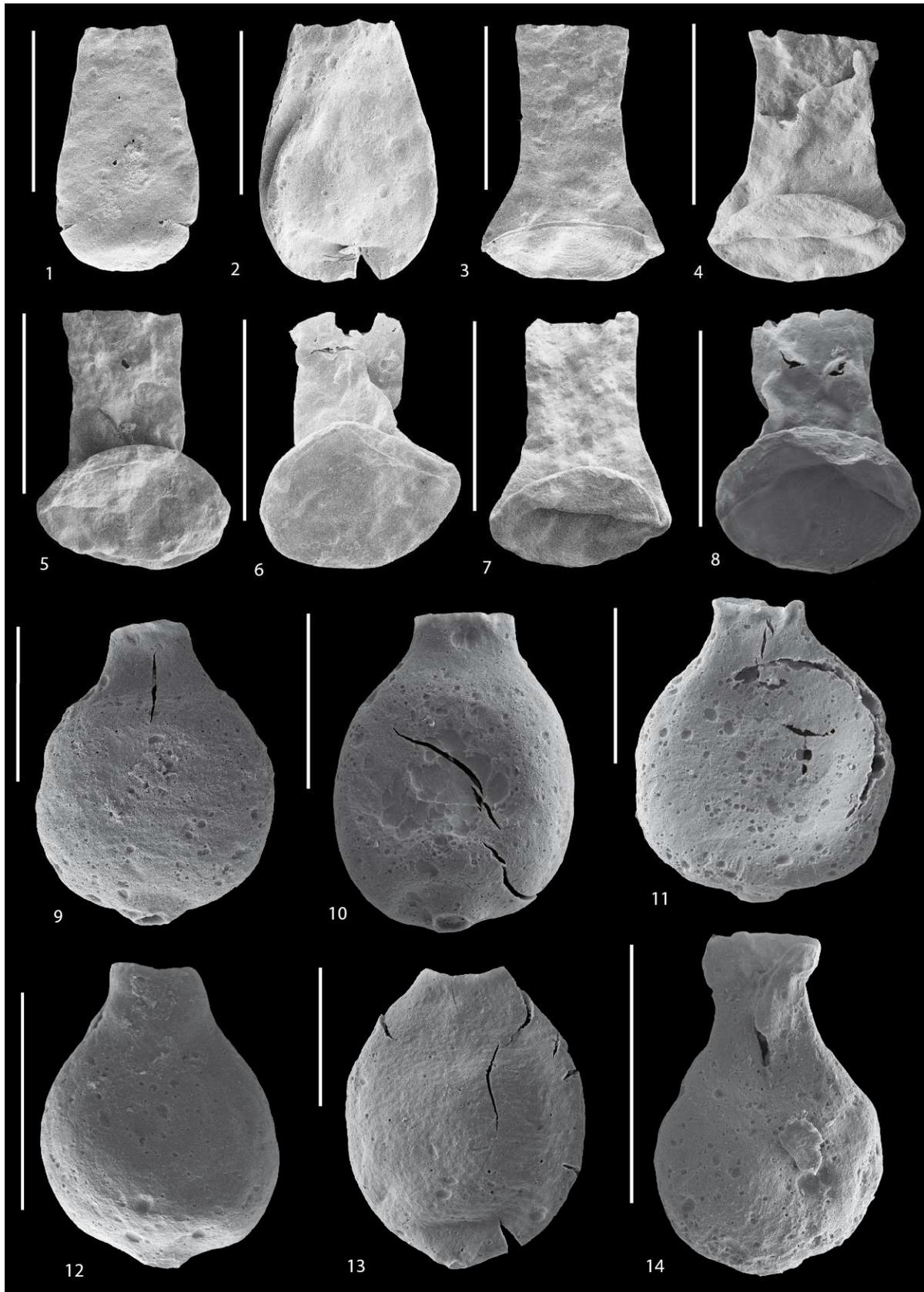


Plate 4: SEM Picture of selected chitinozoans from Meteorite Hotel (Alnif). 1-2: *Conochitina brevis* (TVDB 14-049); 3-8 *Euconochitina vulgaris* (3, 6, 8: TVDB 14-049; 4, 5, 7: TVDB 14-050); 9-14: *Desmochitina bulla* (TVDB 14-049). Scale bars = 100 μ m

