

International Geoscience Programme Project 653 - Opening Meeting





Project 653

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## Welcome from the Chair

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Dear Colleagues,

I am delighted to welcome you, firstly to the opening meeting of IGCP653 and secondly to Van Mildert College, Durham University. Our project, which is funded through 2016-2020, is a truly global effort to explore, investigate and establish the causes, patterns and processes of the 'Great Ordovician Biodiversification Event' (GOBE) and its aftermath. The GOBE completely changed the marine ecosystem, restructuring marine food webs and the mutual relationships between groups of organisms and their environment. The diversifications varied across environments, provinces and even amongst clades; the event itself was rooted in the Cambrian. An international effort, the focus of our project, is essential to improve our data, its management and analysis. The 40 or so participants from nearly 20 different countries represent an amazing kaleidoscope of experience and expertise across all disciplines of geology and palaeontology. The meeting is based on a workshop format, participants seated at round tables to encourage free and wide-ranging discussions with an eye on the conclusion of the project in 2020, and the achievements and goals we might expect. We look forward to a week of exciting and robust exchanges on Lower Palaeozoic topics and the future direction of this key IGCP project.

Van Mildert College, founded in 1965, is one of the largest of the 16 Durham colleges. Set on the 'Hill', nestled in spacious grounds beside the Lake, it has 525 resident students and some 1400 members together with over 8,000 alumni. The atmosphere is relaxed and the ethos, sic vos non vobis, fosters inclusiveness across all the common rooms and drives the many outreach and volunteering projects that makes our College unique. I hope you enjoy your stay here and I am certain our staff will do everything possible to make your visit a memorable one.

Finally I would like to thank Event Durham and especially Van Mildert's Development Officer, Richard Bruce for their organisation skills at many different levels and Thomas Servais for his advice.

David Harper Principal of Van Mildert College Professor of Palaeontology

## Background

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The new project IGCP 653 has now been formally accepted by the IGCP Scientific Board.

IGCP 653 can be considered to be a direct successor project of IGCP No. 410 The Great Ordovician Biodiversification Event and IGCP No. 503 Ordovician Palaeogeography and Palaeoclimate and also to some extent IGCP No. 591 The Early to Middle Palaeozoic Revolution.

As the title indicates, the main objective of our new project is to find the triggers of the different biodiversification events that together constitute the GOBE.

Further information about the project is available at www.igcp653.org

## **Scientific Committee**

David A.T. Harper (Chair, Durham, UK)

Thomas Servais (Lille, France) Olga T. Obut (Novosibirsk, Russia) Christian M.Ø. Rasmussen (Copenhagen, Denmark) Alycia L. Stigall (Athens, Ohio, USA) Zhang Yuandong (Nanjing



### International Geoscience Programme Project 653 - Opening Meeting

Venue
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#### Van Mildert College, Durham University



Van Mildert College was founded in 1965 and is one of the largest of Durham University's Colleges, with ca. 525 residents and over 1300 members.

Situated around a Lake with open grounds, the College is situated approximately 15 minutes from the city centre on foot. The College is located close to the University's Science Site on the southern edge of the historic city.

#### **Durham City**

Few venues in the world can rival the splendour, prestige and heritage of the City of Durham. Located on a dramatic peninsula overlooking the River Wear, Durham's unique Norman Cathedral and Castle not only dominate the skyline, they are also a designated World Heritage Site.

Durham is a small and compact city, and everything is within easy walking distance. Just minutes from the bustling centre, you can enjoy the tranquillity of leafy riverside footpaths along the banks of the River Wear, or the changing seasonal displays at the Botanic Garden. Palace Green Library, the Oriental Museum and World Heritage Site Visitor Centre hold fascinating collections of international significance, as well as offering key insights into local history.





## **Field Excursion - Lake District**

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During this short, two-day excursion we will visit some classic localities on the Avalonian Plate exposed in the north of England, amid some spectacular scenery, that has inspired many artists, poets and writers. We will stay for two nights in Penrith, the ancient capital of the Kingdom of Cumbria; until 1070 AD Cumbria was part of Scotland. On day one, driving directly from Durham, we will visit key localities in the Lake District, west of Penrith. The Skiddaw Group (Lower Ordovician) forms a mountainous zone in the northern part of the Lakes, with Skiddaw itself reaching a height of over 900 m.

We will visit some fossiliferous localities in the thick slate succession. This is overlain by the thick Borrowdale Volcanic Group (Upper Ordovician), dominated by ash flows and lavas generated during subduction and forming some of the most prominent mountains in the region, such as Scafell, Helvellyn and Coniston Old Man. The Upper Ordovician – Silurian Windermere Group contains a wide range of sedimentary rocks, including limestones, sandstones and shales, locally fossiliferous. We will overnight in Penrith.



Lower Ordovician Skiddaw slates exposed on Skiddaw.



Upper Ashgill rocks exposed in Tathyes Gill with Cautley Crags in the distance.

On day two we will visit Ordovician localities in the Howgill Fells (Cautley district), east of Penrith where Ordovician rocks form an eastward extension of the Kendal anticlinorium, abutting against the Dent Fault zone. The classic succession, comprising part of the regional Dent Group (Cautley Mudstone Formation and Ashgill Shale Formation) is lithologically monotonous but richly fossiliferous. The type succession for the Ashgill Series is defined here even although the name is taken from Ashgill Beck in the Lake District. If time permits we will visit the village of Dent, birthplace of Adam Sedgwick. We will overnight again in Penrith before travelling early next morning for Durham City.

## **Restaurants in Durham**

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Durham boasts a wide variety of restaurants throughout the City to visit during your time here, from Italian and tapas to pub grub and schwarma, all within a short distance of Van Mildert College.

Bills - Traditional English £££ https://bills-website.co.uk/restaurants/durham/

*Capriccio* - Italian £ http://www.capriccioristoranteitaliano.co.uk/

*Cellar Door* - Traditional English ££ http://www.thecellardoordurham.co.uk/

*Court Inn* - Traditional English ££ http://www.courtinn.co.uk/

*El Coto* - Spanish ££ http://elcoto.co.uk/

La Spaghettata - Italian £ http://www.fabiosdurham.com/la-spaghettata

*La Tasca* - Spanish ££ http://latasca.com/

Lebaneat - Lebanese £ http://www.lebaneat.com/

*Nadon Thai* - Thai ££ http://www.nadonthai.co.uk/

Tango - Burgers £££ http://tangodurham.co.uk/

Zen - Thai £££ http://www.zendurham.co.uk/

*Zizzi* - Italian £££ https://www.zizzi.co.uk/



Collingwood

## **Brachiopod Diversification**





Patterns of diversification amongst the rhynchonelliform brachiopods.

From Rasmussen in Harper et al. 2013 (Memoir Geol. Soc. London 38).

## **Meeting Programme**

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#### Sunday 25th September 2016

Arrival Reception Van Mildert College, Durham University Fork Buffet and Refreshments

Monday 26th September 2016

\* Indicates keynote

#### What is the GOBE?

9.15 Welcome to Van Mildert College *Dave Harper* 

9.30 Introduction: a new IGCP project *Thomas Servais* and the other IGCP 653 leaders

9.50 *Thomas Servais* and David A.T. Harper: *The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration.* 

10.10 *Timothy P. Topper* and David A.T. Harper: Life strategies of Cambrian brachiopods: providing the foundations for their dominance in the Ordovician.

#### 10.30 Coffee break

11.00 *Björn Kröger* and Lee Hsiang Liow: *\*What is the GOBE? – Three facets of a hypothesis.* 

11.45 **Rasmussen, Christian M. Ø.**, Colmenar, J., Nielsen, M. L. and Kröger, B.: Constructing a high-resolution biodiversity curve through the GOBE interval by applying time slices based on lithostratigraphical ranges of fossil occurrences in the Paleobiology Database.

12.10 *Hints, Olle*, Antonovitš, Liina, Nestor, Viiu and Nõlvak, Jaak: An example of a regional geological database and its application for analyzing diversity patterns of Ordovician and Silurian chitinozoans of Baltoscandia.

## **Meeting Programme**

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Discussion

#### Lunch 12.30-2.00 pm

2.00 Paton, T., Brett, C.E. and **Brookfield, M.E.**: Paleobiology of Ordovician subtidal hardground communities: a contribution to the evolution and development of hard surface biotas with examples from "paleo-Pompei" horizons from the Upper Ordovician of Southern Ontario.

2.20 Van Iten, Heyo, *Gutiérrez-Marco, Juan Carlos* and Sá, Artur A.: Ordovician Conulariids of the Iberian Peninsula.

2.40 *Wang Wenhui*, Xu Chang and Thomas Servais:

A Study on the Ultrastructure and Microscopic Pore Structure of Microfossils with Focused Ion Beam Scanning Electron Microscopy (FIB-SEM).

#### 3.00 Coffee break

3.30 Xuan Ma and Yuandong Zhang:

Graptolite fauna and biostratigraphy of the Hulo and Yuchien formations (Ordovician) in northwestern Zhejiang Province, SE China.

3.50 Suarez, Stephanie E., **Brookfield, Michael E.**, Catlos, Elizabeth J., Stockli, Daniel F. and Batchelor, Richard A.: Precise U/Pb zircons dates of bentonites in Ordovician reference sections in North America and Britain.

4.10 Akodad, Mustapha ; Gutiérrez-Marco, Juan Carlos ; Lehnert, Oliver ; Lefebvre, Bertrand; Martin, Emmanuel L.O.; Nowak, Hendrik; *Servais, Thomas*; Vandenbroucke, Thijs R.A. and Van Roy, Peter: *The Lower Ordovician Fezouata Konservat-Lagerstätte (Morocco): precise age calibration.* 

#### Discussion

## **Meeting Programme**

#### Tuesday 27th September 2016

The geology of the GOBE

9.00 Introductory remarks

9.05 **Conall McNiocaill** : \*What do we really know about Ordovician Palaeogeography?

9.50 *Fang, Xiang*, Ma, Xuan, Li, Wenjie, Lü, Yong and Zhang, Yuandong: *Upper Ordovician of Baoshan and Luxi regions, western Yunnan Province, China* 

10.10 *Zhang Yuandong*, Munnecke, Axel, Chen Xu: Ordovician stable carbon isotope stratigraphy in the Tarim Basin, NW China, and its palaeogeographic implications.

