

Zooming in on the GOBE

2020 Virtual Annual Meeting of IGCP 653

Christian Mac Ørum Rasmussen, Alycia L. Stigall, Arne Thorshøj Nielsen,
Svend Stouge & Niels H. Schovsbo (Eds)

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International Geoscience Programme Project 653: The onset of the Great Ordovician Biodiversification Event

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Table of Contents

1. INTRODUCTION.....	6
2. CONFERENCE SCHEDULE.....	7
3. ABSTRACTS	11

1. Introduction

Welcome online!

So, things did not really work out the way we had hoped they would. We were supposed to have held the official Closing Meeting of [*IGCP project 653: the onset of the Great Ordovician Biodiversification Event*](#), planned as a 'physical event' in the same manner the network has done the preceding four years, only this time it should have been in Copenhagen. And we were looking forward to welcoming you all here. However, 'something happened' and we were suddenly in the unthinkable situation that schools, universities and even national borders were closing. And kept being so for months. In other words, an impossible situation to go ahead with the planning of a normal conference. We were therefore forced to postpone the official closing meeting entitled [*GOBEnghagen: a Baltic perspective on the role of the GOBE*](#). First, we postponed it to September. Now, it is provisionally postponed until May 2021, pending the global development of the COVID-19 pandemic.

Instead of an official closing meeting, an additional, virtual meeting named [*Zooming in on the GOBE*](#) were quickly organized and scheduled to take place on the same September dates as the GOBEnghagen meeting. The 2020 Closing Meeting therefore turned into a Virtual Annual meeting in the hopes that we may still close this successful IGCP-network as a physical meeting in Copenhagen in 2021.

From the first discussions among the IGCP Co-PI's in early June about a virtual event to now, things have moved quickly forward. A 'conference-hungry' network has jumped on to this idea with an overwhelmingly positive response: 45 presentations from all over the world and more than 200 participants have registered, making this the largest meeting held within the IGCP Project 653 community so far.

We are excited to offer this virtual conference. The online environment provides a framework to develop an inclusive conference. The removal of the barrier imposed by travel and registration fees has allowed participants from many countries that have not been able to participate in IGCP 653 meetings previously. Presenters span over some 17 time zones and several continents and the topics reveal a vibrant community that may have been forced to stay at home during the greater part of 2020, but certainly have continued to produce excellent, exciting research.

We hope that you all will enjoy four days of technical sessions, presenting the latest GOBE-research.

GO BE ONLINE!

2. Conference Schedule

Speakers are noted with *. Keynote presentations are in bold and orange. Times are provided at UTC+). For conversion to your local time, visit <https://timeanddate.com>.

Monday, September 7th: Diversity, evolution, and stratigraphy

Session 1. Moderator: Christian M.Ø. Rasmussen			
Time (UTC)		Speaker	Title
1	12:00	Welcome and official opening of meeting	
2	12:20	Rebecca L. Freeman*	Late Cambrian BIMEs, Vicariance, and Extinction: Patterns in Laurentian Linguliform Brachiopods
3	12:40 Keynote	Adriane R. Lam*, Sarah L. Sheffield and Nicholas J. Matzke	Estimating dispersal and evolutionary dynamics in diploporan blastozoans (Echinodermata) across the Great Ordovician Biodiversification Event
4	13:10	Alycia L. Stigall*	How did invasion events promote evolutionary and ecological change during the Great Ordovician Biodiversification Event?
5	13:30	Fernando J. Lavié* and Juan Luis Benedetto	New contributions on the paleobiogeography of linguliform brachiopods from Ordovician of the Precordillera Argentina
6	13:50	Olev Vinn*, Mark A. Wilson, Michał Zatoń and Mikołaj K. Zapalski	GOBE and escalation in symbiosis between large colonial animals and their endobionts
	14:10	COFFEE BREAK	
Session 2. Moderator: Alycia L. Stigall			
Time (UTC)		Speaker	Title
1	14:30	Arnaud Bignon*, N. Emilio Vaccari, Beatriz G. Waisfeld and Brian D.E. Chatterton	Reassessment of the Order Trinucleida and its phylogeny and systematics at familial level
2	14:50	Aske Sørensen*, Arne T. Nielsen, Nicolas Thibault, Zhengfu Zhao, Niels H. Schovsbo and Tais W. Dahl	A cyclostratigraphic analysis of the Late Cambrian Alum Shale
3	15:10	Birger Schmitz*	The breakup of the L-chondrite parent body, its signature in mid-Ordovician sediments in Baltoscandia and the precise timing relative to the Ordovician biodiversity expansion
4	15:30	Marcelo G. Carrera*, Gustavo G. Voldman, Matías J. Mango and Galina P. Nestell	Early–Middle Ordovician Alcyonacean (octocoral) sclerites from the Argentine Precordillera
5	15:50	Tais W. Dahl* and Susanne K.M. Arens	Five major ecological stages during early terrestrialization may distinguish the role of life on Earths atmospheric composition
6	16:10	Christian M. Ø. Rasmussen*, Nicolas R. Thibault, Jan. A. Rasmussen, Svend Stouge, Oluwaseun Edward, Marie-Louise Siggard-Andersen, Mikael Calner, Arne T. Nielsen and Niels Schovsbo	An astrochronological timescale through the GOBE provides Baltic intra-basinal insights on climate and richness

Tuesday, September 8th: Paleontology, oxygenation, and climate

Session 1. Moderator: Arne T. Nielsen			
Time (UTC)		Speaker	Title
1	6:00	Yan Liang*, Olle Hints, Joseph Bernardo, Daniel Goldman, Jaak Nõlvak, Peng Tang and Wenhui Wang	Re-explore the biological affinity of chitinozoans: evidence from morphological variation and exceptional specimens
2	6:20	Juwan Jeon*, Kun Liang, Stephen Kershaw and Yuandong Zhang	Two ‘Silurian-type’ stromatoporoid genera from the Upper Ordovician Beiguoshan Formation of North China, and their tectonic and faunal implications
3	6:40	Francesc Pérez-Peris, Lukáš Laibl*, Lorenzo Lustri, Pierre Gueriau, Jonathan B. Antcliffe, Orla G. Bath Enright and Allison C. Daley	A new Lower Ordovician nektaspid euarthropod from Morocco
4	7:00	Sofia Pereira*, Isabel Rábano, and Juan Carlos Gutiérrez-Marco	The trilobite assemblage of the “Declivolithus Fauna” (Katian) of Morocco: a review with new data
5	7:20	Andrej Ernst* and Hans Arne Nakrem	Early Katian bryozoan faunas of Baltoscandia
6	7:40 Keynote	Joseph P. Botting*, Lucy A. Muir, Stephen Pates, Luke A. Parry and Lucy McCobb	A new, open marine Middle Ordovician Lagerstätte from Wales
	8:10	COFFEE BREAK	
Session 2. Moderator: Tais W. Dahl			
Time (UTC)		Speaker	Title
1	8:30	Qijian Li*, Oliver Lehnert, Rongchang Wu, J. Park, Kun Liang, S. Yu, Y. Mao and Lin Na	The palaeokarst in the Xiazhen Formation (Late Ordovician): a record of the mid-Katian glaciation in South China
2	8:50	Susanne K.M. Arens* and Tais W. Dahl	No consensus on timing and cause of Paleozoic oxygen rise – a case for the significance of respiration.
3	9:10	Álvaro del Rey*, Mikael Calner, Christian M. Ø. Rasmussen and Tais W. Dahl	Understanding the relationship between the global oxygenation state of the oceans and the Great Ordovician Biodiversification Event
4	9:30	Duy Pham* and Jeong-Hyun Lee	Keratose sponge–microbial carbonate consortium in the columnar “stromatolites” and “thrombolite” mounds from the Lower Ordovician Mungok Formation, Yeongwol, Korea
5	9:50	Yuefeng Shen*, Fritz Neuweiler and Le Zhang	Ordovician diversification of calcimicrobes and calcareous algae
6	10:10	Sigitas Radzevičius*, Wiesław Trela, Andrius Garbaras, Donatas Kudžma and Marius Užomeckas	Integrated bio and chemostratigraphy of the upper Homerian (Silurian) from the Kleczanów PIG - 1 well (Holy Cross Mountains, Poland)