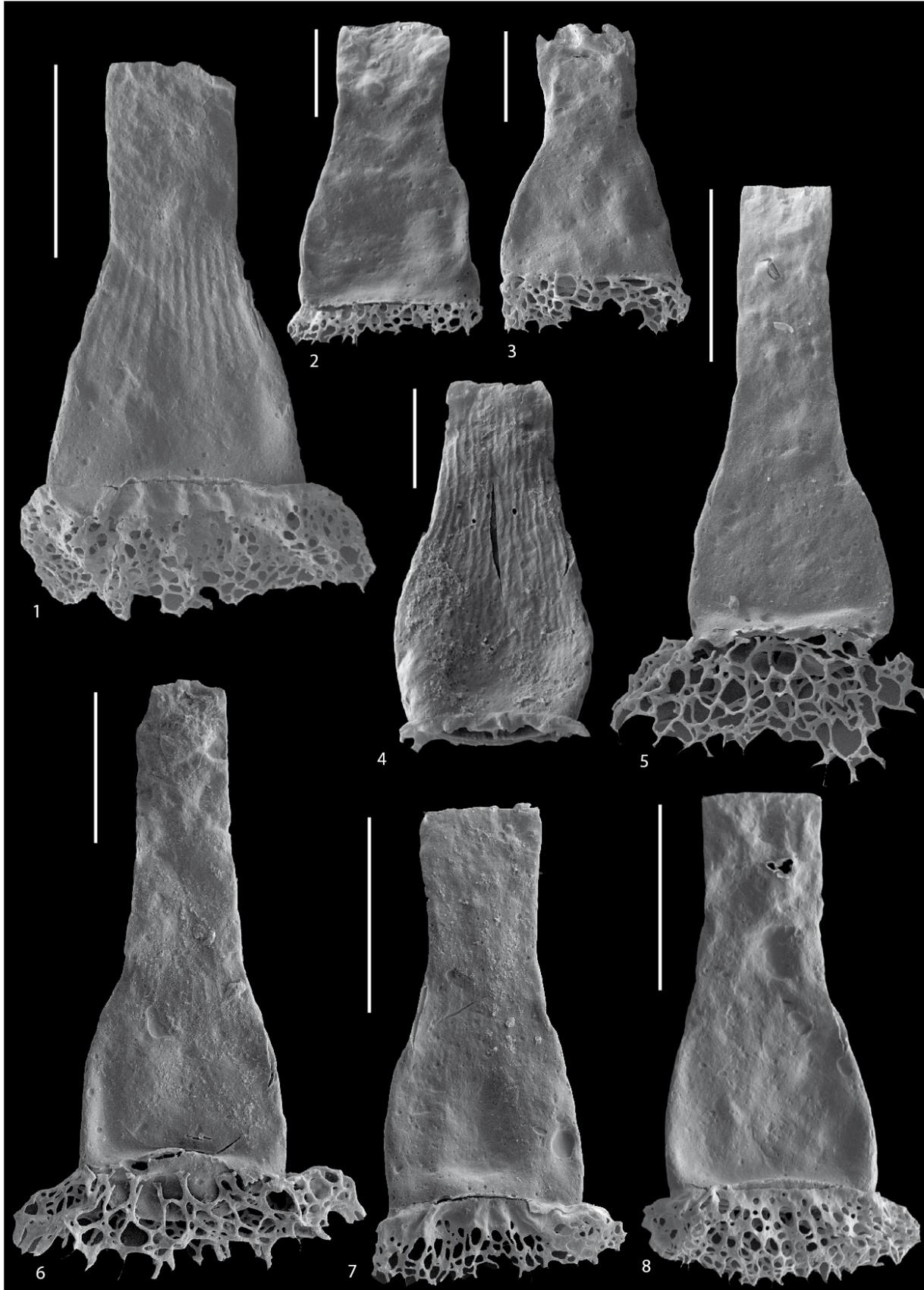


Plate 5: SEM Picture of selected chitinozoans from the Meteorite Hotel (Alnif). 1-8: *Sagenachitina oblonga* (1, 3, 8: TVDB 14-050; 2, 4-7: TVDB 14-049). Scale bars = 100 μm