#### 10.30 Coffee break

11.00 Alexandre Pohl: \*Numerical modelling of Ordovician climate.

11.45 *Dronov, Andrei*, Kanygin, Alexander, Timokhin, Alexander and Gonta, Taras: *Global tectonics as a driving force for the Great Ordovician Biodiversification Event?* 

Discussion

#### 12.15 Lunch

2.00 *Tais Dahl:* \*Geochemical proxies and the history of O2 and CO2 on the early Earth

2.45 *Isozaki, Yukio*: The Ordovician biodiversification and the circum-solar environments.

#### 3.05 Coffee break

Meeting	Programme
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#### 3.30 Barnes, Christopher R.:

*Climate-ocean environmental changes associated with the Great Ordovician Biodiversification Event (GOBE), with emphasis on Laurentian conodont and isotopic data.* 

#### 3.50 Rasmussen, Christian M. Ø.:

Was the Ordovician Radiation fuelled by a present-day type climate?

#### Discussion

#### Wednesday 28th September 2016

#### **Databases and Diversity**

9.00 Introductory remarks

9.05 Claude Monnet:

\*Biodiversity metrics in deep time - a synthesis of taxonomic approaches

9.50 *Alycia L. Stigall* : *How is biodiversity produced?* Examining the influence of geography, ecology, and evolutionary processes on speciation during the GOBE.

10.10 *Rebecca L. Freeman*, James F. Miller, Stephen R. Westrop, Jonathan M. Adrain, Benjamin F. Dattilo and Kevin R. Evans: *Extinction and migration patterns in Laurentian linguliform brachiopods and rhynchonelliform brachiopod "blooms" during the Cambrian–Ordovician transition*.

#### 10.30 Coffee

11.00 *Harper, D.A.T.*, Popov, L.E. and Holmer, L.E. *Early Palaeozoic brachiopod phylogeny: Tracking the GOBE through the trees* 

11.20 Introduction: *Round table discussion: the way forward.* 

#### 12.15 Lunch

Departure for Palace Green after lunch

## The Lower Ordovician Fezouata Konservat-Lagerstätte (Morocco): precise age calibration

<sup>1</sup>Akodad, Mustapha, <sup>2,3</sup>Gutiérrez-Marco, Juan Carlos, <sup>4,5,6</sup>Lehnert, Oliver, <sup>7</sup>Lefebvre, Bertrand, <sup>7</sup>Martin, Emmanuel L.O., <sup>8,9</sup>Nowak, Hendrik, <sup>9</sup>Servais, Thomas, <sup>10</sup>Vandenbroucke, Thijs R.A. and <sup>10,11</sup>Van Roy, Peter

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The Fezouata Biota from the Ordovician of Morocco is preserved in a Konservat-Lagerstätte of major importance, that is today considered as an Ordovician 'Burgess Shale-type Lagerstätte.' The exceptionally preserved biota occur at different intervals within the Fezouata Formation. This Early Ordovician (Tremadocian – Floian) formation is composed mostly of fine-grained siliciclastics and was deposited on the peri-Gondwanan shelf near the palaeo-South Pole. According to recent sedimentological studies (Martin et al., 2016; Vaucher et al., 2016), the benthic communities of the Fezouata Biota lived in an open-marine environment, in a relatively shallow setting (upper offshore to lower shoreface) above storm wave base. The Fezouata Lagerstätte-bearing beds were initially estimated as ranging from upper Tremadocian to upper Floian (Van Roy et al., 2010) and later restricted to the upper Tremadocian (Martin et al., 2016).

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Here we present new biostratigraphical results from several fossil groups, including graptolites, trilobites, acritarchs, chitinozoans and conodonts. These new data provide for the first time a precise biostratigraphical calibration of the Fezouata Biota. Acritarchs of the sub-assemblages of the messaoudensis-trifidum assemblage confirm the late Tremadocian age of the oldest Lagerstätte-bearing beds and allow a correlation with other peri-Gondwanan localities (Nowak et al., 2016). New graptolite studies (Gutiér-rez-Marco and Martin, 2016) allow a detailed view of the most complete Lower Ordovician graptolite succession known from the African continent. They also indicate that most Lagerstätte-bearing beds are present in the late Tremadocian, while another level of exceptional preservation occurs in the ?Baltograptus jacksoni graptolite Biozones of middle Floian age. The conodont assemblages are devoid of any warm/tropical and temperate water taxa and belong to a 'subpolar faunal domain.'The conodont associations of low diversity confirm the late Tremadocian to basal Floian ages of the Lagerstätte (Lehnert et al., 2016).

#### Climate-ocean environmental changes associated with the Great Ordovician Biodiversification Event (GOBE), with emphasis on Laurentian conodont and isotopic data

#### <sup>1</sup>Barnes, Christopher R.

<sup>1</sup>School of Earth and Ocean Sciences, University of Victoria, Victoria, BC V8W 2Y2, Canada

Much data has been gathered related to the Great Ordovician Biodiversification Event (GOBE) and its onset, especially through and since IGCP 410 and the resulting book (Webby et al., 2004). Yet the puzzle remains as to the nature and timing of the environmental changes that presumably largely triggered and controlled this 4-fold explosion of biodiversity at many taxonomic levels, which occurred on a global scale and within a short timeframe of 5-10 Myr in the late Darriwilian-early Sandbian. Many earlier syntheses of Ordovician biodiversity assigned ages of taxa into 5-7 stages/series, which was too coarse to reveal GOBE's remarkably short duration. The latter was better documented through later isotopic studies with detailed stratigraphic sampling and biostratigraphic controls. However, securing long sections through this interval has long proven challenging given the associated Whiterock Regression that limited such sections to most cratonic margins, with many now in deformed orogenic belts. Sections in undeformed parts of Laurentia, Baltica and China offer potential opportunities.

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Studies with colleagues based on excellent sections in the Canadian part of Laurentia, particularly in the Appalachian, Cordilleran and Innuitian (Arctic) carbonate outer platform and slope environments have been extensively sampled in studies of conodont biostratigraphy, paleoecology, and paleobiogeography. These collections, along with those from other sampled paleoplates and microcontinents, served as the basis for Sr, Nd and O isotopic studies. Sr work showed an extreme excursion (87Sr/86Sr ratios: 0.7087 to 0.7078 between 470-460 Ma) that argues for a major ocean floor spreading, LIP, or superplume event. One key challenge is to identify a process/location that was of sufficiently short duration and not subjected to subduction. With Nd work, the ENd values for water masses associated with Laurentia are strongly negative (-28 to -18) in the Early Ordovician, changing near GOBE to higher values (-13 to -5), suggesting limited input from older cratonic sources and marking the influx of transgressive lapetus Ocean waters. More recent O isotope studies showed a change at the GOBE interval from excessively high equatorial ocean temperatures (38-40C) during the Tremadocian-Dapingian to ones approximating today's values (28-32C during 470-450 Ma). These high temperatures likely suppressed biodiversification through the Early Ordovician until the GOBE onset.

The combination of primary climate/ocean environmental factors leading to the onset of GOBE could thus include: a) lowered sea levels of the Whiterock Regression followed by the initial Sandbian-Katian transgression with increased ecospace and nutrient upwelling; b) change from hot to today's ("normal") equatorial ocean temperatures; and c) probably a corresponding reduction in hypersalinity in cratonic epeiric seas. This "normal" condition lasted through the remainder of the Ordovician, but was drastically changed by the terminal Ordovician glaciation and regression resulting in a 50% reduction in biodiversity for many clades.

#### \*Geochemical proxies and the history of O<sup>2</sup> and CO<sup>2</sup> on the early Earth

#### <sup>1</sup>Tais W. Dahl

<sup>1</sup>Natural History Museum of Denmark, University of Copenhagen, DK-1350 Copenhagen, Denmark

The history of life is linked to the evolution of the environment. Specifically, the partial pressure of atmospheric  $CO^2$  and  $O^2$  have played a central role in shaping Earth's climate and the oxygenation state of the oceans.

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These parameters are coupled through the global biogeochemical cycling of carbon between Earth's crust, atmosphere and oceans. Several models suggest that the Cambrian-Ordovician CO<sup>2</sup> levels were one order of magnitude higher than today and that atmospheric pO<sup>2</sup> were one order of magnitude lower (Bergman et al., 2004; Lenton et al., 2016). A major transition is thought to have occurred between the Ordovician emergence of bryophytes and the Devonian-Carboniferous expansion of forests on land. However, the governing factors are not straightforward and Earth's climate and oxygenation state may not always have evolved in parallel.

Evidence for the Paleozoic environmental history is derived from a combination of Earth system models, geochemical proxies and the fossil record. Any one line of evidence involves large uncertainties and various assumptions, but together they can paint a clearer picture of the past. To illustrate this, I will present evidence for a major rise of atmospheric oxygen associated with the late Ordovician-Silurian invasion of rootless plants on land (Lenton et al., 2016).

The new study suggests that atmospheric oxygen levels first reached modern levels in the early Devonian, fully oxygenating the deep oceans. This is significantly later than argued in recent reports of a Neoproterozoic-Early Cambrian (>550 Ma) oxygenation event (Chen et al., 2015; Lyons et al., 2014; Sperling et al., 2013), and significantly earlier than predicted from the rise of forests in the Late Devonian-Mississippian (Bergman et al., 2004). Basically, the modelled consequence of bryophytes present on land fits with evidence from fossil charcoal and several geochemical compilations (incl.  $\delta^{13}$ C in carbonates and  $\delta^{98}$ Mo in organic-rich mudstones) suggesting anoxic water masses were more common in the Ordovician oceans than in the Devonian and modern oceans (Dahl et al., 2010). How robust are these findings and what can we do to further validate it? Several geochemical proxies may apply, for example one route is to map out anoxic marine zones in the Paleozoic oceans, and follow the waxing and waning of the anoxic marine zones with time. Do we see correlations between the oxygenation state of the oceans and evolving marine animal ecosystem on local scales? There are examples of animal extinctions when oxygen levels decline, and oceanic anoxic events represent a plausible kill mechanism during some Paleozoic biotic crises (Gill et al., 2011; Knoll et al., 1996). Another question is whether animal radiations were caused by increasing oxygen availability in the environment. Could the animal-habitable zone expand and lead to animal radiations at this time (Dahl and Hammarlund, 2011; Sperling et al., 2015)? I suggest the integration of a more complete paleontological and geochemical record with unifying Earth system models can illuminate these questions and improve our understanding of the co-evolution of animal life and our planet.