Wednesday, September 9th: Paleoeology and geochemistry

Session 1. Moderator: Cole T. Edwards			
Time (UTC)		Speaker	Title
1	14:00	Jana Bruthansová* and Heyo Van Iten	Ordovician conulariids as host organisms for epibionts (Prague Basin, Czech Republic)
2	14:20	Benjamin F. Dattilo*, Roy E. Plotnick and Dale Springer	Tracking the water depth habitat range of <i>Megalograptus</i> through the Katian from the Appalachian Basin to the Cincinnati Region
3	14:40	Sarah R. Losso* and Javier Ortega-Hernández	Recent developments in the paleobiology and taphonomy of trilobites from the Walcott-Rust Quarry (Upper Ordovician)
4	15:00	Ceara K.Q. Purcell* and Alycia L. Stigall	How do ecological niches evolve during Ordovician environmental change? A test using Laurentian brachiopods
5	15:20	Alejandro Corrales-García, Jorge Esteve and Matheo Lopez-Pachon	Burrowing assessment of <i>Iliaenus sarsi</i> Jaanusson, 1957 and <i>Megistaspis extenuata</i> (Wahlenberg, 1821) from the Middle Ordovician of Sweden
6	15:40 Keynote	Jorge Esteve* and Matheo López-Pachón	Swimming and enrolment in a mesopelagic trilobite: new ecomorphological advantages in the Middle Ordovician Ocean
16:10 COFFEE BREAK			
Session 2. Moderator: Sarah R. Losso			
Time (UTC)		Speaker	Title
1	16:30	Joshua B. Zimmt*, Steven M. Holland, Seth Finnegan and Charles R. Marshall	Recognizing pulses of extinction from clusters of last occurrences: A Late Ordovician case study
2	16:50	Cole T. Edwards*, Clive M. Jones, Page C. Quinton and David A. Fike	Oxygen isotope ($\delta^{18}\text{O}$) trends measured from conodont apatite using Secondary Ion Mass Spectrometry (SIMS): implications for paleo-thermometry studies
3	17:10	Richard M. Robinet*, John T. Haynes, Steven A. Leslie and Achim D. Herrmann	Examining the Climate/Tectonic Implications of Sandbian-Katian Environmental Change in the Southern Appalachians Utilizing K-bentonite Apatite Phenocryst Geochemical Correlations
4	17:30	Richard G. Stockey*, Feifei Zhang, Noah J. Planavsky, Junxuan Fan, Lin Na, Seth Finnegan, Cole Edwards, Sam Goldberg, Matthew Saltzman, Tais W. Dahl, Kristin Bergmann, Erik A. Sperling, Hua Zhang, Ying Cui, Xiangdong Wang and Shu-zhong Shen	On ocean anoxia and the onset of the Great Ordovician Biodiversification Event
5	17:50	Erik A. Sperling*, Michael J. Melchin, Tiffani Fraser, Richard G. Stockey, Una C. Farrell, Liam Bhajan, Tessa N. Browne, Devon B. Cole, Benjamin C. Gill, Alfred Lenz, David K. Loydell, Joseph Malinowski, Austin J. Miller, Stephanie Plaza-Torres, Beatrice Rodewald, Alan D. Rooney, Sabrina A. Tecklenburg, Jacqueline M. Vogel, Noah J. Planavsky and Justin V. Strauss	An exceptional record of early Paleozoic redox change from the Road River Group, Yukon, Canada
6	18:10	Gustavo Voldman* and Aldo L. Banchig	Conodonts from siliciclastic rocks: a case study from the Portezuelo del Tontal Formation, Ordovician of the Western Argentine Precordillera

Thursday, September 10th: Diversity, paleoecology, and isotopes

Session 1. Moderator: Björn Kröger			
Time (UTC)		Speaker	Title
1	10:00	Tomas Želvys*, Antanas Brazauskas, Aandrej Spiridonov, Donatas Kudžma, Andrius Garbaras and Sigitas Radzevičius	Preliminary report on $\delta^{13}\text{C}_{\text{carb}}$ isotope excursion through the Silurian of Jočionys-299 borehole, Eastern Lithuania
2	10:20	David A.T. Harper*, Jiayu Rong, Bing Huang and Rongyu Li	Hirnantian brachiopods in time and space: New insights on an old fauna
3	10:40	Richard Hofmann*	Why was there no GOBE in Western Laurentia?
4	11:00	Bertrand Lefebvre*, Elise Nardin and Martina Nohejlová	The great Ordovician diversification of echinoderms: deciphering a complex global signal
5	11:20	Thomas Servais*, Borja Cascales-Miñana and David A.T. Harper	Early Palaeozoic diversifications: ‘explosions’ and ‘events’ or a continuum of change?
6	11:40	Ursula Toom*, Olev Vinn and Olle Hints	Ordovician Bioerosion Revolution on Baltica
	12:00	COFFEE BREAK – Astrogeobiology Laboratory tour and Ordovician fossil meteorites with Birger Schmitz	
Session 2. Moderator: Richard Hofmann			
Time (UTC)		Speaker	Title
1	12:20 Keynote	Amelia M. Penny*, Olle Hints, André Desrochers and Björn Kröger	Marine substrate change and biodiversity in the Ordovician
2	12:50	Farid Saleh*, Orla G. Bath-Enright, Allison C. Daley, Bertrand Lefebvre, Bernard Pittet and Jonathan B. Antcliffe	Untangling the ecology and fossil preservation knot for Paleozoic biotas
3	13:10	Björn Kröger* and Amelia M. Penny	Early – Middle Ordovician seascape-scale aggregation pattern of sponge-rich reefs across the Laurentia Palecontinent
4	13:30	Olle Hints*, Aivo Lepland, Merlin Liiv, Tõnu Meidla and Leho Ainsaar	Paired carbonate and organic carbon isotope records from the Ordovician of Estonia: local, regional or global drivers?
5	13:50	Bertrand Lefebvre* and Yves Candela*	Introducing the next IGCP-proposal
6	14:00	Closing ceremonies	

3. Abstracts

No consensus on timing and cause of Paleozoic oxygen rise – a case for the significance of respiration

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Geochemical proxies and models suggest O₂ levels began a rise to near modern levels in the Ordovician. Earth system models suggest the O₂ increase was driven by the long-term O₂ source, represented by organic carbon burial in marine sediments. This would have demanded an increase in the riverine P flux to the oceans. Arguably, non-vascular plants could have preferentially weathered P relative to bulk rock weathering and caused the oxygenation. We propose an alternative solution in which the emergence of land plants put a brake on a major O₂ sink by promoting respiration in soils. To test this, we developed a 1D reactive transport model to quantify the effect of respiration in soils on the oxidative weathering sink on land. The solution depends on uplift rate, porosity and distribution of labile soil organic matter. Yet, our model shows that respiration indeed does stave off oxidative weathering, causing a rise in atmospheric O₂ until it reaches a level, where oxidative weathering again balances the O₂ source. Our results suggest that land plants played a significant role in bringing up atmospheric O₂ levels – not only by sourcing O₂, but also by reducing its major long-term sink.

Reassessment of the Order Trinucleida and its phylogeny and systematics at familial level

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The Superfamily Trinucleoidea is an iconic trilobite group of the GOBE, but its evolutionary history has received little attention. In recent decades, this group has been included in the Order Asaphida. In a recent phylogenetic analysis, we have shown that this group is more closely related to Ptychopariida. As Ptychopariida is paraphyletic, we suggested that trinucleoids should be raised to ordinal status, the Trinucleida, with the aim to define a higher-level taxon based only upon synapomorphies. A preliminary phylogenetic study raised several unexpected issues with regard to definition of some of the families within Trinucleida. Most important among these was that the Family Alsataspididae, as currently defined, is paraphyletic. Hence, we performed another phylogenetic analysis, focussed on this family. Two suborders appeared, Trinucleina encompassing the families Orometopidae, Raphiophoridae and Trinucleidae; and the other one being Dionidina, including the families Dionididae, Heterocaryonidae, Myindidae, and Alsataspididae. Interestingly, because of some similarities to trinucleids, we included several Harpetida in the analysis. As might be expected, most of the harpetids stay close to the outgroup taxa, but the basal family of harpetids, the Heterocaryonidae is included in the analysis as a basal member of the Dionidina. The family Liostracinidae is more closely related to Ptychopariida, so we have excluded them from the Trinucleida, making it easier to posit the characters of a hypothetical ancestor of the Order Trinucleida. These analyses offer new views of the evolutionary history of trinucleid trilobites. Indeed two lineages (suborders of Trinucleida) evolved rapidly during the Late Cambrian/Early Ordovician generating several families that are less diverse when compared to earlier views of Alsataspididae (that included all of these families, excepted Heterocaryonidae). Moreover, our analysis suggests that the bilaminar perforated fringe evolved separately (more than once) in distinct taxa (Trinucleidae, Dionididae and Myindidae). These taxa, despite having similar cephalic morphological innovations did not share equal evolutionary success. Indeed, only Trinucleidae and Raphiophoridae (the latter does not have a perforated fringe but does have a marginal suture) are characteristic of the GOBE (Whiterock fauna). Most derived Dionididae were not as successful (Ibex 2 fauna). However, the systematics of this family need to be examined in more depth and detail to understand better its evolutionary history. Myindidae bearing these features (perforated bilaminar fringe with marginal suture) are restricted to only two genera (Ibex 1 fauna).

A new, open marine Middle Ordovician Lagerstätte from Wales

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Ordovician Konservat-Lagerstätten are extremely diverse in palaeoenvironment, taphonomy and palaeoecology, ranging from modified Burgess Shale-type faunas in the Early Ordovician to a suite of shallow-marine marginal deposits, unique lagoonal facies, and deep-water assemblages. There are, however, no Middle or Late Ordovician examples of diverse soft-bodied faunas representing an offshore, open marine environment that can be compared with the Burgess Shale-type faunas or illustrate ecological development in this habitat during the main phase of the GOBE. The closest we have is the diverse suite of deposits in the Darriwilian to basal Sandbian Builth Inlier of Wales (Llanfawr Lagerstätte, Holothurian Bed and Llandegley Rocks), each of which is limited in either diversity or preservational quality. These faunas were preserved in a volcanic island setting, and together with numerous other localities in the area, provide a uniquely broad palaeoecological picture, but preserve only part of the total diversity.