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8. General discussion and perspectives

General discussion and perspectives

A detailed study of the chitinozoan assemblages from the Lower-Middle Ordovician in Morocco, Wales, England and Norway, and from the Upper Ordovician in Norway, improved our understanding of the chitinozoan biostratigraphy in this interval, and a framework has been built enabling correlations between Baltica and Laurentia on the one hand, and Avalonia and Gondwana on the other. Despite the increased information now available from the Arenig type area, there still is insufficient data to identify the response of the chitinozoan assemblages, or provinces, to climate fluctuations, both on the large scale between separate areas on Gondwana, Avalonia and Baltica, as on the local scale as was attempted for the rhythmites on Baltica. However, the new data do serve to constrain an erosional event potentially related to glacioeustasy in Gondwana. Below, the results obtained are discussed, in function of the objectives laid out at front of this volume:

1. The investigation of the rhythmites in the Oslo-Asker District in Norway from the Huk, Arnestad, Frognerkilen, Solvang and Skogerholmen formations, using diagenetically inert parameters such as the distribution of chitinozoans coupled to the concentration insoluble elements cannot confirm a primary cyclic signal in these marl-limestones alternations. A diagenetic origin can therefore not be ruled out, for these Katian, Sandbian and Floian deposits. The bed-by-bed statistical analyses of the chitinozoans distribution show no differences between the marl and the limestone samples except for one sole species, *Ancyrochitina bornholmensis*, but this small signal is considered to be not significant enough as a proof. The geochemical results are generally in agreement with the palynology, with similar slopes of the trend lines, indicating a high correlation of the diagenetically stable elements normalized to Al_2O_3 between the lithologies.

However as indicated by Westphal *et al.* (2008), we know that such results are insufficient to prove an entirely diagenetic origin of the rhythmites, and that an original difference between the lithologies may have existed but was erased by the diagenesis, or that the proxies studied may have been insufficiently sensitive to potential environmental signals. For instance, to be able to observe a difference in the chitinozoan assemblage composition, which depends on SSTs more than sea level variations (Vandenbroucke *et al.*, 2010a), the studied area should be situated in the latitudinal zone where the boundaries between climate belts (e.g., subpolar and polar) are shifting during climate changes. If our studied area is not crossed by such a boundary and stays within the same climate belt (e.g., subpolar), during the studied interval, we will not observe significant variations within the assemblage. However, the studied area was situated at mid palaeolatitudes (approximately 50 °S to 45 °S during the Early Ordovician and 30 °S during the Late Ordovician) and thus should be appropriately located to detect such variations.

The chemostratigraphy also revealed that the formation with the highest coefficient of correlation between the lithologies was the Huk Formation, which suffered most from diagenesis in comparison with the other rhythmites, whereas formations with a lower

diagenetical overprint (i.e., Skogerholmen Formation) sometimes present slight differences between the slopes of the trend lines indicating a potential minor difference in the precursor sediment. It is clear that (late) diagenesis has affected the results, and to further investigate the nature of the rhythmites, the same methodological bed-by-bed analyses should be applied to other rhythmites found in the Oslo-Asker District, such as in the lower Sandbian Elnes and Vollen formations or in the middle Katian Grimsøya Formation, with a lower diagenetical overprint.