## Global tectonics as a driving force for the Great Ordovician Biodiversification Event?

<sup>1</sup>Dronov, Andrei, 2Kanygin, Alexander, <sup>2</sup>Timokhin, Alexander and <sup>2</sup>Gonta, Taras

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Although the "Great Ordovician Biodiversification Event" (GOBE) represents the most intense phase of species radiation during the whole Phanerozoic, the ultimate cause of this event remains elusive. Several drivers have been suggested including both intrinsic (biotic) and extrinsic (abiotic) factors. Among the abiotic factors, a cooling climate (transition from greenhouse to icehouse conditions) is regarded as the most powerful. It was suggested that icehouse conditions increased latitudinal and bathymetrical temperature and oxygen gradients initiating an oceanic conveyor belt, which intensified upwelling (Rasmussen et al., 2016). The latter fuelled the GOBE not only because upwelling zones created new ecospace for primary producers, but also because the cooler oceanic waters did penetrate, in the Mid and the Late Ordovician, waste areas covered in the Cambrian and Early Ordovician by warm-water epicontinental seas. Two large Ordovician cratons situated in tropical settings (Laurentia and Siberia) demonstrate this scenario. Penetration of cool-water oceanic masses into former warm-water realms caused drastic changes in their hydrological regimes creating an enormous increase in amount of new ecospace for cool-water benthic organisms.

The general pattern of long-term lithological changes is similar in the Ordovician of Laurentia and Siberia. On both continents the Ordovician succession starts with warm-water tropical carbonates, passes through siliciclastic sandstones, and is terminated by cool-water carbonates. Nevertheless, the onset of cooling, marked by the distribution of cool-water carbonates is not contemporaneous in Siberia and Laurentia. In Siberia it starts earlier in the Darriwilian. That observation contradicts the hypothesis that the onset of cool-water carbonates in Laurentia reflects a global cooling event. Rather, regional cooling events induced by upwelling in Siberia and Laurentia started at different times and merge at later stages, leading to global cooling of the Earth's system.

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Regional upwelling events were apparently caused by regional and/or global plate tectonic reorganization. Recent data from the Ordovician of Siberia suggest that evidence for the Taconian orogeny was much more widespread along the western and southern margins of Siberia (in present-day orientation) than it was previously believed. This global or semi-global orogenic event is broadly coincident with the main phase of the GOBE. That suggests that the ultimate driving force for Ordovician climatic change and the GOBE was actually tectonic activity. It is also interesting to note a close coincidence between the GOBE and the major asteroid breakup event that enhanced meteorite flux on Earth by one to two orders of magnitude for at least a few million years after the disruption event in Darriwilian (Schmitz et al., 2008). These astronomical perturbations probably led to Solar System gravity disturbances that may have created a sudden reorganization of tectonic plate movements on Earth in the Mid Ordovician and consequently triggered orogeny, volcanism, initiating an oceanic conveyor belt, upwelling, cooling and biodiversification in that order.

### Upper Ordovician of Baoshan and Luxi regions, western Yunnan Province, China

<sup>1,2</sup>Fang, Xiang, <sup>1,2</sup>Ma, Xuan, <sup>1,2</sup>Li, Wenjie, <sup>3</sup>Lü, Yong, <sup>1,4</sup>Zhang, Yuandong

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The Baoshan and Luxi Regions, tectonically known as the Baoshan Terrane, formed a critical part of the Sibumasu Block in Ordovician and Silurian time, and is the significant area for studying the tectonic relationship and history of the South China, Indochina and South Tibet blocks. Recently we investigated and collected three sections of basically clastic facies and of mid Katian to Hirnantian (Upper Ordovician) age in the Baoshan and Luxi regions, western Yunnan, including the Laojianshan Section (Baoshan), Xiangshuiao Reservoir A Section (Shidian, Baoshan), and Shaodihe Section (Mangshi, Luxi). A biostratigraphical study of the sections is conducted and a comparison to the equivalent reference sections of South China, shows that there is a significant disconformity between the Pupiao Formation in Baoshan (equivalently Luxi Formation in Mangshi, Luxi) and the overlying Renhochiao Formation (equivalently Wanyaoshu Formation in

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Mangshi, Luxi) in western Yunnan, which spans the Dicellograptus complanatus Biozone, Dicellograptus complexus Biozone and largely the Paraorthograptus pacificus Biozone of late Katian. A rich and well-preserved shelly fauna, dominated by brachiopods Hirnantia and trilobites Mucronaspis (Songxites), occurred in the Wanyaoshu Formation in the Shaodihe Section, Mangshi, Luxi, but was completely absent in the Laojianshan and Xiangshuiao Reservoir A sections, Baoshan. The fauna is correlated to the Metabolograptus extraordinarius Biozone and the lower Met. persculptus Biozone, as constrained by the yielded graptolites in the underlying and overlying beds. The stratigraphic hiatus in the western Yunnan seems likely to result from the sea-level drop of Late Ordovician Gondwanan glaciation, and thus represents the first significant evidence of the event in Sibumasu Block.

# Extinction and migration patterns in Laurentian linguliform brachiopods and rhynchonelliform brachiopod "blooms" during the Cambrian–Ordovician transition

**Rebecca L. Freeman**<sup>1</sup>, James F. Miller<sup>2</sup>, Stephen R. Westrop<sup>3</sup>, Jonathan M. Adrain<sup>4</sup>, Benjamin F. Dattilo<sup>5</sup>, and Kevin R. Evans<sup>2</sup>

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Linguliform brachiopods, a key component of the Cambrian Evolutionary Fauna, have a well-preserved record in late Middle Cambrian to earliest Ordovician strata of the outer shelf of western Laurentia. Last occurrences of linguliform taxa in the outer shelf often coincide with well-known trilobite extinctions, which were accompanied by decreased brachiopod diversity. Linguliform taxa with extra-Laurentian affinities appear in the aftermath of extinction intervals, parallelling changes commonly seen in trilobite faunas. The pattern of change in the cratonic shelf of Texas and Oklahoma is variable. The end-Steptoean trilobite extinction is associated with the appearance of an endemic fauna that is apparently unrelated to the coeval, pandemic, outer-shelf fauna of western Laurentia.

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In contrast, the end-Sunwaptan trilobite extinction was marked by the appearance of cosmopolitan linguliform taxa that are similar to faunas of the outer shelf.

Rhynchonelliform brachiopods of the "Paleozoic Evolutionary Fauna" are generally scarce in both inner and outer shelf settings but they become intriguingly abundant for brief intervals in the wake of trilobite extinctions. These rhynchonelliform "blooms" are expressed by shell beds, often as transgressive lags in shallow water facies. They imply large populations that contrast with the rarity of rhynchonelliforms at other times. The blooms are well documented in the literature, and some, such as the "Eoorthis coquina" of the early Sunwaptan, have been used as biostratigraphic markers throughout Laurentia. The environmental and ecological conditions that generated the blooms are unclear. It is difficult to envisage a scenario in which declining diversity of trilobites led to the expansion of rhynchonelliforms. It is tempting to suggest that declines in linguliforms might have favoured rhynchonelliforms, but that hypothesis is seemingly contradicted by abundant linguliforms in the Eoorthis coquina in Texas.

Extinctions in the Cambrian and Ordovician of Laurentia were complex events characterized by turnover and immigration of trilobites and linguliforms and short-lived expansions of rhynchonelliforms. The "blooms" of the latter can be viewed as harbingers of the diversification of rhynchonelliforms at the onset of the GOBE. Understanding the environmental and ecological changes that fostered the blooms without leading to any lasting evolutionary radiation will likely provide fresh insight into the causes of the GOBE.

#### Early Palaeozoic brachiopod phylogeny: Tracking the GOBE through the trees

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The Brachiopoda is one of the most successful animal phyla, dominating marine environments for much of the Palaeozoic Era and continuing to the present day with more restricted distributions and diversities.

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Based on a relatively simple body plan, the phylum achieved a remarkable diversity of form and range of life styles. There are, however, three key challenges in understanding the early history of the phylum: a) identifying the origin, morphology and life modes of the first brachiopods; b) understanding their relationships to higher sister taxa and c) unravelling the roles of the Cambrian and Ordovician radiations that set the agenda for much of subsequent brachiopod evolution. The latter, the GOBE, has been the focus of sustained research over nearly three decades. To date assessments of biodiversity have been based mainly on taxon counts. We present here a new phylogeny for the Early Palaeozoic Brachiopoda indicating that: a) the three Brachiopod subphyla may have split from each other at an early stage in brachiopod evolution, and probably prior to the acquisition of a mineralized shell in the early Cambrian; b) a "tubular" sessile life habit may be primitive within the lophotrochozoans; c) obolellates retain a position at the base of the rhynchonelliform clade, whereas e) the kutorginates emerge as a sister group of all strophomenates and f) the clear split of the rhynchonelliforms into the rhynchonellates and strophomenates is confirmed. Our phylogenetic hypothesis charts the success of the rynchonellates through the GOBE and beyond, occupying increased morphospace and establishing the basic anatomy and architecture of the modern articulated brachiopod.

## An example of a regional geological database and its application for analyzing diversity patterns of Ordovician and Silurian chitinozoans of Baltoscandia

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The understanding of diversification and extinction events has been greatly advanced thanks to the assembly of large data sets and the use of computers to analyze these data. The most important global palaeontological database is the Paleobiology Database (http://paleobiodb.org), which has a large community of users and contributors and covers a rapidly growing number of published fossil occurrences from the Early Paleozoic. However, regional or otherwise focused databases may also be very useful for analysing diversity patterns. In Estonia a national geoscience database has been developed and used by multiple academic institutions. Started primarily as a collection management system its scope has gradually widened to cover also, e.g., fossil occurrence records and primary geochemical data from numerous Early Paleozoic sections of Baltoscandia.

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The system is built using open source components and most of the data are publicly accessible through the main data portal (http://geocollections.info), custom API, and a number of specialised front-ends. One example of the latter is the Baltoscandian chitinozoan portal (http://chitinozoa.net), which aims to facilitate studying the diversification history of this enigmatic group and make the large Baltic collections and data more accessible and usable.