A new Builth Inlier locality, Castle Bank, yields a rich exceptionally preserved fauna from the Darriwilian *Didymograptus munchisoni* Biozone. It is stratigraphically and environmentally intermediate between Llandegley Rocks and the Holothurian Bed, and represents an open marine environment near storm wave base. The small quarry exposes siltstones and substantial volcanic ash layers, the sediments composed of laminated, densely graptolitic background beds and (in a two-metre-thick interval) slightly coarser event beds. Numerous exceptionally preserved sponges occur through this interval, in both background and event layers. Most of the other exceptionally preserved organisms are limited to thin event layers in a particular interval that is 30 cm thick.

The fauna is very diverse, including dozens of sponge species (often with soft tissue remains as well as full articulation of skeletons), exceptional preservation of other biomineralised animals such as fully articulated trilobites (with limited soft tissue mineralisation), palaeoscolecid, asterozoans and a conodont bedding-plane assemblage, but also diverse non-biomineralised worms, arthropods, cnidarian-like and lophophorate-like animals, and problematica. Soft tissues such as cuticle and labile tissues (e.g. tentacles) appear to be preserved as Burgess Shale-type carbon films and/or pyrite, but taphonomy is yet to be investigated in detail. The brachiopods, trilobites and graptolites are typical of the time interval, and suggest a normal marine community. Castle Bank therefore offers a unique opportunity to study an open marine Ordovician community that lived during the the peak of the biodiversification interval.

Ordovician conulariids as host organisms for epibionts (Prague Basin, Czech Republic)

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Approximately 4% of just over 5000 examined conulariids from Ordovician formations in the Prague Basin (Czech Republic) exhibit invertebrate epibionts and/or attachment scars. The commonest epibionts are craniid brachiopods followed by bryozoans and edrioasteroids. Less abundant are monoplacophorans and diverse holdfasts. Epibionts occur on *Anaconularia anomala*, *Archaeoconularia*, *Conulariella* sp., and *Pseudoconularia grandissima*, though predominantly on *A. anomala* and *Archaeoconularia* from open shelf deposits in certain Upper Ordovician formations, in which conulariids are substantially more abundant than in other formations. Except for monoplacophorans, epibionts occur on the external surface of the conulariids, in some cases with brachiopods, bryozoans, or edrioasteroids present on all four faces. Edrioasteroids and brachiopods on some specimens are preferentially centered on or near the facial midline. These results highlight the importance of Ordovician conulariids as biological substrates, especially in Perunica and South Polar Gondwana, and indicate that encrustation occurred both on live individuals and on dead ones. The corners and midlines influenced the settlement and subsequent growth of brachiopods and edrioasteroids, and conulariids bearing these epibionts were buried catastrophically. The record of conulariid epibionts indicates that the increase in their diversity during the initial stages of the GOBE was very low.

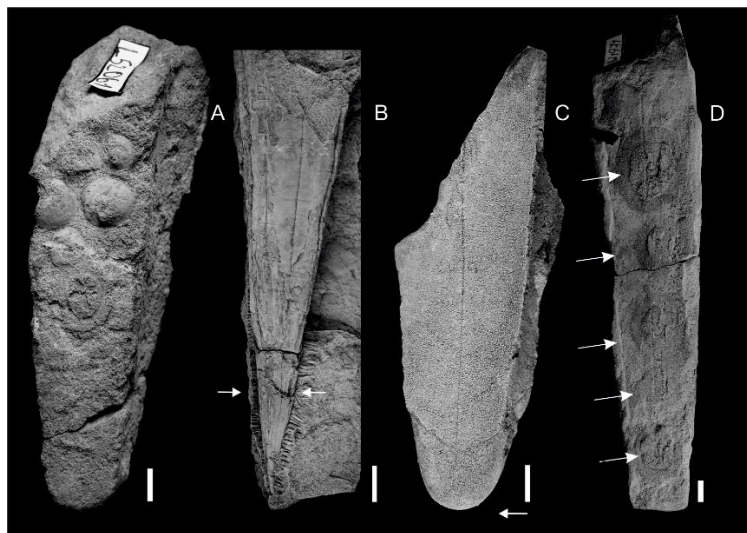


Figure 1: A - Craniid brachiopods and edrioasteroid on the faces of *Anaconularia anomala*, Sandbian, NML 52061. B - Trepastome colony encrusting *Archaeoconularia fecunda*, Sandbian, NML 51780, C - Cystoporate bryozoans fully covering a schott-bearing specimen of *A. anomala*, Sandbian, NML 37814. D - Edrioasteroids encrusting *Archaeoconularia munita*, Sandbian, NML 21971.

Early–Middle Ordovician Alcyonacean (octocoral) sclerites from the Argentine Precordillera

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Alcyonacean octocoral sclerites present a highly incomplete stratigraphic distribution, probably reflecting biases in the fossil record related to the difficulties of finding and extracting these tiny calcareous fossils. Its oldest established record is the form genus *Atractosella* Hinde, present in the Llandovery-Wenlock (Silurian) of Gotland (Sweden), England, Scotland, and from an erratic boulder in Germany. In the present contribution, we analyse the occurrence of silicified Early and Middle Ordovician alcyonacean sclerites in the San Juan Formation of the Argentine Precordillera. The sclerite assemblage consists of spindle morphotypes, ranging from slightly fusiform elongated, rod-like forms to oval or strongly ellipsoidal. They are ornamented with small regular granules or tubercles, and some sclerites are linearly connected by their tips. The recovered sclerites occur in different stratigraphic levels and localities of the Argentine Precordillera and therefore could represent associations of different species or genera. Notwithstanding that, they provide clear evidence on the Floian (Early Ordovician) occurrence of Alcyonacean sclerites in the fossil record. The variable morphologic characteristics of these fused and unfused Alcyonacean sclerites are present in the suborders Alcyoniina (soft corals) and the Scleraxonia (horny octocorals). Although any of these groups assignment is still speculative at this state of knowledge, it may imply that these basal forms could be elements of a possible Alcyoniina-Scleraxonia stem-group.

Burrowing assessment of *Iliaenus sarsi* Jaanusson, 1957 and *Megistaspis extenuata* (Wahlenberg, 1821) from the Middle Ordovician of Sweden

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During the GOBE there was a change from a general Cambrian morphology towards a greater variety of morphological novelties. A good example of this is the variety of cephalic forms found in various groups of trilobites, seemingly allowing them to occupy different levels within the sediment and, therefore, different lifestyles. Nevertheless, the form-function-environment linkage has rarely been tested despite being widely known in the field of paleontology. To elucidate if these adaptations confer a functional advantage we have to mechanically assess such morphological differences.

Here we evaluate the capacity of burrowing and compare the biomechanical properties of two contemporary trilobites from the Middle Ordovician of Sweden: *Iliaenus sarsi* Jaanusson, 1957 and *Megistaspis extenuata* (Wahlenberg, 1821), which diverge enormously in their body architecture and likely in their lifestyle. While *I. sarsi* is an iconic example of an infaunal organism due to its round frontal shape, *M. extenuata* bears dagger-shaped anterior border which may be adapted to infaunal lifestyle. However, given that biomechanical assessment by means of Finite Element Analysis (FEA) of these organisms has not been carried out yet, so far, we can only hypothesise the real function of these forms. Therefore, we have carried out a 3D FEA in order to understand the function behind these morphological designs. FEA shows that the design of *I. sarsi* was very effective to withstand greater stresses than *M. extenuata*. In fact, *M. extenuata* shows a very poor design for burrowing and seems likely that the dagger-shaped anterior border had other functions rather than burrowing.

Five major ecological stages during early terrestrialization may distinguish the role of life on Earth's atmospheric composition

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On geological time scales the atmosphere is constantly recycled through the biosphere and Earth's interior. Yet, the atmosphere has supported life for more than 3.5 billion years demanding regulatory feedbacks at play within the Earth system. Both biological and geological processes influence the atmospheric composition and thereby the climate and oxygenation state of our planet. The colonization of land by plants, fungi and animals took place in several stages that each may have increased Earth's O₂ levels and acted to cool the Earth's climate by drawing down atmospheric CO₂. Here, we call attention to five distinct ecological stages associated with the emergence of new traits in land plants:

1) non-vascular plants, 2) vascular plants with lignified tissue, 3) plants with shallow roots, 4) arborescent vegetation with deep and complex root systems, and 5) seed plants. A review of the existing paleoenvironmental records is consistent with a profound transition from a hot and poorly oxygenated atmosphere to a world more similar to the modern Earth. Further scrutiny of the available records and relative timing of O₂ rise and CO₂ drawdown during these ecological shifts will constrain the processes that have governed Earth's atmospheric composition.