The same chitinozoan assemblages from the Oslo region yielded additional biostratigraphic information. When coupled to stable carbon isotope data, they allowed us to correlate the base of the Hirnantian between Baltica and Laurentia, integrating the established chitinozoan biozonation from both palaeocontinents with $\delta^{13}\text{C}$ curve from Anticosti Island (Desrochers *et al.*, 2010; Delabroye *et al.*, 2011, 2012). The presence of *Belonechitina gamachiana* in the Hovedøya Member of the Skogerholmen Formation (Oslo) allowed us to place this formation within the eponymous chitinozoan biozone. Combined with a modest $\delta^{13}\text{C}$ excursion within the same strata, these new data permitted to correlate the Hovedøya Member to the lower part of the Ellis Bay Formation in Anticosti. This suggests a revised stratigraphic position for the Katian-Hirnantian boundary in Baltica, i.e., at the base of the *B. gamachiana* chitinozoan Biozone instead of the base of the *Spinachitina taugourdeaui* chitinozoan Biozone (e.g., Nölvak 1999, Brenchley *et al.*, 2003), which is in agreement with the interpretation of Melchin *et al.* (2013) and Holmden *et al.* (2013).

These results prove that for stratigraphical correlation, even across long distance and especially in combination with chemostratigraphic methods, the chitinozoans remain a powerful tool. In addition, and following the earlier documentation of $\delta^{13}\text{C}$ excursions in some of the rhythmites of the Oslo-Asker District (i.e., across the Arnestad-Frognerkilen formations boundary and in the Solvang Formation, where Bergström *et al.* (2011) recorded respectively the GICE and the Kope), it appears that these rhythmites may (all?) be linked to major perturbation in the carbon cycle. Chemostratigraphy is a good tool for local and long distance stratigraphical correlations, but so far most of the studies focused on the HICE and the GICE (Bergström *et al.*, 2008). Therefore $\delta^{13}\text{C}$ analyses should also be carried in the rhythmites of the Elnes and Vollen formations and the Grimsøya Formation to confirm the hypothesized excursions within these units.

2. The detailed analyses of the chitinozoan assemblage of a section exposing a major incision at Jbel Signit Nord in Morocco, i.e., the near field area from a supposed ice cap, revealed an abundant and well preserved assemblage indicating the middle Arenig *E. brevis* chitinozoan Biozone in the infill of the incision, as well as under the incision and from the sediments postdating the infill. This is indicating a relatively short-term event potentially related to glacio-eustatic sea level variations. The same potentially-lowstand sedimentary features have been observed at about 50 km in Alnif within the same *E. brevis* chitinozoan Biozone or slightly younger, suggesting that this is at least a regional event and which supports the climatic hypothesis. To confirm the hypothesis, sedimentological analysis of those sections

investigating the architecture and stacking pattern of the potentially glacio-related deposits, are ongoing by our colleagues-sedimentologists from Strasbourg, Bordeaux and Rennes.

To test the hypothesized glacial event at a more global scale, we should be able to trace this glaciation in the far field from a supposed ice cap, i.e., in Wales, situated at that time in the peri-Gondwana area, where evidence of contemporary lowstand deposits should also be visible. To be able to correlate precisely the sections from Morocco with Wales, a new biostratigraphical framework using chitinozoans was established for Avalonia.