The regional database contains information on all chitinozoan taxa occurring in Baltoscandia, as well as relevant publications and most type-, cited-, and figured specimens. The occurrence data are available for more than 100 drill cores and outcrops, particularly from the eastern Baltic area. Most of these data have been used in publications, but all initial identifications have been checked and where necessary revised, forming a coherent data set for analysing the regional diversification pattern.

The public web portal allows searching for taxa, references, localities, samples and individual specimens by various criteria. Where available, links and digital images are included in the query results. In case of georeferenced localities, distribution maps are provided and a tool for automatic generation of range charts, exportable to desktop drawing programs, is available. For analysing chitinozoan diversity patterns the system allows generation of input files for CONOP9 quantitative stratigraphic analysis. The latter has proved very efficient in producing high-resolution taxon richness curves devoid of binning problems.

Various conventional diversity measures are automatically calculated for time slices based on the same data. The integrated nature of the database also allows easy access to other types of data available from the same sections; for instance, stratigraphic subdivisions, sedimentological data, K-bentonite layers and results of stable isotope analyses. The regional data show that the main diversification episode for chitinozoans in Baltoscandia falls into the Darriwilian and the peak standing diversity occurred in the Sandbian. All main crises through the Late Ordovician and Silurian show close matches with carbon isotope events. Data from the Early Ordovician and Dapingian are still very scarce and further sampling and taxonomic work are needed to fully reconstruct the early history and biogeographic links of Baltoscandian chitinozoans.

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### The Ordovician biodiversification and the circum-solar environments

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Immediately after the Cambrian turmoil, the Ordovician period witnessed the most remarkable animal diversification in the middle as well as the first mass extinction of the Phanerozoic at the end. The continuation of a base-line warm climate during the Early-Middle Ordovician was punctuated rapidly by the appearance of the end-Ordovician (Hirnantian) glaciation. Most researchers agree that this long-term change in global climate likely affected the secular change in biodiversity; nonetheless, the universal driver of such a global climate change, both warming and cooling, has not yet been identified. Widely claimed changes in atmospheric CO2 content and the associated greenhouse effect still needs solid evidence on fundamental driver/mechanism.

An alternative explanation can be explored in a much wider viewpoint, i.e. the relative position of our solar system with respect to a large dark cloud; in particular, the effect of galactic cosmic radiation (GCR) to global cloud coverage (the Svensmark effect) cannot be overlooked. The more GCR penetrates the atmosphere, the more cloud forms to block solar heat flux, i.e. to drive cooling. Recent astronomical researches enabled us to perceive a rough pattern of distribution and migration of high-energy dark clouds.

As to the Ordovician, there are two independent lines of supporting evidence from our planet for the encounter with a dark cloud; i.e., the long-term stability in geomagnetic field (Moyero Reverse Superchron) during the Early-Middle Ordovician and the occurrence of meteorite showers during the mid-Ordovician. The former likely corresponds to an intense geomagnetic shield, while the latter recorded gravitational instability around the Earth. A similar scenario was proposed for the Permian and its extinction events; the global environmental changes and relevant biodiversity shift during the Ordovician can be re-interpreted from a totally different aspect.

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#### \*What is the GOBE? - Three facets of a hypothesis

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The term "Great Ordovician Biodiversification Event" (GOBE) was coined during IGCP 410 (1997–2002). Today "GOBE" is the canonical term for the hypothesis of the existence of a distinct and unique spectacular Ordovician increase in marine biodiversity at all taxonomic levels. The GOBE hypothesis provides a strong framework to tackle major problems in the understanding of the evolutionary history of the Palaeozoic. At the same time it serves as a frame to highlight a number of open problems and conflicting ideas.

The GOBE hypothesis has three basic facets:

(1) The GOBE was distinct and unique. It is hypothesized that the diversification processes and pattern during the Ordovician differ fundamentally from earlier and later Palaeozoic radiations. The GOBE is seen as reflecting the most sustained and greatest diversity increase of the Phanerozoic, and which established a Palaeozoic diversity plateau. This view, however, is a perspective from within a specific scale. When the scale is broadened or narrowed the GOBE disappears within larger trends or in a complex succession of short-term diversifications.

(2) The GOBE was an event. An event can be defined as an episode where something unexpected occurs. In this context, it can be hypothesized that the Ordovician diversification was not a necessary consequence of the Cambrian Explosion and had (a) trigger(s) in its own right or (an) independent cause(s). The search for the cause(s) of the GOBE is a central aspect of current research programmes. Nevertheless, it remains a matter of debate if the processes that led to the diversification in the Ordovician can be readily distinguished from processes of the Cambrian Explosion.

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(3) The GOBE was an evolutionary radiation. The GOBE can be seen as an extraordinary broad taxonomic diversification. This implies underlying changes in evolutionary rates of speciation and extinction across diverse taxa. Most authors directly or indirectly assume that increased rates of speciation during the GOBE are caused by geographic differentiation or triggered by climatic changes. In some cases the GOBE is explicitly equated with adaptive radiations. Despite these assumptions, estimates of evolutionary rates unmodified by sampling biases are rarely employed and the significance of reduced extinction rates during the Ordovician remains to be tested.

### \*What do we really know about Ordovician Palaeogeography?

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Ordovician plate reconstructions have become much more sophisticated over the past decade or so, both in terms of the level of paleogeographic detail they contain, and in the quality of presentation. This increase in sophistication has come about, in part, because of improvements in reconstruction software, which enable reconstructions to be produced with 'realistic' topography and can incorporate lithofacies and faunal evidence. There has also been an increased awareness that paleogeographic reconstructions must conform to some simple plate tectonic 'rules' and must follow a logical temporal progression from older to younger time. While earlier reconstructions typically depicted only continental outlines separated by rather barren-looking oceans, more recent reconstructions are much more tightly integrated with other geological and geophysical datasets, and depict volcanic arcs and intra-oceanic islands. As a result the reconstructions look much more like modern tectonic maps, but also have some predictive power in stratigraphic correlation, and as paleogeographic templates for studying biogeography and palaeoclimate.

It is important to note, however, that even the most sophisticated paleogeographic reconstructions are only as reliable as the data that underpin them, and that all such reconstructions embed assumptions that are not always explicit or clear to the general user of such maps. Ordovician paleogeographic reconstructions are anchored by relatively reliable paleomagnetic data from Laurentia (6 poles); Baltica and Russian Platform (12 poles); Siberia (13 poles); and Gondwana (8 poles).

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These poles are not uniformly distributed through the Ordovician, and data gaps require interpolation across large spans of time. The very best studies have errors on the pole positions of about 7-8°, which translate into latitudinal uncertainties of ~  $\pm$ 4° for equatorial continents such as Laurentia and Siberia, and ~  $\pm$ 10° for continents located at mid latitudes such as Baltica. Many of the other Ordovician landmasses are represented by only one or two poles which provide a 'snapshot' of their paleogeography rather than a coherent picture. The North and South China Blocks, many of the Asian terranes, the peri-Gondwanan terranes, and the accreted terranes of South America can only be located from faunal and geological correlations, which may provide circular arguments if those same paleogeographies are used to assess biodiversity or radiation events.

Several recent Carboniferous to Cenozoic paleogeographic reconstructions have attempted to tie the locations of the eruptive sites of Large Igneous Provinces to deep mantle structures identified by seismic tomography. This may provide an element of longitudinal control in plate reconstructions that is not possible from using paleomagnetic data alone, and these correlations are now being extended as far back as the Cambrian. These methods offer considerable potential in refining Ordovician paleogeographies, but require that significant assumptions are made regarding the longevity and stability of the deep mantle structures we see in modern-day tomography.

### Graptolite fauna and biostratigraphy of the Hulo and Yuchien formations (Ordovician) in northwestern Zhejiang Province, SE China

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The Great Ordovician Biodiversification Event displays a high dichroneity, characterized by different timing and rates among different regions and fossil groups, as evidenced by many previous studies (Zhan et al., 2013). As a major member of the early Paleozoic Evolutionary Fauna, graptolites underwent rapid phylogenetic evolution, a burst of new taxa and the appearance of various morphological types of graptolites during the Middle-Late Ordovician (Zhang et al., 2008).

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In recent years, an ideal area with well-reserved graptolite faunas of Middle to Late Ordovician ages have been discovered in northwestern Zhejiang Province, which may significantly enhance our knowledge of the graptolite evolution and biostratigraphy of offshore to upper slope facies in South China. Well-exposed and continuous successions from 6 sections are characterized by dominant graptolitic shale facies intercalated with some other biofacies and yield abundant fossils. Graptolites occur abundantly in the Hulo Formation of middle-late Darriwilian to early Sandbian age and the Yuchien Formation of late Katian age, while shelly faunas dominate the late Sandbian to early Katian interval.

Altogether, 43 species of 25 genera from the Hulo Formation in the Jiumulong, Shengcun and Songtian sections and 29 species of 11 genera from the Yuchien Formation in the Pancun, Qingshibu and Langjia sections, have been identified and illustrated with taxonomic, stratigraphic and biogeographic remarks.

In ascending order, these faunas can be assigned to the following graptolite biozones: the Acrograptus ellsae, Nicholsonograptus fasciculatus, Pterograptus elegans, Jiangxigraptus vagus and Nemagraptus gracilis biozones from the Hulo Formation, and the Dicellograptus complexus and Paraorthograptus pacificus biozones from the Yuchien Formation. A refined graptolite biostratigraphy of Middle-Late Ordovician of this area has been attained and can be well correlated with its equivalents in the world elsewhere. Further study on the spatial and temporal distribution of Middle-Late Ordovician graptolites and the clear picture of graptolite systematic evolution in South China are still in progress.

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### \*Biodiversity metrics in deep time - a synthesis of taxonomic approaches

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One major product of paleontology is the description of past biodiversity and its fluctuation in space and deep time. This is famously exemplified by Sepkoski's biodiversity curves for the number of marine taxa through the Phanerozoic. These curves are derived from his global compendia of marine animal families and genera, and have been used to, and still continue to motivate a tremendous amount of paleobiological research. Among many examples, such biodiversity curves enabled identifying the major ("Big Five") mass extinctions, the three "Great Evolutionary Faunas" that sequentially replaced one another as dominant groups during the Phanerozoic, possible periodicity in biodiversity fluctuations, and also the major biodiversification events such as the "Cambrian Explosion" and the "Great Ordovician Biodiversification Event".