Figure 1: Atmospheric CO₂ and O₂ constraints from models and proxies during the five major ecological stages of early terrestrialization.

Tracking the water depth habitat range of *Megalograptus* through the Katian from the Appalachian Basin to the Cincinnati Region

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Megalograptus from the Cincinnati region and Appalachian Basin is the best-known Ordovician eurypterid and thus key to understanding the environmental history of the clade. Previous discussions of the habitat of eurypterids have focused on the question of whether they lived in open marine, restricted-marine, or even non-marine environments. Given that they are consistently associated with normal marine faunas, it is uncontroversial that megalograptids generally occupied open marine environments *sensu lato*.

Since the 1960s more effort has been made to differentiate these Ordovician open marine environments into finer subdivisions. Using sedimentological and paleontological criteria the Ordovician ramp can be divided into peritidal, lagoonal, barrier/biohermal, shoreface, shallow subtidal, and deep subtidal. Recent sequence stratigraphic work has resulted in multiple thin time slices throughout the Cincinnati Ordovician. This allows finer environmental and temporal placement of *Megalograptus* occurrences.

Original localities and stratigraphic descriptions are precise and most occurrences in the Cincinnati can thus be located to the nearest few meters stratigraphically. Megalograptid occurrences projected onto this high-resolution sequence stratigraphy show a consistent association between megalograptids and the lagoon-barrier-to-shoreface facies. Appalachian Basin occurrences in the Martinsburg Formation appear to be of comparably shallow depths based on fossil evidence.

The megalograptid lineage apparently invaded the Cincinnati region from the Appalachian region. Martinsburg occurrences are dated Edenian or Maysvillian, whereas the earliest Cincinnati occurrence is in the later part of the Maysvillian. Both the Cincinnati Region and the Appalachian basin received sediments from the Taconic Orogen and in that way they are the same sedimentary system. During the Edenian the Cincinnati sea was far too deep for megalograptids, but the Appalachian Basin region was shallow. These suitably shallow water habitats prograded from the Appalachians to the Cincinnati basin –and occurrences of megalograptids track the facies northward and westward through the Cincinnati region, with the older being further SE, and the younger being further NW.

Megalograptus is often reconstructed as a fierce predator. The thin and fragile spines of their grasping appendages make it unlikely, however, that they fed on robust prey. Instead, they are well-suited for trapping gelatinous organisms, such as jellyfish, which should have been abundant in the near-shore waters of the Ordovician.

Understanding the relationship between the global oxygenation state of the oceans and the Great Ordovician Biodiversification Event

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The Middle Ordovician witnessed the most rapid and sustained increase in marine family- and genus-level diversity in Earth's history: the Great Ordovician Biodiversification Event or GOBE. And with such an event, the question is simple: what caused this dramatic increase in marine diversity? And although a very straightforward question, it is fundamental in the understanding of the relationship between life and the environment. How does life relate to the environment? What causes life to suddenly change so much that the face of Earth was never the same anymore? Several hypotheses have been proposed to explain why during this particular time interval life unfolded; including one, planetary cooling leading temperatures in the oceans more favorable for life to thrive. And two, an increase in atmospheric oxygen because animal life requires oxygen to survive; thus, more oxygen would have allowed more life. In this project we assess how the oxygenation state of the oceans could have been related to the diversification event by analyzing the uranium (U) isotope composition of a marine carbonate sequence across the Middle Ordovician within the Baltoscandian paleobasin. A shift towards heavier U isotopes would indicate a more oxygenated state of the oceans and vice versa. Our results show that the recorded U isotope signatures remained stable (no observable important swings) the time interval leading to the maximum diversification rate. An increase in global oxygenation was not related to the rapid increase in diversification. A relative stable redox landscape accompanied the ecological change that led to the highest diversification rates of the GOBE.

Oxygen isotope ($\delta^{18}\text{O}$) trends measured from conodont apatite using Secondary Ion Mass Spectrometry (SIMS): implications for paleo-thermometry studies

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The oxygen isotopic compositions ($\delta^{18}\text{O}$) of minimally altered phosphate minerals and fossils, such as conodont elements, are used as a proxy for past ocean temperature. Phosphate is thermally stable under low to moderate burial conditions and is ideal for reconstructing seawater temperatures because the P-O bonds are highly resistant to isotopic exchange during diagenesis. Traditional bulk methods used to measure conodont $\delta^{18}\text{O}$ include multiple conodont elements, which can reflect different environments and potentially yield an aggregate $\delta^{18}\text{O}$ value derived from a mixture of different water masses. *In-situ* spot analyses of individual elements using micro-analytical techniques, such as secondary ion mass spectrometry (SIMS), can address these issues.

Here we present 108 new $\delta^{18}\text{O}$ values using SIMS from conodont apatite collected from four Lower to Upper Ordovician stratigraphic successions from North America (Nevada, Oklahoma, and the Cincinnati Arch region). The available elements measured had a range of thermal alteration regimes that are categorized based on their conodont alteration index (CAI) as either low (CAI = 1–2) or high (CAI = 3–4). Though individual spot analyses of the same element yield $\delta^{18}\text{O}$ values that vary, most form a normal distribution around a mean value when spot locations are optimized. Variability of individual spots can be minimized by avoiding surficial heterogeneities like cracks, pits, or the near the edge of the element, and the uncertainty can be improved with multiple (≥ 4) spot analyses of the element. Samples from closely spaced beds or multiple conodonts from the same bed also have variable mean $\delta^{18}\text{O}$ values of individual elements (0.0 to 4.3‰, median 1.0‰), regardless of low or high CAI values. Oxygen isotopic values measured using SIMS in this study reproduce values similar to published trends, namely, $\delta^{18}\text{O}$ values that increase during the Early–Middle Ordovician and plateau by the mid Darriwilian (late Middle Ordovician). Twenty-two of the measured conodonts were from ten sampled beds that had been previously measured using bulk analysis. SIMS-based $\delta^{18}\text{O}$ values from these samples are more positive by an average of 1.7‰ compared to bulk, consistent with observations by others, who attribute the shift to carbonate- and hydroxyl-related SIMS matrix effects. This offset has implications for paleo-temperature model estimates, which indicate a 4°C per $\delta^{18}\text{O}$ (‰) ocean water temperature correlation. Although this uncertainty precludes precise paleo-temperature measurements, it is valuable for identifying spatial and stratigraphic trends in temperature that might not have been previously possible with bulk approaches.

Early Katian bryozoan faunas of Baltoscandia

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Bryozoan diversity increased during the Ordovician and peaked in the late Sandbian. The early Katian bryozoan communities prospered on the shelf of Baltica, but suffered heavy losses at the end of this time interval. Studied localities of the early Katian age in Estonia, Sweden, and Norway exhibit high diversity and abundance of bryozoans represented by various stenolaemate groups. Bryozoans occupied various biotopes including reefs. The taxonomic composition of the studied bryozoan communities shows low level of endemism. Among other factors, the low level of geographical isolation seems to be responsible for the mass extinction at the end of the early Katian.

Swimming and enrolment in a mesopelagic trilobite: new ecomorphological advantages in the Middle Ordovician Ocean

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Trilobites were marine arthropods with an extraordinary capacity to adapt to their environment. They occupied most ecological niches as early as the Cambrian, including benthic and pelagic environments. Despite a few redlichiids and ptychopariid examples, pelagic environments were not widely occupied by active trilobite swimmers until the Ordovician. Trilobites reached their maximum ecomorphological compass among pelagic trilobites during the Ordovician, where we have found a high number of pelagic and mesopelagic trilobites with non-streamlined and well-streamlined morphology. We focused our work on a well-streamlined trilobite, the Ordovician cyclopygid *Microparia*. In contrast to the nekto-benthic *Hypodicranotus*, which displayed a secondary loss of enrolment capacity, this little trilobite retained the capacity to encapsulate its body perfectly (i.e. enroll) like many benthic trilobites. However, most of the living free-swimming arthropods are unable to enroll, with the exception in some larvae, such as those of the mantis shrimp, or in some copepods which show an incomplete enrolment style (i.e. no encapsulation). We examine whether enrolment represented an advantage for a mesopelagic trilobite like *Microparia*, and how it did so. A numerical simulation based on computational fluid dynamics (CFD) was used to explore the hydrodynamic behavior of *Microparia* and give a new framework for understanding the ecomorphological evolution of well-streamlined trilobites. The results show very low drag coefficients in all simulations in a prone position suggesting that this trilobite was a good swimmer. In enrolled position drag coefficients are still lower, because when the trilobite is enrolled the shape becomes markedly oval, a form that is very efficient to reduce drag. On the other hand, the oval shape of *Microparia* generates no lift ($C_L \sim 0$), therefore currents neither push *Microparia* towards the sea surface nor to the seafloor; its wakes are symmetric. These results show high stability in the horizontal plane (parallel to the flow currents) and suggest that *Microparia* could be almost stable in the water column when it was enrolled. This represents a new way to use enrollment in trilobites, not only for protection against predators or environment but also as a hydrodynamic tool to maintain stability within the water column.