3. The palynological study of selected sections in the historical type area of the Arenig in Wales allowed us to define four chitinozoan assemblages in the upper Tremadoc, the Arenig and the lowermost Llanvirn. The species recorded in Wales are similar to those found by Paris (1990) in Gondwana, although they sometimes occur in different chronostratigraphic units in the Arenig type area than those they were originally assigned to. The first assemblage contains *Lagenochitina destombesi*, diagnostic of the lower Tremadoc eponymous chitinozoan biozones in Gondwana (Paris, 1990; Webby *et al.*, 2004; Videt *et al.*, 2010), but also found in the lower Tremadoc in Baltica (Nölvak 1999, Nölvak *et al.*, 2006). *Lagenochitina brevicollis* is also found in the assemblage and also diagnostic of the eponymous upper Tremadoc chitinozoan Biozone in Gondwana (Videt *et al.*, 2010). The second assemblage contains many species found in the middle Arenig *E. brevis* chitinozoan Biozone in Gondwana (Paris 1990), although the index taxon is not found in the assemblage. The absence of *E. brevis* is remarkable, as it has been observed in many areas, Morocco and Algeria (Paris 1990; Videt *et al.*, 2010), in the Brabant Massif by Samuelsson and Verniers (2000), in Estonia (Nölvak & Grahn, 1993, Nölvak 1999) and in Argentina (De La Puente, 2010). The third assemblage contains several eponymous species of upper Arenig chitinozoan biozones from Gondwana, such as *Desmochitina ornensis* and *Belonechitina henryi* (Paris 1990; Webby *et al.*, 2004; Videt *et al.*, 2010), but also *Tanuchitina granbyensis*, an upper Arenig species described in Baltica (Grahn, Nölvak and Paris, 1996). The fourth assemblage yielded key species of the Arenig-Llanvirn boundary, but the presence of *Cyathochitina protocolix*, diagnostic of the eponymous biozone straddling the Arenig-Llanvirn boundary, could not be confirmed.

To further the use of those assemblages, a detailed taxonomic work ought to be established for these (and additional) specimens in order to define proper biozones that could be used for correlations and more sections, especially in the lower-middle Arenig, should be studied. The preliminary study of the upper Tremadoc Watch Hill Formation from the English Lake District reveals the presence of *Euconochitina symmetrica*, eponymous species of the lower Arenig chitinozoan biozone in Gondwana and Laurentia.

The correlation of the lowest, Tremadoc assemblage with Gondwana is not surprising given the close palaeogeographical position of Avalonia at that time. The absence of *E. brevis* in the middle Arenig second assemblage could result from (local) oceanic parameters (such as non-deposition during lowstand event) rather than an increasing faunal provincialism in an increasingly isolated and nomadic Avalonia, as the fauna becomes similar again in the third

assemblage, presenting strong affinities with Gondwana as does the fourth assemblage. But the stratigraphical position of *E. brevis* has already been questioned (Nowak *et al.*, 2016) and point to an issue in the biostratigraphy of the chitinozoans which can be attributed to the fact that many morphologically similar specimens within approximately coeval stratigraphical positions, but in different palaeocontinents, have been assigned to different species and sometimes even to different genera. This considerably hampers the power of correlation of the biozonation schemes, as in result they result to become too regional.

Harper (1996) demonstrated that during the Early Ordovician the Celtic Fauna, based on Arenig brachiopods from North Wales, was found on microcontinents derived from Gondwana (e. g. Avalonia), an island arc found in the Southern margin of the Iapetus Ocean and maybe in the Laurentian terranes or margin. In Harper *et al.* (2013), the brachiopod fauna is divided in three climate belts: the Southern Fauna (high latitudes), the Northern Fauna (low latitudes) and Baltic provinces. During the Tremadoc, the Southern Fauna was found up to 60 °S in the Iapetus Ocean, including in Avalonia and almost up to equatorial latitudes in the Northern part of the Gondwana land (e. g. actual South America). During the Floian (early Arenig), a major change in faunal affinities occurs and the Southern Fauna became restricted to high latitudes (> 80 °S) and the Dapingian (middle Arenig) witnessed the local extinction of several genera, especially in low latitudes. The Dapingian-Darriwilian boundary (late Arenig) is characterized by the apparition of the Celtic Fauna, which largely consist of endemic species, and a high degree of diversification.