Because the fossil record is the only direct evidence of past biodiversity, reconstructing such curves is an important task, which has seen the development of multiple metrics to account for the various facets of biodiversity and correct for the various biases of an incomplete fossil record. Biodiversity generally refers to the variety and variability of life on Earth; this can refer to genetic variation, ecosystem variation, or species variation (number of species) within an area. In deep time, the most commonly applied approach due to its easy availability relies on the Linnæan hierarchical classification.

Here, I will review (1) the various metrics based on taxonomic frameworks, (2) how these metrics account for the different types of data (occurrence vs. abundance), for the different relative and discontinuous ranges of taxa in space and time, and for the incompleteness of the fossil record, (3) how the various facets of biodiversity are estimated (richness, evenness, similarity, community composition, origination, extinction, etc.), (4) how to analyze the resulting time series and their correlates, and (5) what are the systems available (databases, software) to compile data and perform this vast range of indices of paleobiodiversity.

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Paleobiology of Ordovician subtidal hardground communities: a contribution to the evolution and development of hard surface biotas with examples from "paleo-Pompei" horizons from the Upper Ordovician of Southern Ontario

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Subtidal marine hardgrounds with diverse encrusting and boring biotas are common in many carbonate successions but have scarcely been studied as biological communities. Our aim is to plot the distribution and relationships of these biotas, using biological and archaeological methods and concepts, to the morphology and the palaeoenvironments in which they developed. In this way we can not only compare ancient hard surface communities with modern ones but also infer the possible development and evolution of hard surface communities through time. We begin (and to illustrate our methods) with extraordinarily preserved Upper Ordovician (Katian) hardgrounds in the Kirkfield Member of the Bobcaygeon Formation, Simcoe Group, southern Ontario, Canada which offer an unprecedented opportunity for a high-resolution study of in situ fossil organisms. The hardgrounds are mounds up to several meters long with 1 to 15 cm of relief, and with sheltered overhangs, small caverns, and a hummocky lower surface. These seafloor microhabitats were colonized by a diverse echinoderm- and bryozoan-dominated community that is preserved in life position owing to mud burial events.

These unusual surfaces let us work out normally indeterminable characteristics such as community succession, microhabitats distribution, diversity comparisons between variably-sized mound "islands," and the modes of life of several enigmatic and rare echinoderms representing at least eight classes. The hardground surfaces are photographed in high resolution and reconstructed in 3D using structure-from-motion and multi-view-stereo algorithms. This approach, never before used in palaeoecological modelling, permits precise analysis of spatial distributions of fossil taxa and characterization of the hardground surface topography. These Ordovician hardground surfaces also give an insight into a time when the biosphere was undergoing an unprecedented diversification and the Earth's carbon cycle was undergoing drastic changes.

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### \*Numerical modelling of Ordovician climate

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The Ordovician (485–444 Ma) is a geological period characterized by the coincidence of a major glaciation and one of the "Big Five" mass extinction events that punctuated the Earth's history.

A new analysis of the event has focussed on three key areas: Firstly, during the Ordovician continental configuration has led to distinctive ocean dynamics, which stimulates in turn the development of climatic instability that allows global climate to cool suddenly in response to subtle changes in the atmospheric partial pressure of CO<sup>2</sup> (pCO<sup>2</sup>). Secondly, an innovative climate-ice sheet coupled model has produced the first simulation of the glaciation that is supported by geological data, in the context of a decrease in pCO2. Results show that glacial onset may have occurred as early as the Mid Ordovician (465 Ma), i.e., some 20 million years earlier than thought initially. In this scenario, climatic instability is reached during the latest Ordovician and accounts for the onset of the Hirnantian glacial maximum (445–444 Ma). Experiments conducted with a non-vascular vegetation model reveal that the origination and expansion of the first land plants significantly intensified continental weathering during the Ordovician and potentially generated the drop in atmospheric CO<sup>2</sup>.

Finally, the interactions between climate and the marine biosphere were investigated based on two complementary approaches. (i) New constraints on the palaeobiogeography of marine living communities are provided by the publication of maps showing the ocean surface circulation modelled at various pCO<sup>2</sup> levels during the Early, Middle and Late Ordovician. (ii) The relationships between climatic variations and the redox state of the ocean were studied using a Recent ocean model with biogeochemical capabilities (MITgcm). The simulations suggest partial and global oceanic anoxic events during the Katian and the early Silurian respectively. But they also show that anoxia is probably not responsible for the latest Ordovician mass extinction event.

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#### Was the Ordovician Radiation fuelled by a present-day type climate?

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Biodiversity in deep time, as well as its drivers, continue to be the subject of intense debate. Various statistical techniques have been applied to calculate the fluctuating species richness through the Phanerozoic and both extrinsic and intrinsic factors have been suggested as possible drivers. The Ordovician radiation stands out as the most dramatic period in Earth history with respect to species richness fluctuations. The initiation of this radiation during the earlier parts of the Ordovician facilitated the largest and most sustained jump in marine species richness through the entire Phanerozoic, only to be interrupted by a catastrophic, multi-phased mass extinction event during the terminal Ordovician Hirnantian Stage.

The Ordovician was long regarded as being part of a prolonged super-greenhouse interval encompassing the Cambrian, Ordovician and Silurian periods. Hence, just a decade ago, it was the consensus that the Ordovician was one of the warmest periods of the Phanerozoic. Extreme levels of pCO<sup>2</sup> were estimated, as were raging high temperatures. The main reason for the supposed Ordovician super-greenhouse originates from the fact that the period experienced intense volcanic activity possibly leading to a Phanerozoic sea level maximum. This would concur with high levels of CO<sup>2</sup> outgassing due to the chemical weathering of rocks which could not be consumed there were, for instance, no land plants to absorb the higher CO<sup>2</sup> levels. Therefore, geochemical models, such as the famous GEOCARB model, estimated pCO<sup>2</sup> levels as high as 16–20 times higher than the present atmospheric levels (PAL) – but basically without having any solid data points by which such an estimate could be calibrated against. This enigma has had some serious implications: how could the supposedly short-lived end Ordovician ice age form during runaway greenhouse conditions? A climate paradox that made this event in deep time a prime argument against the ongoing debate as to the role of man-made CO<sup>2</sup> emissions on climate change during the industrial period as the Ordovician analogue apparently shows that ice caps can form on the poles even during extremely high  $CO^2$  levels. Hence, those opposing the views of, for instance, Mr. Al Gore, have centered their arguments on this apparently scientifically impossible icehouse interval.

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Recent studies, however, suggests a very different scenario. During the last decade a growing body of notably palaeontological and geochemical evidence suggests that the Ordovician Period experienced a much colder climate than previously believed. New studies even suggest that the Ordovician radiation was intimately linked to the cooling climate and thus, as such, the Ordovician climate was perhaps quite similar to that of present day.

#### Constructing a high-resolution biodiversity curve through the GOBE interval by applying time slices based on lithostratigraphical ranges of fossil occurrences in the Paleobiology Database

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The main outcome of IGCP projects 410 and 503 has been the impressive documentation of the rise in biodiversity during the Late Cambrian - Late Ordovician interval. The temporal resolution of these data, however, are, for the greater part, binned in global stages spanning 5–6 myr at best. This, is a temporal resolution in line with analysis, such as that of Sepkoski (1981; 2002), that span the entire Phanerozoic. Whereas Sepkoski's monumental effort focused on showing the standing diversity through the Phanerozoic, the landmark papers of John Alroy and co-authors (Alroy et al., 2008; 2010) presented an updated Phanerozoic biodiversity curve based on the Paleobiology Database (PaleoDB) that further included a novel approach to account for sampling artifacts. This produced a rather different view on Phanerozoic biodiversity changes compared to the well-known Sepkoski curve. Notably of interest to the IGCP 653 project, the Great Ordovician Biodiversification Event (GOBE) was shown to be initiated in the Late Cambrian, as opposed to Sepkoski's Mid Ordovician radiation. The differences arise because counteracting for sampling artefacts was done by standardizing the samples using so-called sub-samples. However, in doing so, they were forced to bin their datasets in 10-11 myr time slices. Hence, temporal resolution was lost in the effort to gain a more realistic estimate. However, for high-precision studies on species richness through, for instance, the interval of interest to IGCP 653, this is not desirable.

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So, when asking specific questions with respect to the onset of the GOBE – such as when was the onset – should we then look to the classic Sepkoski curve based on ~30,000 genera, or, the modern estimate by Alroy and co-authors in which almost 300,000 specimens are distributed between ~19,000 genera that have been subsampled to account for sampling artifacts? Undoubtedly, the latter is more likely to represent a more realistic signal. However, the temporal resolution is better in the former.

Actually, the PaleoDB does hold the information needed to achieve a much higher temporal resolution, as all kinds of stratigraphical information associated with a given fossil collection can be entered. The data are there so to speak. However, it is somewhat difficult to extract these data. The current project therefore has tried to circumvent this issue by extracting all lithostratigraphical information that is associated with the fossil occurrences through the Early Palaeozoic that are entered in the PaleoDB, and correlate these to a set of time slices. These time slices are partitioned so that they can be globally recognized based on well-defined biostratigraphical boundaries, and so that they are relatively even in duration and of high temporal precision (with an average duration of ~2 myr), thus enabling a high-precision, sample standardized, analysis based on the PBDB of when the GOBE was initiated.

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## The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration

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In order to understand the evolution of life during Earth History, many authors have performed diversity counts of fossil organisms. The curve of Phillips (1860) was divided into three stratigraphically based marine faunas, the first of them corresponding to 'Palaeozoic life.' More than a century later, the diversity counts of Sepkoski (1978-2002) confirmed the two major radiations of marine diversity during the Phanerozoic, and clearly pointed out that the most spectacular increase of animal marine diversity at the family level took place during the Ordovician. Not only a rapid increase of the diversity was obvious, but also the dramatic changes in a palaeoecological context, with the development of the 'Paleozoic Evolutionary Fauna' in the Ordovician, that replaced progressively the 'Cambrian Evolutionary Fauna' (e.g. Sepkoski and Sheehan, 1983; Sheehan, 1996).