Microparia, as well as several other cyclopygids, shows important morphological novelties (e.g. stream-lined body, eyes do not project and presence of “snout”) but also takes advantage of a “plesiomorphic” behavior (i.e. enrolment) to occupy a special ecological niche in the mesopelagic habitat.

Late Cambrian BIMEs, Vicariance, and Extinction: Patterns in Laurentian Linguliform Brachiopods

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Global biodiversity plateaued in the wake of the Cambrian Explosion before dramatically increasing during the Great Ordovician Biodiversification Event (GOBE). Recent studies (e.g., Stigall et al., 2017) have demonstrated that accumulation of species was enhanced through an alternating regime of speciation through dispersal (biotic immigration events; BIMEs) and vicariance, speciation occurring as ranges are subdivided.

In Laurentia, this interval is characterized by alternating periods of extinction and immigration and periods of regional-scale diversification among trilobites, the so-called “biomeres”. The same pattern is seen in the linguliform brachiopods of this interval. Ongoing studies examine two of these biomere boundaries, the Steptoean/Sunwaptan, and the Sunwaptan/Skullrockian. The study areas contrast paleoenvironments in Laurentia, including the deep outer shelf environment of Utah and Nevada, and the higher-energy shallow shelf environment of Texas and Oklahoma.

In all study areas, and at both boundaries, the biomere boundaries involve complete turnover of linguliform species. At the lower Steptoean/Sunwaptan boundary, globally distributed species then temporarily replaced the now-extinct endemic fauna in the outer shelf environment, while new endemic species appeared in the cratonic environment, potentially demonstrating the role of both BIME’s and vicariance in rebuilding biodiversity after this extinction event. The second Sunwaptan/Skullrockian biomere extinction event again produced complete turnover of the linguliform brachiopods at apparently the same time as trilobite extinction, but during this interval the replacement faunas were cosmopolitan in all study areas. These repeating patterns of BIMEs and vicariance are essentially identical to patterns seen in many clades later during the Middle Ordovician. This pattern suggests that at least some critical factors for producing biodiversity were in place earlier than the GOBE, even though repeated extinction events that depleted alpha and beta diversity contributed to lower gamma diversity.

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Hirnantian brachiopods in time and space: New insights on an old fauna

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Distributional analysis of Hirnantian brachiopod faunas, based on a new, comprehensive dataset from over 20 palaeoplates and terranes, confirms that within the Hirnantian Stage there were two successive faunas: 1. The widespread and diachronous *Hirnantia* Fauna related to a glacial acme in the early–mid Hirnantian; shallow, deeper and deep-water communities diversified in much more complicated environmental conditions than hitherto envisaged; and 2. The Edgewood–Cathay Fauna thrived during post-glacial, warmer, shallow-water regimes with both carbonate and siliciclastic facies in low latitudes during the late Hirnantian–early Rhuddanian. This faunal succession tracks two climatic perturbations, one with a glaciation, associated with climatic cooling and a global low-stand, during which the *Hirnantia* Fauna flourished, almost globally, and a second characterized by melting ice, global warming, and sea-level rise (with global anoxia), aligned to the development of the Edgewood–Cathay Fauna and the repopulation of the seas by animals adapted to warmer water. Intense climate changes, sea-level fluctuations, and oceanographic ventilation and anoxia, had important roles in brachiopod evolution through the Hirnantian extinctions; higher originations of new taxa may be linked to intervals of accelerated speciation due to extreme climatic conditions.

Paired carbonate and organic carbon isotope records from the Ordovician of Estonia: Local, regional or global drivers?

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Carbon stable isotope excursions are widely used as correlation tool in Ordovician stratigraphy as well as for reconstructing climatic and environmental history. The mechanisms behind individual carbon isotopic excursions are, however, not fully understood and their geographic scope, facies dependence and synchronicity need further assessing. The Baltic region has been a reference area for studying Ordovician carbon isotope records for several decades. Most previous works in the region are based on data from bulk carbonate rocks ($\delta^{13}\text{C}_{\text{carb}}$), whereas the stratigraphic variability of the isotopic composition of organic matter ($\delta^{13}\text{C}_{\text{org}}$) has remained poorly studied.

Here we document paired carbonate and organic carbon isotope records from the Middle Ordovician to basal Silurian from Estonia. The primary aims of this work were to: (1) assess the variability and stratigraphic usefulness of the $\delta^{13}\text{C}_{\text{org}}$ curves, in comparison with $\delta^{13}\text{C}_{\text{carb}}$ data from the same sections and records from other regions; (2) examine the offset between the carbonate and organic matter isotope curves ($\Delta^{13}\text{C}$) in order to reveal any temporal trends; (3) test the spatial variation of paired isotope data within the Baltoscandian basin. For this 470 samples at c. 1 m resolution were analysed from the Lelle, Viki and Tartu cores, each characterising somewhat different facies within the Baltoscandian basin.

The $\delta^{13}\text{C}_{\text{carb}}$ curves from the three sections reveal the isotopic excursions well-known globally and/or from the region: MDICE, LSNICE (Kukruse low), GICE, Rakvere, Saunja, Moe and the prominent HICE. The $\delta^{13}\text{C}_{\text{org}}$ data show more varying patterns than $\delta^{13}\text{C}_{\text{carb}}$, ranging between c. -33‰ and -26‰. Compared to data from other regions, however, the new Estonian $\delta^{13}\text{C}_{\text{org}}$ data sets stand out by relatively small scatter. The main $\delta^{13}\text{C}_{\text{carb}}$ events can usually be identified in the $\delta^{13}\text{C}_{\text{org}}$ curves; the agreement between the two curves is particularly good in the Darriwilian and Sandbian. Starting from the Katian, the paired curves tend to show different magnitudes, and occasionally slightly diachronous nature or even opposite trends. Few $\delta^{13}\text{C}_{\text{org}}$ anomalies observed in one section only are likely related to specific facies conditions, restricted biota, or early diagenetic effects. On a basinal scale, the average $\delta^{13}\text{C}_{\text{org}}$ (as well as $\delta^{13}\text{C}_{\text{carb}}$) values increase towards deeper-water settings. The $\Delta^{13}\text{C}$ curves show an overall increasing trend by 1–2‰ in the Viki and Lelle sections, which agrees with the global data compilation and may suggest a global driver, such as change in $p\text{CO}_2$ and $p\text{O}_2$. However, a more pronounced $\Delta^{13}\text{C}$ increase occurs in the early Katian post-dating GOBE, and in places the broader trend is masked by stratigraphically constrained local/regional shifts of up to 5‰. In summary, the new paired carbon isotope records reveal mixed signatures from global changes in carbon sequestration and environments, as well as basinal trends and locally induced shifts. The latter two have limited value for stratigraphy, but may aid understanding facies changes and diagenetic environments.

Why was there no GOBE in Western Laurentia?

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Most recent studies have shown that, on a global scale, the main phase of the Great Ordovician Biodiversification Event (GOBE) can be tied to the Dapingian and early Darriwilian substages. The Upper Cambrian to Middle Ordovician Pogonip Group of the Basin and Range Province (western U.S.) represents one of the most fossiliferous shallow marine successions that straddle this critical time interval.

Superb outcrop conditions in the Ibex Area in western Utah allow for almost continuous sampling of benthic communities throughout much of Lower and Middle Ordovician strata. It thus holds great potential to shed light on early phases of the GOBE. Quantitative palaeoecological analysis of mainly benthic communities was used to reconstruct diversity patterns on the local community level.

First of all, the late Dapingian to Darriwilian Kanosh Formation fails to record a notable within-clade diversification among benthic groups (i.e. brachiopods, trilobites, gastropods), which is seen elsewhere in Laurentia and worldwide.

Palaeocommunities are fairly uniform and low in alpha (within community) diversity and beta (differential diversity between communities) diversity. These patterns are most readily explained by comparable harsh local environmental conditions that are prevalent in the Kanosh system including high siliciclastic input (accompanied by possible salinity fluctuations), and intertidal to supratidal habitats.

The stratigraphically older Wah Wah (late Floian) and Juab (early Dapingian) Formations show that this low diversity (and hence the delayed radiation) may be deeper rooted in larger scale environmental controls. The communities of the Wah Wah Formation are the most diverse of the Pogonip Group but decline towards the upper part of the unit. The transition to the overlying Juab Formation, which straddles the Floian–Dapingian boundary, is marked by a notable drop in species richness and a complete turnover in both trilobite and brachiopod faunas. The fact that much of the brachiopod diversity before this boundary “event” was aggregated at low systematic levels (genera and families) provides evidence for an early stage of the GOBE already taking place in the late Floian in western Laurentia. The hypothesized Floian–Dapingian boundary event could have reset the nascent emergence of fairly diverse, typically Palaeozoic-type communities. Data from Baltica show a similar pattern suggesting that the Floian–Dapingian transition could be of interregional significance.