This evolution of the palaeobiogeographical patterns is comparable to those of the chitinozoans now that we have documented the assemblages in Wales with a similar fauna to Gondwana during the Tremadoc. During the middle Arenig, the assemblages in Wales are remarkable by lacking endemic species of Gondwana, although some common species allow a comparison. But the upper Arenig-Lower Llanvirn great similarity in the chitinozoan assemblage between Wales and Gondwana differs from the establishment of the local brachiopod Celtic Fauna. This could be explained by the different position in the water column, as most of brachiopods are attached to the substrate whereas chitinozoans are thought to be pelagic and thus to be prone to transport by water current. Cold water masses induced by a cooling in Gondwana could flow northward, driving ocean current controlling the dispersion, as it is supposed for the acritarchs (Molyneux *et al.*, 2013). The acritarchs are thought to be more dependent on difference in water masses or oceanic current than on climate belts, as they are found all along the Gondwanan margin from high to low latitudes. During the Early Middle Ordovician, the acritarchs from the Peri Gondwana province was also present in Avalonia, but not in Baltica (Molyneux *et al.*, 2013).

It has to be noted that in the upper Arenig Lysaker Member of the Huk Formation in the Oslo Region, the chitinozoan assemblage does not correspond to the established biozonation for Baltica, but is in contrast relatively similar to the assemblage 3 from Wales, with a fauna constituted almost exclusively of Cyathochitinids.

We can see from these changes in provincialism that there is an event in the middle upper Arenig (Dapingian-Darriwilian boundary) that modifies the distribution of the organisms, phytoplankton and zooplankton and lead to hiatus and unconformities (e. g. Dabard *et al.*,

2015; Gutiérrez-Marco *et al.*, 2014), which could represent a phase of cooling during the Early-Middle Ordovician. In addition, it is interesting to note that Rasmussen *et al.* (2016) described a sea level drop in the lowermost Darriwilian, which is contemporary to the distal deposition of the Huk Formation in the Oslo Region.

9. Conclusions

Conclusions:

To conclude, my contribution to the understanding of the complex Ordovician system is as follows: When testing the potential of the chitinozoans to track climate variations and possibly the start of an Early Palaeozoic Ice age during the Early-Middle Ordovician the results are variable: In Norway, the results were not conclusive, as the chitinozoan assemblages from the Darriwilian, Sandbian and Katian did not allow to detect variations in the rhythmities that could be related to SST variations and climate fluctuations. Only one species in the upper Sandbian showed a significant difference of abundance in the two lithologies, being more abundant in the marls than in the limestones but that was not convincing enough to confirm the expression of climate variations. In Morocco, the results are convincing, as the chitinozoan assemblages recovered in the incisions clearly point to a rather short term event constrained in the middle Arenig which is at least regional, and therefore could be related to glacioeustasy. However, other mechanisms for such incisions do exist and the glaciogenic hypothesis requires further confirmation from ongoing sedimentological analysis. The four assemblages defined in Wales allow for a solid correlation with Gondwana, as it reveals a very similar fauna for the upper Tremadoc and middle upper Arenig, but some key species, found elsewhere in the peri-Gondwana domain, are lacking in Wales. The newly described fauna also lead to draw limited paleobiogeography conclusions when comparing with Gondwana, Baltica and Laurentia, although a full analysis would require a more complete dataset still.

As summarized in figure 10, it is clear that the fauna from Avalonia in the Lower-Middle Ordovician is an integral part of the Gondwanan/polar province as, despite its drifting toward Baltica, the affinities are stronger with the fauna from Gondwana, apart from one common species found in the upper Arenig in Baltica (i.e., *Tanuchitina granbyensis*). Taken at face value, there seems to be a widespread fauna, with species in common between most of the palaeocontinents during the Tremadoc. The chitinozoan assemblages then seem to become much more restricted during the middle to upper Arenig, e.g., the Arenig assemblages as we found them in Wales are restricted to high southern latitudes. I suggest that this shift from widespread to restricted faunas, or increasing palaeoprovincialism, could reflect changing palaeoenvironmental conditions during the middle upper Arenig. SST has been invoked as a main control on chitinozoan distribution patterns (Vandenbroucke *et al.*, 2010) and the timing would fit the hypothesized onset of the EPI cooling (or one of its phases) during the Early and Middle Ordovician as it is suggested by other proxies (i. e. Trotter *et al.*, 2008, Turner *et al.*, 2011, 2012; Rasmussen *et al.*, 2016).

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