The term 'Great Ordovician Biodiversification Event' (GOBE) was proposed by Webby and others to identify an IGCP project (IGCP 410, 1997-2002; Webby et al., 2004a). This term is now commonly used to designate this rapid diversification of marine life. It is clear that the individual fossil groups show different curves with diversity peaks at different stratigraphic levels. Some important Palaeozoic fossil groups, such as, for example, brachiopods, show a dramatic increase of diversity during a relatively short time span in the Floian-Darriwilian (Early and Middle Ordovician) (e.g., Harper et al., 2004; Rasmussen et al., 2016). Other fossil groups, such as corals, for example, diversify much later, but also very rapidly, during the Sandbian, in the Late Ordovician (Webby et al., 2004b). On the other hand, while the spectacular Ordovician diversification in some fossil groups is clear, other organisms did not show such rapid and dramatic increases in the Ordovician, but a continuous and long-term biodiversification that, for some fossil groups, had already started in the Cambrian. Such groups include some subphyla of the echinoderms (e.g., Nardin and Lefebvre, 2010) and the phytoplankton (e.g., Servais et al., 2008).

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The GOBE was thus a (relatively rapid) radiation of marine life that obviously started in the latest Cambrian and was only interrupted by the end-Ordovician extinction. At a larger scale, the Ordovician biodiversification is, together with the 'Cambrian Explosion,' part of a longer-term radiation that commenced in the Late Precambrian and peaked during the early Devonian radiation.

The GOBE as such can thus not be regarded as a single event, but as a sum of different rapid diversity increases of planktonic and benthonic organisms at different time intervals and on the margins of different palaeocontinents. Clearly the term 'Great Ordovician Biodiversification Event' requires redefinition to keep pace with the huge volumes of new data and interpretations generated by subsequent research post Webby et al. (2004). We suggest expansion of the term's remit to encompass the radiation of all marine organisms during the entire Ordovician, whereas other radiations within this frame might be designated separately, for example the short and rapid increase of brachiopod families during the Darriwilian, as the Middle Ordovician Brachiopod Event (MOBE).

## How is biodiversity produced? Examining the influence of geography, ecology, and evolutionary processes on speciation during the GOBE

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The Great Ordovician Biodiversification Event (GOBE) was an extraordinary radiation of marine animal life that records one of the most dramatic diversity increases of the entire Phanerozoic Eon. Because the accumulation of diversity is effectively a function of the production (and subsequent continuation) of new species, it is important to examine global diversity increase as the sum of a series of individual speciation events.

In this contribution, current speciation theory developed within the extended evolutionary synthesis is reviewed based on a series of paleontological case studies. Speciation is a complex process involving multiple contributory factors, including drivers both internal and external to the species under consideration. Significantly, the primary controls on speciation in the case studies are external, environmental factors.

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Abiotic factors (tectonics, sea level, climate change) were the dominant controls on speciation, but external biotic factors (species invasions, ecosystem turnover, habitat patchiness vs. continuity) were also prominent. Notably, these external biotic factors relate to entities in the economic hierarchy that occur at higher levels than the organismal/population level where microevolutionary influences occur. Due to the discrete nature of information flow in the genealogical and economic hierarchies, the impacts of ecosystem or community-level change must be filtered to the genealogical hierarchy via organisms or populations (where deme = avatar) before resulting in the gene flow breakdown required for speciation.

The secondary controls on speciation across case studies also have commonalities. The relative breadth of a species' niche impacts species survival and adaptability during intervals of environmental change. Species with broad ecological niches display reduced levels of niche evolution and higher levels of persistence across disturbance intervals. This indicates that species-level emergent characters may play a key role in speciation dynamics and argues for the importance of species selection in determining diversity patterns through time.

The three case studies presented herein emphasize the centrality of large-scale environmental changes acting over long time scales in driving speciation and thus major patterns in biodiversity and thereby relegating microevolutionary processes to a more limited role in speciation initiation. The explicit incorporation of additional hierarchical levels and the interplay between the economic and genealogical hierarchies provides a dynamic perspective to analyze speciation. In particular, incorporation of a broader evolutionary theory with explicit consideration of abiotic environmental changes, species selection, details of species geographic ranges and niche breadth, and migration of species provides a robust framework to assess cross-faunal speciation dynamics.

Understanding the processes that produced the GOBE will require careful consideration of the oceanic and tectonic processes operating during the early Paleozoic as well as the speciation process itself. Reviewing current areas of knowledge and knowledge gaps will help facilitate discussion of future research agendas moving forward.

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Precise U/Pb zircons dates of bentonites in Ordovician reference sections in North America and Britain.

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The Ordovician contains both the Great Ordovician Biodiversity Event and one of the greatest of the Earth's mass extinctions. One problem in documenting biosphere changes during these events is the scarcity of modern precise U-Pb dating of bentonites and lavas interstratified in reference sections, which would help in both the correlation of separate biostratigraphic schemes and in their calibration to an absolute time scale.

Our study aims to systematically get more precise U-Pb zircon ages from biostratigraphically constrained bentonites and lavas in reference sections of Ordovician series, starting with eastern North America and Western Europe, which will allow the various independent series to be precisely correlated. Zircon grains in bentonites are separated with heavy minerals and the zircons U-Pb dated. Normally at least 40 individual grains are dated using the Laser Ablation-Inductively Coupled Plasma-Mass Spectrometer at the University of Texas-Austin – the youngest concordant age should give a maximum age for the eruption (a bed can not be older than the youngest thing in it - though it can be younger). Weighted mean ages, which are frequently used to date such ashes, give ages which may include older material from the volcanic pile through which the eruption came, and thus give indeterminably biased older ages, which are not only spuriously precise but inaccurate. We report here 3 U-Pb zircon ages from the Trenton Group, Ontario, Canada, and Dob's Linn, Scotland. The youngest concordant age from the top of the unmetamorphosed Kirkfield Formation in Ontario (Chatfieldian, early Katian) is 448.0 +/- 18 Ma, which fits with existing ages bracketing the Katian: the weighted mean age is too old at 466.0±3.4 Ma but corresponds with the mean age of the Red Indian Lake continental magmatic arc in the Appalachians to the east.

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At Dob's Linn, Scotland, the site of the Ordovician/Silurian Global Boundary Stratigraphic Section and Point (GSSP), the metamorphosed section gives a youngest concordant age of 402±12 Ma (weighted mean 435.6±4 Ma) for DL7, a bentonite 5 meters below the GSSP and 358.2±7.9 Ma (weighted mean 425.4±5.9 Ma) for DL24L, a bentonite 8 meters above the GSSP. These youngest ages are Devonian on the current timescales – at Dob's Linn, the current age for the GSSP is 443.8 +/- 1.8 Ma, based on an U/Pb dates from a bentonite 1.6 meters above the GSSP. We are confident that our techniques rule out contamination and the most likely explanation is that the small zircons we analyzed either suffered Pb loss, or were overgrown during low grade hydrothermal metamorphism of the sediments during the Caledonian orogeny. These Devonian ages suggest that the 443.8 +/- 1.8 Ma age may also be suspect. The Dob's Linn site is therefore unsuitable for calibrating the biostratigraphic horizons. If completed, ages from bentonites in the Mohawkian/ Cincinnatian of northeastern North America and the Llanvirn of Wales will also be reported.

## Life strategies of Cambrian brachiopods: providing the foundations for their dominance in the Ordovician

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Brachiopods are among the first animal phyla to emerge from the Cambrian explosion, rapidly diversifying to all major palaeocontinental blocks within an interval of 20 million years. The group underwent another steep diversification during the Early-Mid Ordovician and their relative abundance and diversity made them one of the most successful invertebrate groups during the early Palaeozoic. During this time brachiopods lived in a range of environments, and represented a significant component of Cambrian-Ordovician early marine ecosystems, yet information regarding their modes of life and ecology is somewhat limited.

Recent studies, primarily from the Chengjiang and Burgess Shale Lagerstätten have revealed that by the middle Cambrian (Series 3, Stage 5) brachiopods from across the phylum had already developed a wide range of ecological strategies and life modes. Cambrian brachiopods occupied distinct trophic niches on soft and hard substrates and exhibited at least four types of lifestyles: pedicle-anchoring, pedicle-attachment, free-lying and semi-infaunal.

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Despite the explosion of brachiopod genera witnessed in the Early Ordovician, with the exception of the appearance of burrowing and cementing brachiopods, life strategies of brachiopods remained largely the same, indicating that the majority of life modes observed in brachiopods had rapidly evolved and was already in place prior to the Great Ordovician Biodiversity Event.

#### Ordovician Conulariids of the Iberian Peninsula

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Conulariids (class Scyphozoa, phylum Cnidaria) are relatively rare fossils which are widely distributed in Ordovician marine strata of North Gondwana and adjacent peri-Gondwanan terranes. However, Ordovician conulariids of the Iberian Peninsula (Spain plus Portugal), then part of the Gondwanan margin, have not yet been formally described or tabulated. Our examination of samples collected throughout the Iberian Massif revealed the presence of Archaeoconularia and Pseudoconularia. Pale yellowish-brown shales of Floian age in the Barrancos Formation (Ossa-Morena Zone) of Spain yield extremely rare, small flattened specimens of Archaeoconularia sp. Darriwilian dark grey shales in six formations in the Central Iberian and Cantabrian zones collectively host rare specimens of at least two species of Archaeoconularia, one with fine nodes and the other with nodes that are coarse, and at least one species of Pseudoconularia. A third species of Archaeoconularia, characterized by very high apical angles, may also be present. A distinctive bed in Katian dark gray shales within the Cantera Formation yields at least one species of Archaeoconularia. Many specimens of Archaeoconularia from Darriwilian strata are inflated (uncompacted) and preserve the apertural region, which exhibits partial plicated closure of the oral end of the periderm. Plicated closure may have occurred in response to catastrophic burial of live conulariids.

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While taxonomically similar to Ordovician conulariid assemblages of other high latitude, Gondwanan and peri-Gondwanan localities, the Ordovician conulariid assemblages of Iberia differ from many of them, for example the Ordovician assemblages of Morocco and the Upper Ordovician assemblages of Bohemia, France and Jordan, in that they apparently do not exhibit monospecific mass occurrences. Additionally, gigantic Archaeoconularia such as those present in Morocco have not been found in Iberia. In these respects the Iberian conulariids are perhaps most similar to those of Wales (Avalonian terrane), which likewise are rare, relatively small and occur in dark gray shales.