However, the diversity loss may not be perceived as “extinction” because the diversity has been low throughout the Early Ordovician anyway. The analysis of local communities reveals that such events, in fact, reset the clock for intra-clade diversification which, in sum, could explain the damping of diversity dynamics before the sudden radiation of clades since the middle Ordovician. Probable environmental controls that would explain this pattern are recurrent anoxic phases and generally high sea surface temperatures in Early Ordovician shallow marine waters.

Two ‘Silurian-type’ stromatoporoid genera from the Upper Ordovician Beiguoshan Formation of North China, and their tectonic and faunal implications

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Stromatoporellid *Simplexodictyon* and clathrodictyid *Plexodictyon* are widely distributed in Silurian and Devonian strata. They are considered to be typical ‘Silurian-type’ stromatoporoids, and thought to have originated in the Wenlock and Ludlow epochs, respectively. In this study, we report these two genera from the Upper Ordovician Beiguoshan Formation at Tiewadian, on the southern margin of the Ordos Basin, Shaanxi Province of North China. The age of the formation is estimated to be middle Katian, judging from the presence of conodont *Taoqupognathus beiguoshanensis*, as well as fossil assemblages including corals, brachiopods, and graptolites. This finding represents the earliest known record of these genera, and extends significantly their stratigraphic ranges to earlier times. Their incomplete fossil records in North China, i.e. the missing of Silurian and Devonian occurrences, are here interpreted as largely due to the regional sea-level fall in response to the tectonic uplift of North China during the Late Ordovician, known as the Huaiyuan Epeirogeny, which led to the absence or erosion of the contemporary stratigraphic records. In addition, our taxonomic restudies show some of the previously described Ordovician-Silurian ‘*Clathrodictyon*’ from peri-Gondwana might not be true ‘*Clathrodictyon*’ and require further taxonomic investigations. The discovery of *Simplexodictyon* and *Plexodictyon* from the Upper Ordovician adds to our knowledge on the early diversification of clathrodictyids and clathrodictyid-stock (i.e. stromatoporellids) taxa, and is crucial for a better understanding of the early evolutionary history and paleobiogeography of stromatoporoids.

Early–Middle Ordovician seascape-scale aggregation pattern of sponge-rich reefs across the Laurentia Paleocoast

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During the late Cambrian – Early Ordovician the predominant non-microbial reef builders were sponges or sponge-like metazoans. During the Early – Middle Ordovician interval metazoans became dominant reef builders. A comparison of sponge-rich reefs from eight sites of the Laurentia paleocoast demonstrates that reef deposition pattern changed across reef – seascape scales in this time interval. The oldest reefs in this study were deposited during the earliest Tremadocian and contain abundant microbialites. They grew directly on hard substrate and formed meter-thick coalescent banks and sheets. Younger reefs are commonly bioturbated with less microbial textures. These late Tremadocian – Middle Ordovician reefs form discrete patches and clusters and their growth is not exclusively associated with underlying hard substrate. Three different seascape level reef growth patterns can be distinguished: (1) mosaic mode of reef growth, where reefs form a complex spatial mosaic dependent on hard substrate; (2) episodic mode, where patch reefs grew exclusively in distinct unconformity bounded horizons within non-reefal lithological units that have a much larger thickness; and (3) belt-and-bank mode, where reefs and reef complexes grew vertically and laterally as dispersed patches largely independent from truncation surfaces. We speculate that the early – Middle Ordovician trend from mosaic to belt-and-bank mode of reef growth was partly driven by intensified bioturbation.

A new Lower Ordovician nektaspid euarthropod from Morocco

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Nektaspids are non-biomineralized euarthropods that were at the peak of their diversity during the Cambrian Period. Post-Cambrian nektaspids are a low-diversity group with only a few species described so far. *Tariccoia tazagurtensis* is a new species of small-bodied nektaspid (of the family Liwiidae) from the Lower Ordovician Fezouata Shale of Morocco. This species is characterized by a sub-circular cephalon with pointed genal angles and with a marginal rim; a thorax consisting of four tergites, the 1st and 2nd of which are overlapped by the cephalic shield; and by a pygidium with its anterior margin curved forwards, a rounded posterior margin and a long medial keel that does not reach the posterior pygidial border. *T. tazagurtensis* differs from the type (and only other known) species from the Ordovician strata of Sardinia (Italy), *Tariccoia arrusensis*, mainly in its cephalon and pygidial morphologies. The two specimens of *T. tazagurtensis* preserve remains of the anterior part of the digestive tract, which are comparable to the ramified digestive glands seen in the Cambrian nektaspids *Naraoia* and *Misszhouia canadiensis*. The rare occurrence of *T. tazagurtensis* in the Fezouata Shale and the distribution of other liwiids suggest that these liwiids were originally minor members of open-marine communities during the Cambrian, and migrated into colder brackish or restricted seas during the Ordovician.

Estimating dispersal and evolutionary dynamics in diploporan blastozoans (Echinodermata) across the Great Ordovician Biodiversification Event

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Robust statistical inference of early Paleozoic macroevolutionary patterns of invertebrate taxa have been primarily focused on brachiopods and trilobites. These taxa, along with other clades, have been used to infer the drivers and impacts of Ordovician diversification events, namely the Great Ordovician Biodiversification Event (GOBE). To date, echinoderm paleobiogeographic patterns have been excluded from these statistical analyses. In this study, we use a phylogenetic hypothesis of early Paleozoic diploporous blastozoan echinoderms to estimate ancestral biogeographic histories and dispersal pathways across the GOBE to infer their drivers of evolution and dispersal. The number and type of dispersal events for three Ordovician time slices that encompass the time before, during, and after the GOBE was estimated using Biogeographic Stochastic Mapping (BSM) within BioGeoBEARS. The best-fit model incorporated jump dispersal, and indicated several source regions for blastozoans, with deep nodes within the tree indicating a Gondwana or Baltic origin. From the BSM analysis, the most dispersal occurs in the Early to Middle Ordovician, with several events occurring between Gondwana and Laurentia, and Laurentia and Baltica. There are reduced dispersal events within the Middle Ordovician GOBE interval, but it is clear that Baltica and Laurentia exchanged taxa during this time. During the Late Ordovician, there is again an increase in dispersal events between Baltica, Laurentia, and Gondwana. These reconstructed dispersal events indicate that oceanic gyre systems, currents, and upwelling regions were likely important factors to facilitate species movement on a global scale. Speciation events plotted against $\delta^{18}\text{O}$ and other geochemical data indicate the blastozoan speciation events are not clustered during times of global cooling, unlike speciation events for brachiopods and trilobites. Additional phylogenetic hypotheses of this group will further reveal drivers of echinoderm speciation through the early Paleozoic.

New contributions on the paleobiogeography of linguliform brachiopods from Ordovician of the Precordillera Argentina

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In the last decade, several analyzes on the biogeographic distribution of Ordovician linguliform brachiopods have been carried out (e.g. Popov et al., 2013; Holmer et al., 2016). In the present study, we reassess the biogeographic affinities of the Middle and Upper Ordovician linguliform genera recorded globally, including new data from the Precordillera of western Argentina (Cuyania terrane). Clustering analyzes and PCoA (Principal Coordinate Analysis) were performed using the Dice and Raup-Crick indices in two sets of taxa, one including the genera present in the Middle Ordovician and the other those present in the Upper Ordovician (both excluding endemic genera). Results obtained in this paper based on linguliform brachiopods mostly match with the patterns observed in other benthic groups from Cuyania (mainly rhynchonelliformean brachiopods). During the Darriwilian, many of the genera from the Precordillera show clear Laurentian and Baltic affinities, sharing with these regions at least 13 genera (excluding cosmopolitan and widely distributed taxa). Additionally, there are several genera in common with the Kazakhstani terranes. Another remarkable feature is the appearance in the Precordillera of some endemic taxa, which also have been recorded in the Famatina Range, on the western margin of Gondwana. By the Late Ordovician, however, despite the scarcity of data at the global scale (Popov et al., 2013), many genera become restricted to Laurentia and are absent in the Argentine Precordillera. This pattern may be due to the fact that at this time the Cuyania terrane was already close to the western margin of Gondwana (the so-called “pre-accretion stage”, Benedetto et al., 1999).

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The great Ordovician diversification of echinoderms: deciphering a complex global signal

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The most dramatic increase in echinoderm diversity and disparity took place during the Ordovician, with a peak of about 15 classes instead of e.g. only 5 in the latest Cambrian (Furongian) and in post-Palaeozoic seas. The global analysis of about 2,000 Ordovician echinoderm taxa recovered from over 300 areas worldwide suggests that their diversity remained relatively low from the Tremadocian to the Dapingian, before rising from the Darriwilian to the Katian, and finally collapsing in the Hirnantian. Taxonomically, this pattern largely depicts the major diversification of crinoids, which represent from 30 to 70 percent of the whole echinoderm diversity, and become, during the Ordovician, one of the major components of marine ecosystems. However, the analysis of the geographic origin of included taxa indicates a strong historical and/or sampling bias towards Laurentian faunas (e.g. North America, Scotland; 20 to 50 percent of the data), themselves largely dominated – faunistically – by crinoids. Zooming in on the situation in other well-represented areas in the database (e.g. Avalonia, Baltica, high-latitude Mediterranean Province) provides distinct regional temporal patterns of biodiversity, and especially on non-crinoid-dominated faunal compositions. However, Ordovician echinoderm faunas remain very poorly known in many other areas in the world (e.g. Australia, Central and Southeastern Asia, China, South America, Siberia). In recent years, significant sampling efforts in some areas (e.g. Morocco) have significantly modified our knowledge of some regional faunal assemblages and contributed to fill in databases, which, however, still remain largely dominated by data from a single palaeocontinent.

The palaeokarst in the Xiazhen Formation (Late Ordovician): a record of the mid-Katian glaciation in South China

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Sedimentary record and oxygen isotope data from different palaeocontinents display multiple episodes of moderate glaciation and deglaciation during Katian (Late Ordovician) times with a glacial peak in the middle Katian. In South China, the Katian palaeokarst in the Xiazhen Formation at Zhuzhai, briefly reported several years ago, was recently investigated in detail. There, the Xiazhen Formation has been re-studied and divided into four informal members: a lower limestone member, a lower shale member, a middle mixed-lithology member, and an upper shale member. The palaeokarst occurs in the top part of the middle mixed-lithology member, where karstified limestones are capped by greenish to brownish shales of the upper shale member displaying a significant sea level rise. The palaeokarstic surfaces show an irregular topography, with shale fillings in potholes and cracks descending down at least 7.5 metres. Based on new conodonts collections, the *Yaoxianognathus yaoxianensis* Zone has been confirmed in the limestones below the palaeokarst surface, corresponding in age to stage slices Ka2 and top of Ka1. This biostratigraphic result coincides with published conodont data from the type section at Tashan (Waicun), implying that the lower part of the Xiazhen Formation should be correlated to the early Katian rather than late Katian as previously assumed. High resolution $\delta^{13}\text{C}_{\text{carb}}$ data record the Kope and Fairview excursions in the middle mixed-lithology member. These chemostratigraphic data show stratigraphical overlaps between the sub-sections at Zhuzhai. Published graptolite data suggest a late Katian (Ka4) age for the upper shale member infilling the cracks and cavities cutting down from the karst surface into the underlying limestones and overlaying this surface. Thus, the time of subaerial exposure falls into the mid-Katian when the corresponding, dramatic and globally recognized glacio-eustatic sea-level fall affected and widely karstified tropical and subtropical carbonate platforms (e.g., Baltica, Laurentia).

Re-explore the biological affinity of chitinozoans: Evidence from morphological variation and exceptional specimens

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As an extinct group of cryptic organic-walled microfossils, chitinozoans widely distributed in Ordovician to Devonian marine sedimentary rocks, however, with a hitherto debated biological affinity. Since the first description in the 1930s, they have been classified as multiple groups of protists, metazoans or egg capsules of metazoans. A fungi hypothesis, possible polyphyletic origin, vegetative reproduction, and ontogenetic development have also been hypothesized, however, with less general acceptance. Over the last three decades, chitinozoans have almost exclusively been interpreted as eggs of unknown marine metazoans, possibly some wormlike animals. Nevertheless, no further discussions related to their affinity have been advanced.

In our recent study, three-dimensionally preserved specimens of *Hercochitina violana* show a highly variable morphological variation. A compiled size variation dataset of chitinozoan species and a dataset of coefficients of variation (CV) in eggs of extant aquatic metazoan have been carried out. The result shows that the magnitude of the size variation within chitinozoan species is larger than observed in fossil and modern eggs, which indicates, more plausibly, chitinozoans are not eggs. Furthermore, the previously reported abnormal specimens which preserved as “vesicle-in-vesicle” turn out to be the key specimens during the life history of chitinozoans. All of those specimens are distinguished by occupying regularity and repeatability, i.e., a complete vesicle carrying one or several “less-complete” but highly similar one(s) at the base. With more details decoded by the Field Emission Scanning Electron Microscope and X-ray micro-computed tomography, the “less-complete” specimens are verified to be or to have the potential to develop into a complete specimen, which points to a reproduction stage. Herein, chitinozoans should not be eggs, instead, they are an independent group of microorganisms.

Recent developments in the paleobiology and taphonomy of trilobites from the Walcott-Rust Quarry (Upper Ordovician)

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Trilobites are the dominant group of macroscopic euarthropods throughout the Paleozoic, and are known primarily from their biomineralized dorsal exoskeletons. Despite their impressive diversity (ca. over 20,000 described species) the appendicular ventral anatomy of trilobites is only known from 31 taxa, most of which consist of highly compressed macrofossils. In 1879, Charles Doolittle Walcott reported the preservation of trilobite appendages preserved in 3D from the Upper Ordovician Spillway Member (Rust Formation; Trenton Group) in Herkimer County, New York. Over 280 thin-sections from this site are housed at the Museum of Comparative Zoology at Harvard, most of which belong to the phacopids *Ceraurus pleurexanthemus* and *Flexicalymene senaria*. Walcott-Rust trilobites show that non-biomineralized tissues are exceptionally preserved by an isopachous rim of fibrous calcite perpendicular to the exoskeleton, and sparry calcite crystals that completely fill the void formed by the body. The occurrence of calcite had previously been attributed to a microenvironment created during decay (Brett et al., 1999). This peculiar mode of calcite preservation captures exceptional detail, including delicate structures such as exopod lamellae and endopod endites. However, the precise appendicular morphology of *C. pleurexanthemus* and *F. senaria* has been controversial given the difficulty of interpreting the preserved anatomy from obliquely-cut thin sections. Here, we provide an updated account of the work on this iconic locality, focusing on the taphonomy of soft tissue preservation, distribution of calcite preservation within the Rust Formation, and trilobite limb morphology. Extensive restudy of the thin-sections shows that calcite occurs in veins and nodules throughout the matrix, and are not isolated within the fossil specimens. Whereas all previous findings of calcite preservation were from Layer 3 in Spillway Member, new discoveries demonstrate a stratigraphically wider distribution. Comparisons of thin-sections with computed tomographic scans of partially enrolled trilobite specimens allow to better understand the orientation of the thin sections, and facilitate precise morphological interpretations. Future work will characterize the taphonomic pathway through use of elemental and isotopic analysis, compare the calcite preservation of Walcott Rust with that of the Silurian Herefordshire Biota in England, and reconstruct the 3D limb morphology of *C. pleurexanthemus* and *F. senaria*. The Walcott-Rust specimens provide a unique opportunity to study exceptional Ordovician 3D preservation of animal soft tissues.

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Marine substrate change and biodiversity in the Ordovician

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The Ordovician was a time of tremendous evolutionary and environmental upheaval, incorporating both the unprecedented marine diversification of the GOBE, and substantial changes in shallow marine environments at both local and global scales, mediated by a complex interplay between biotic and abiotic processes. Understanding how early Palaeozoic environments constrained biotic evolution is a major topic of palaeoenvironmental research, though knowledge of the magnitude and nature of the feedbacks between proliferating macroscopic life and global environments is less completely developed.

Among the regional-scale environmental changes of the Ordovician were the development of extensive shallow marine carbonate shelf environments, together with the expansion of novel habitats generated by metazoan ecosystem engineers. Drawing on data from both Baltica and Laurentia palaeocontinents, we evaluate the impact of regional substrate changes on diversity at a variety of spatial and temporal scales.

We used the Ordovician-Silurian record of the Baltic palaeobasin as a case study, using hierarchical diversity partitioning to evaluate the impacts of environmental heterogeneity and temporal turnover on brachiopod diversity patterns, using data from the Paleobiology Database and the database of the Geoscience Collections of Estonia. We find that the development of an extensive carbonate shelf in the Baltic palaeobasin during the Sandbian-Katian had a major influence over regional diversity patterns because of the relatively high heterogeneity (beta diversity) of assemblages in these carbonate-dominated environments.

The development of widespread metazoan reefs in the Baltic paleobasin occurred alongside this diversification, and imposed small-scale habitat heterogeneity on marine seascapes. The Middle Ordovician rise of metazoan reefs enhanced complexity in shallow marine environments, which can be investigated in areas of exceptional exposure. With reference to metazoan reefs of the Mingan Archipelago, Quebec, we explore the forms of seascape heterogeneity generated by this change in carbonate deposition at community scale.

Developing understanding of the interactions between environmental and faunal heterogeneity is required for a mechanistic picture the long-term development of marine ecosystems. The early Palaeozoic marks the inception of major metazoan impacts on marine environments, and developing knowledge of these links could have general implications for our understanding of the feedbacks between macroscopic life and global environmental change.