These results extend the paleogeographical extent of a low diversity, cold-water, South polar Gondwanan/peri-Gondwanan conulariid realm, generally dominated by Archaeoconularia, which differs markedly from the low to mid latitude, mid-late Ordovician Baltic and Laurentian realms, which were characterized by substantially higher taxonomic diversity at both the genus and species levels. Additional effort should be extended to regions such as southwestern Libya, where collecting by one of us (JCG-M) in upper Katian rocks has produced fragmentary specimens of Archaeoconularia, Conularia Miller in Sowerby, 1821 and, possibly, Conulariella Bouček, 1939, previously known from Bohemia and Armorica.

This is a contribution to the projects CGL2012-39471 and IGCP 653.

## A Study on the Ultrastructure and Microscopic Pore Structure of Microfossils with Focused Ion Beam Scanning Electron Microscopy (FIB-SEM)

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Focused ion beam scanning electron microscopy (FIB-SEM) is a dual beam system which combines focused ion beam (FIB) and scanning electron microscopy (SEM) to cut samples and display real-time images at nanometer scale. FIB-SEM has been widely used to observe the pore structures of shale and in the reconstruction of three-dimensional distribution of nanometer-sized organic-matter pores in shale. Morphological and ultrastructural studies of some Palaeozoic microfossils such as chitinozoans and spores have been investigated by SEM and transmission electron microscopy (TEM).

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The two skills have limitations in the study of intra-structures of microfossils. Another key field, X-ray three-dimensional imaging techniques, has the advantage of being nondestructive, and has been adopted in the study of embryo fossils in recent years. For microfossils such as chitinozoans and acritarchs which can be found in great abundance in shales, FIB-SEM (which is destructive) can be treated as a good technique to check the inside ultrastructure and microscopic pore structure of these microfossils. We observed several kinds of microfossils from the Coronograptus cyphus graptolite Biozone in the Lungmachi Formation (Llandovery, Silurian) from a borehole in Sichuan Basin (southern China) with FIB-SEM. The investigated taxa are: the conodont Paltodus unicostatus; the chitinozoans Conochitina edjelensis and Eisenachitina inanulifera; the acritarch Leiosphaeridia sp. and the scolecodont Kozlowskiprion sp.

The results reveal that submicron-nano pores, are well developed in the analysed conodonts, chitinozoans and acritarchs. The conodont shows a dense distribution of cylindrical and ellipsoidal pores. The texture of the vesicle wall of the chitinozoan specimens are characterized by an undivided two-layer structure which is denser in the interior. The vesicle wall of the acritarch specimen is composed of disordered fibrosis structures. Pores inside the acritarch vesicle are well connected with each other and are submicron to nanometer in size. No obvious pores are found in the vesicle of the scolecodont taxon. Disparities of micro-pores in different microfossil groups shown in this study will help to explain the cause of organic pore heterogeneity.

#### Ordovician stable carbon isotope stratigraphy in the Tarim Basin, NW China, and its palaeogeographic implications

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The Tarim Basin, located in northwestern China, represents one of China's major palaeoplates. The palaeogeographic position of the block in the Ordovician, however, is debated. In this study we present biostratigraphically controlled stable carbon isotope data from some 600 samples spanning almost the entire Ordovician, in order to provide a tool that can be used for future chemostratigraphic correlations.

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The data correlate well with the results from South China, and several major global  $\delta^{13}$ C excursions such as the MDICE (Dw2/3), SAICE (Sa2), GICE (Ka1), and Whitewater excursion (Ka4) are documented for the first time from the Tarim Basin. Major sedimentary gaps are identified based on an integration of the chemostratigraphic results and graptolite and conodont biostratigraphy: (1) in the lower Floian between the Penglaiba and Yinshan formations, (2) in the upper Darriwilian to lower Sandbian between the Dawangou and Saergan (or Kanling) formations, and (3) in the latest Sandbian between the Kanling and Qilang formations, as well as (4) between the Tumuxiuke and Lianglitag formations. The mid-upper Ordovician rocks recording high  $\delta^{13}$ C values have been deposited during transgressive or highstand intervals, whereas the regressive intervals are mostly missing. This results in a stacking of several positive excursions, and thus it seems guite likely that chemostratigraphic correlation without biostratigraphic control may produce misleading results, especially for shallow-water carbonates. A comparison of the stratigraphic sequences in Tarim, North China and South China suggests that the three blocks may be close to each other in the northeastern peri-Gondwanan region during the Ordovician, and that the Kuangsian Orogeny, which initiated in the Sandbian in South China, also significantly affected Tarim and North China and resulted in the stratigraphic gaps of similar ages.

## **Poster Presentations**

#### GOBE provides new enrolment mechanisms in trilobites

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Enrolment in trilobites was a defence strategy against predators but also against unfavourable environmental conditions. Recent studies demonstrate that Cambrian trilobites already had a very efficient enrolment mechanism. Nevertheless, these trilobites had few enrolment structures or interlocking devices. Such devices allowed them to enrol using two different styles: 1) Sphaeroidal-type with the pygidium resting under the cephalon, and 2) spiral-type with the pygidium tucked beneath the cephalon and, therefore, not visible when the trilobite is enrolled. This scenario of only two enrolment types suddenly changed in the Ordovician. Cambrian genera had on average

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16% of the total known interlocking devices, whereas Ordovician genera had on average 28% of the total known interlocking devices. As a result of this increase in the percentage of interlocking devices, both main enrolment types (i.e. spiral and sphaeroidal) were modified into a number of new types and subtypes during the Ordovician.

Herein we present 3D modelling of two familiar Ordovician trilobites from Gondwana and Avalonia: Neseuretus and Placoparia. Neseuretus displays an "unrolled spiral enrolment-type" while Placoparia shows a new enrolment-type in Ordovician times, the "inverted spiral enrolment". Unrolled spiral enrolment is a subtype within the spiral enrolment type. This is because the spiral is partly unrolled, so that part of the pygidium is visible even in the fully enrolled animal. The inverted spiral type resembles the sphaeroidal type but differs from the latter in the fact that terminal pygidial lobes reached the vincular pits on the dorsal side of the cephalon.

Preliminary results of the 3D modelling provide two different kinematics for both trilobites. Whilst Neseuretus encloses its body with very low constant angles (between 16.5 and 17.2 degrees) between adjunct segments, the angles between adjunct segments of Placoparia are higher and range between 20 and 28 degrees. Different enrolment types of these two trilobites explain the difference between low and high angles. Fitting the pygidium beneath the cephalon is a short-haul, while allocating the pygidium on the top of the dorsal surface of the cephalon is a longer-haul. Comparison between the kinematics of Neseuretus and a typical Cambrian trilobite with spiral enrolment-type (JE, unpublished data) demonstrates that Cambrian trilobites needed to flex gradually every single segment to place the pygidium beneath the cephalon. However, a constant angle is needed to achieve a spiral partly unrolled. This allows a faster movement to enclose the body. On the other hand, enclosing the body spirally inverted prevents open gaps in the trilobite exoskeleton. These facts coincide with the GOBE and are clearly an advantage against new predators, such as cephalopods and fishes, which appeared and diversified in the same period.

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Upper Middle Ordovician – (?)lower Upper Ordovician conodonts from offshore Kårehamn wind park, north-east Öland, Sweden

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A new collection of upper Middle Ordovician (Darriwilian) - perhaps extending into lower Upper Ordovician - conodonts is taken from the offshore P4 well (56058'47.9"N, 17o1'11.9"E). The core of the P4 well is of high quality, complete, 40 m long and 12 cm in diameter. The P4 well was drilled 4 to 5 km just off and to the east of the small fishing village Kårehamn, north-eastern coast of the Swedish island Öland, in the preparation for the construction of the offshore Kårehamn wind park - the largest offshore wind park in Sweden. The succession of the upper 20 m of the P4 core is composed of mainly grey limestone referred to the Folkeslunda, Furudal and Dalby limestones, where the Folkeslunda Limestone conformably overlies the grey to vague-red Seby Limestone. Today, the Folkeslunda and Dalby limestones are barely exposed on Öland and are best known from older borings (i.e. Böda Hamn, Gammalsby and Skärlöv borings), whereas a tongue of the Furudal Limestone is exposed at the now abandoned Källa quarry and referred to the locally named Källa Limestone. The transgressive strata are mainly composed of mud-dominated carbonate facies and argillaceous partings and represent a deepening upward succession, whereas the uppermost part of the core is characterized by a falling stage. The grey limestones yield abundant, diverse and characteristic conodont faunas and 20 samples have been investigated from them. Currently 17 genera and 23 species have been identified, comprising the nominate taxa Pygodus serra, Eoplacognathus robustus, Eoplacognathus lindstroemi and Pygodus anserinus.

Associated taxa are Baltoniodus prevariabilis, Sagittodontina kielcensis, and species of Costiconus, Panderodus, Protopanderodus, Dapsilodus, Drepanodus, Drepanoistodus and Semiacontiodus. Periodon aculeatus, Decoriconus, Erraticodon and Triangulodus are present - but rare. These characteristic assemblages are referred, respectively, to the Pygodus serra (with two subzones) and Pygodus anserinus conodont zones of the Baltoscandian conodont zonal system. The succession from the core of the P4 well and the conodont faunas are similar to those known from the Böda Hamn core situated ca. 40 km to the north of Kårehamn.

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However, the Kårehamn P4 well is the first record investigated from the offshore of eastern Öland and thus provides important new information to the upper Middle Ordovician succession and biostratigraphy of Öland and in turn allows for precise comparisons with the coeval successions of Baltoscandia.

## Phytoplankton dynamics during the Great Ordovician Biodiversification Event (GOBE): project outline

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Most early Palaeozoic acritarchs are thought to represent a part of the marine phytoplankton and therefore may constitute a significant element at the base of the marine trophic chain during the 'Cambrian Explosion' and the subsequent 'Great Ordovician Biodiversification Event.' It has been argued that a higher concentration of phytoplankton in the early Palaeozoic oceans triggered the major evolutionary events and had an important impact on metazoan diversification. Servais et al. (2008, 2016) argued that the evolution of the phytoplankton triggered a 'plankton revolution' through the Cambrian–Ordovician boundary interval at the beginning of the GOBE. The expanding and increasingly diverse phytoplankton could have served as food for the developing zooplankton, but also for various clades of suspension feeders and detritus feeding organisms.

Ordovician acritarch occurrences have been recorded in a great number of studies. However, the Ordovician radiation of the acritarchs is far from being completely understood, because the datasets are not yet comprehensive. Servais et al. (2004) reviewed the Ordovician acritarch literature and plotted the number of scientific publications on a palaeogeographical map in order to document the areas and regions that have been studied in detail and those that still need further investigation. Only three areas are so far sufficiently well analysed to allow the drawing of diversity curves. Vecoli and Le Hérissé (2004) produced a curve with the acritarch diversity of North Africa (a part of the margin of Gondwana in high latitudes). Li et al. (2007) and Yan et al. (2011) provided the diversity trends for the phytoplankton from South China. Hints et al. (2010) presented the biodiversity patterns of Ordovician marine microphytoplankton from Baltica and compared them with other fossil groups and sea-level changes.

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Here, we present a new research project, based on a PhD research programme, to analyse the phytoplankton dynamics during the Great Ordovician Biodiversification Event, following the publication on the Cambrian by Nowak et al. (2016) : « Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity. » Similar to the Cambrian project, we propose to reconstruct taxonomic diversity trends that can be compared with the biodiversity of marine invertebrates during the GOBE. We will attempt to compile a complete database and calculate various diversity indices at global and regional scales. The stratigraphic bins should be as precise as possible, and follow the Ordovician time-slices.

## RNames – A new stratigraphical database and a tool for occurrence based palaeobiological analyses

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What is RNames? RNames (http://rnames.luomus.fi/) is a relational database linking stratigraphic names with each other that are considered to be time-equivalent or time-overlapping. Stratigraphic names are named units that represent specific time intervals. There are different types of units, such as chronostratigraphic, biostratigraphic, and lithostratigraphic names. Even an absolute time tag of a unit can be considered as a specific type of name. In our database we consider all these types as "name qualifier". One name can have several qualifiers, such as the "Trenton", which can be a lithostratigraphic unit, the "Trenton Group" and a regional chronostratigraphic unit, the "Trentonian". The combinations of name and qualifier exist in a specific geographic area. In our database the name, the qualifier, and the location form together a "structured\_name" For each structured\_name exist many published opinions of how it relates to other names. There are thousands of opinions expressed in the literature, which together result in a very complex network of relations. RNames is a database in which all these relations are compiled by reference.

What is RNames for? (1) The main utility of RNames comes when structured\_names should be correlated with other structured\_names by specific criteria, such as the most actual opinion, or the best compromise between conflicting opinions, or the biostratigraphy only. The relations compiled in RNames allow for queries based on

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explicit criteria (called "rules" herein). We query via MySQL and R. Currently three R scripts exist by which the structured names of Rnames are correlated to main Ordovician chronostratigraphic time frames (Ordovician Global Stages; Stage Slices; Time Slices). The resulting lists are published at http://rnames.luomus.fi/. The R code and the rules of the queries will be published separately in the near future. (2) The structured\_names compiled in RNames can be matched with stratigraphic names in other databases, such as the Paleobiology Database (https://paleobiodb.org). We did this and as a result have for the first time a high-resolution time binned (Global Stages, Stage Slices, and Time Slices) list of all Ordovician fossil genus occurrences (c. 86.000) compiled in the Paleobiology Database.

Who can use the data and contribute? Currently the database is restricted to names of the Ordovician Period and only three correlation lists are published. In the near future additional search features will be successively added and it is planned to expand the stratigraphic range of the database. RNames will be opened to collaborators when it is citeable. A paper with initial research results is in preparation.

## Extrinsic factors controlling the GOBE: new evidence from the slope facies of the Argentine Precordillera

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The Great Ordovician Biodiversification Event (GOBE), the major diversification episode of marine life in Earth history, is frequently considered as a combination of intrinsic (biological) and extrinsic (environmental) factors. Regarding the latter, the global distribution of Middle Ordovician megabreccias and debris flows has been related to destabilization of continental margins by meteorite impacts or earthquakes associated to plate-tectonic processes, such as terrane accretions or riftings, which produced environmental perturbations that favoured the GOBE intrinsic mechanisms. Therefore, a precise biostratigraphic scheme is essential to temporally adjust the disorganised sedimentary deposits. As such, the age of the Los Sombreros Formation at the continental slope and rise of the Argentine Precordillera is controversial, frequently argued as Ordovician or either Devonian, based on the complex structure and the inherent reworked character of its components. Furongian, Tremadocian, and late Floian conodont elements have been recovered from the slope facies, frequently associated

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with middle Darriwilian specimens (Lenodus variabilis and Eoplacognathus pseudoplanus zones). The recent record of specimens referable to the Hirsutodontus simplex Subzone of the Cordylodus intermedius Zone (upper Furongian) and from the Macerodus dianae Zone (upper Tremadocian) in gravity-flow deposits with synsedimentary deformation features from the Los Sombreros Formation imply that a slope connected the carbonate platform to the east with a deep-water (oceanic) basin to the west at least since late Cambrian times. The new conodont data presented is consistent with episodic extensional tectonic processes that controlled the development of the Precordilleran passive continental margin during most of the Furongian-Middle Ordovician, despite an elevated flux of extraterrestrial material that cannot be neglected during the Darriwilian, as observed in the Precordillera platform and several thousand kilometres away from coeval horizons in Scotland, Sweden and central China.

## New evidence of predator-prey relationships in the planktic ecosystem during the GOBE: A report of a suggested predator of graptolites

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A new discovery in the lower Martinsburg Formation (Late Ordovician) near Harrisburg, PA has uncovered evidence of Burgess-type soft-tissue preservation revealing a rare glimpse of a planktic ecosystem comprising enigmatic cone-shaped organisms and associated graptolites. The simple shape of these enigmatic fossils, along with the slight structural alteration of the Martinsburg Fm (silica-rich cleavage artifacts causing minor degradation of minute features) has made assigning taxonomic affinity challenging. However, the fossil's biotic association, sedimentological setting, and temporal placement, suggests the organism's affinity. Their resemblance to modern thecosome pteropods (cm scale bathy-pelagic gastropod predators) includes similar body plan, morphology, and mode of preservation. Despite these similarities, these fossils are unlikely to be related to true pteropods, which have a sparse fossil record with first occurrences in the latest Mesozoic (radiating after the K-Pg extinction).

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However, molecular clock studies suggest that Opisthobranchia (includes the clade Thecosomata) could have originated as early as the mid-Paleozoic. Here, we propose that these non-shelled homoplastic gastropod forms are 'pseudopteropods' that evolved as graptolite predators during the expansive emergence of epifaunal suspension feeders during the Great Ordovician Biodiversity Event.

#### Late Ordovician ostracods from Anticosti Island, eastern Canada

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Within the lower Palaeozoic succession of Anticosti Island, the Late Ordovician Ellis Bay Formation contains a particularly rich and well-preserved podocope ostracod fauna preserved in shelf deposited mudstones and limestone. Here I illustrate some of the key ostracod morphologies, record their stratigraphical ranges, and suggest ways in which the ostracods might be used to explore environmental change during the Late Ordovician.

# Early to Middle Ordovician diversification dynamics while simultaneously modeling sampling probabilities and palaeoenvironmental dependence: updates after 1.5 decades.

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The timing and extent of changes in biodiversity have to be accurately estimated if we want to understand processes leading to the dramatic increase in biodiversity during

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the Great Ordovician Biodiversification Event (GOBE). The palaeontological data we have available for estimating biodiversity are biased and incomplete. Hence, when using these data to estimate diversity changes, we need to explicitly consider the incompleteness of the fossil record, as well as sampling biases. Capture-mark-recapture (CMR) approaches explicitly take variable sampling probabilities into account. In addition they allow us to understand how palaeoenvironmental factors may affect diversity and/or sampling through covariate modeling. For instance, sampling and diversification differences amongst habitats can be detected, if present.

Here, we illustrate how we will apply CMR approaches to palaeontological data using Ordovician data from the Paleobiology Database (PBDB). Our plan, in essence, is to re-visit Connolly and Miller's studies (Paleobiology 2001, 2002), using new data and introducing new models. Our new estimates will provide insights in how different taxa contributed to the GOBE on a global and a palaeocontinental scale. By doing this, we will get a better temporal and spatial understanding of the patterns of the GOBE. These results will enable us to tease apart possible triggers or drivers of the GOBE.

## A Gondwanan perspective for the onset of the GOBE: preliminary brachiopod alpha-diversity data from the Iberian Peninsula

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The Cambrian Explosion and the "Great Ordovician Biodiversification Event" (GOBE) represents one of the greatest rises in marine biodiversity during the history of the Earth. Recent studies suggest that both events may in fact be part of a single, large-scale radiation. Thus, the onset of the GOBE likely has its roots within Cambrian Period (Servais et al., 2016). So far, three major diversification pulses have been recognized during the GOBE. The first diversity increase occurred during the latest Cambrian – earliest Ordovician (Floian Stage). The second happened during the Darriwilian, when global marine species richness tripled. Finally, a third pulse culminated in the Katian. Studies that specifically focus on brachiopods further document this stepwise succession of radiations. These reach a peak during the Katian, just prior to the Hirnantian extinctions. Detailed brachiopod species richness data are now available from three of the major palaeogeographic regions during the Ordovician (Baltica, Laurentia, China). However, as of yet, little focus has been on the high-latitude regions within Gondwana.

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Therefore, species richness data from these regions presently remains almost unknown. Here, we present a brachiopod alpha-diversity curve from the microcontinent of Iberia. We compiled all available brachiopod data from this region through the Cambrian "Series 3" to the uppermost Katian interval. The species richness data was compiled based on the literature, as well as our own field observations. Our preliminary results show a rapid rise in diversity going from two species in the Dapingian/lower Darriwilian interval to 19 in the middle–upper Darriwillian (D. murchisoni–H. teretiusculus zones, Dw2–Dw3 stage slices).

This significant burst in brachiopod diversity corresponds to the second diversity pulse of the GOBE and may be correlated with the diversity increase observed in the lower-middle Darriwilian (L. variabilis-Y. crassus zones) of Baltica (Rasmussen et. al., 2007) and the H. holodentata Zone in Laurentia (Trubovitz and Stigall, 2016). A second brachiopod diversity increase is seen in the middle Katian of Iberia. The extrinsic or intrinsic causes behind the first diversity increase observed in Iberia are under investigation, but the second one was likely triggered by the global warming event, known as the Boda event and its related factors, such as the development of carbonate platforms, the heating of the oceanic waters and the sea level rise (Colmenar, 2015 and references).

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## **Ordovician By The Lakes**

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