The trilobite assemblage of the “*Declivolithus* Fauna” (Katian) of Morocco: a review with new data

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The very peculiar Upper Ordovician trilobite *Declivolithus* Přibyl & Vaněk (Trinucleinae) was defined in the Voltuš Fm (Rožmitál trough) of the Czech Republic and later recognized in the High Atlas and the Anti-Atlas of Morocco. Within the Prague Basin, it occurs in the Bohdalec Fm (upper Berounian), and, putatively, in the underlying Zahořany Fm (middle Berounian). Previous records of *Declivolithus*-bearing assemblages from Morocco (Destombes 1971; Fortey & Edgecombe, 2017) were assigned to the middle Katian based on trilobite biostratigraphical correlation with the Bohdalec Fm. This unusually large trinucleid is the most conspicuous element of an assemblage occurring in the Bofloss locality, a local biofacies development of pelagic mudstones and sandstones cropping out in a small anticline, isolated by faults, in the Tizi n'Oufite area. Its stratigraphical correlation remains problematic due to the structural setting, but it probably corresponds to the upper part of the Lower Ktaoua Fm, although a correlation with the lower half of the Upper Tiouririne Fm cannot be excluded.

The assemblage is composed almost exclusively of trilobites preserved either in grey fine mudstones or in coarse-grained sandstones, with scattered representatives of graptolites, machaeridians, echinoderms and brachiopods. The “*Declivolithus* fauna” trilobite assemblage is herein revised, being dominated by *Declivolithus* and abundant cyclopygids (*Cyclopyge*, *Symphysops* and *Heterocyclopyge*), with fewer representatives of *Dionide*, *Eudolatites*, *Nobiliasaphus*, *Phacopidina*, *Prionocheilus*, *Selenopeltis* and a new species of *Ulugtella*? The preservation allows a systematic revision of some species previously known from Bohemia, but the biostratigraphical data are not definite. Although some support the previous assignment of the Moroccan assemblage to the upper Berounian, a middle Berounian age cannot be excluded. The type-locality of *Declivolithus* is also of difficult correlation, due to its location within a faulted block (Rožmitál) and has been mostly assigned to the middle Berounian due to the presence of the brachiopod *Aegiromena aquila*. Its trilobite assemblage has seven of ten species in common with the Bofloss assemblage. The recent revisions on the Upper Ordovician trilobites of Morocco suggest that this region and the Czech Republic are within the same cluster of high Gondwanan latitude. At least from Sandbian until mid Katian, the fossil assemblages of Bohemia are greatly correlated at species level with those from Morocco.

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Keratose sponge–microbial carbonate consortium in the columnar “stromatolites” and “thrombolite” mounds from the Lower Ordovician Mungok Formation, Yeongwol, Korea

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Lower Ordovician “stromatolites” and “thrombolites”, composed of keratose sponges and microbial carbonates, are reported from the Mungok Formation (Tremadocian), Yeongwol, Korea. The columnar “stromatolites” are up to 10 cm in width and height, and consist of the inner core with lower-angled (10–45°) layers that are covered by higher-angled (>45°) layers. The inner core is made up of keratose sponges alternating with microbial carbonates, whereas microbial carbonates dominantly consist of the outer cover. The “thrombolite” mounds are up to 100 cm high and 40–60 cm wide domes embedded within ribbon rocks. These thrombolite mounds comprise the keratose sponge-microbial carbonate “clots” and minor lithistid sponge-microbial carbonate “clots”. The columnar “stromatolites” formed under high-energy subtidal setting, where laminoid keratose sponges alternate with microbial carbonate and form the columns. On the other hand, “thrombolite” mounds developed under low-energy environments possibly below normal wave base, where bulbous to globular keratose sponges formed the “clots”, and microbial carbonates developed within the sponges by soft-tissue degradation, probably by sulfate-reducing bacteria. Lithistid sponges and microstromatolites developed small “clots” in between the keratosan-microbial clots.

The current study demonstrates the importance of hydrodynamic controls on overall reef morphology and configurations during the Early Ordovician. Columnar “stromatolites” represent tight laminar frame reefs, formed under high-energy environments, whereas “thrombolite” mounds are similar to cluster reefs developed in low-energy environments. Coeval lithistid-microbial reefs mainly developed under intermediate-energy conditions. The keratose and lithistid sponges rarely occur together in the reefs, suggesting that there could have been ecological or environmental factors affecting the distribution of these sponges in reef habitats. The increasing reports of keratosan-microbial consortium from the early Paleozoic successions worldwide suggest that these may be an integral component of the Great Ordovician Biodiversification Event, together with the coeval lithistid sponge-microbial consortium.

How do ecological niches evolve during Ordovician environmental change? A test using Laurentian brachiopods

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The Ordovician was a complex interval of Earth history, characterized by dramatic environmental changes including climatic shifts, sea level fluctuations, and explosive biotic diversification. In order to understand the impact these changes had on ancient ecosystems, it is necessary to investigate the temporal correlation between species ecological responses and changing environmental factors. This project addresses this complex relationship by using ecological niche modelling (ENM) to quantify patterns in Laurentian brachiopod niche occupation over the course of multiple environmental changes in the Ordovician.

ENM analysis requires taxon occurrence and environmental layer data. Brachiopod occurrence data were downloaded from the Paleobiology and iDIGBio Databases (Fig. 1). Major gaps in the records were supplemented with field investigation of under-sampled Ordovician strata. Environmental layers were created using detailed stratigraphic records published in relevant literature or collected in the field. Niche models were generated for stage-level time slices over the entire Ordovician Period using Maxent. For genera that could be modelled in multiple time slices, niches were compared among distinct intervals. The degree of similarity between models of adjacent time slices was analysed, and patterns of niche stability versus evolution were compared with contemporaneous local and global environmental change.

Patterns in niche occupation reveal that rates of niche stability differed during intervals of abiotic versus biotic environmental change. Similarly, trends in niche evolution differ between generalist and specialist taxa, particularly in response to rapid competitive pressures. The results of this study indicate that species respond differently based on different types and rates of environmental change, and suggest that major environmental changes in the modern can have similar long-term ecological results.

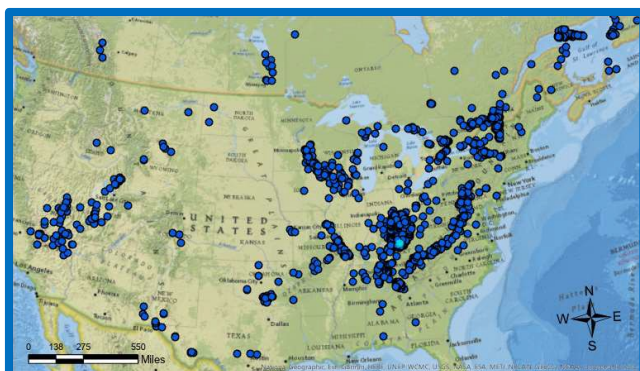


Figure 1: Occurrence data for Ordovician brachiopods downloaded from the PBDB and iDIGBio Databases. This initial dataset comprises over 33,000 discrete occurrence points.

Integrated bio- and chemostratigraphy of the upper Homeric (Silurian) from the Kleczanów PIG - 1 well (Holy Cross Mountains, Poland)

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A distinctive biotic crisis (including graptolite and conodonts) referred to as the Mulde Event was recognized worldwide in the upper Homeric of Silurian period. It has a conspicuous carbon isotopic signature referred to the middle-late Homeric glaciation and climate aridity.

New carbon isotope data have been obtained from Silurian dark shales of the Prągowiec Beds in the Kleczanów PIG – 1 borehole (depth 206 – 178 m), which is located in the southern Holy Cross Mountains (Poland). Samples for $\delta^{13}\text{C}_{\text{org}}$ analysis were collected approximately every 1 m. They were grinded and dissolved using 5 N of HCl acid to remove carbonate material, and then washed with distilled water and dried. The stable carbon isotope values from organic material were measured using Thermo Gasbench II coupled with a Thermo Delta V isotope ratio mass spectrometer.

The stratigraphy of studied well was established based on graptolites, which indicates the presence of the *lundgreni*, *parvus* - *nassa*, *praedeubeli*, *deubeli*, *ludensis* and *nilssoni* biozones.

The $\delta^{13}\text{C}_{\text{org}}$ values are stable in the lower part of investigated interval of the Kleczanów PIG – 1 borehole and rise from -31.7 ‰ (*lundgreni* Biozone) to maximum of -29.22 ‰. The maximum value of $\delta^{13}\text{C}_{\text{org}}$ is reached at the *lundgreni/parvus* biozonal boundary and falls to -30.81 ‰ near the boundary of the *nassa/praedeubeli* biozones. The $\delta^{13}\text{C}_{\text{org}}$ values rise again to -29.78 ‰ in the *deubeli* Biozone and decrease to -31.36 ‰ in the upper part of the *ludensis* biozone. There are stable values of $\delta^{13}\text{C}_{\text{org}}$ in the upper part of *ludensis* and lower part of *nilssoni* biozone, varying from -31.21 to -31 ‰.

According to these findings, the *lundgreni*, *parvus*, *nassa*, *praedeubeli*, *deubeli*, *ludensis* and *nilssoni* biozones are distinguished in the studied interval of Kleczanów PIG – 1 borehole. The thickness of the graptolite biozones are very narrow compared with those in carbonate facies (e.g. the East Baltic Basin). Both positive $\delta^{13}\text{C}_{\text{org}}$ value peaks of the Mulde Event are identified in the investigated interval of Kleczanów PIG – 1 borehole.

An astrochronological timescale through the GOBE provides Baltic intra-basinal insights on climate and richness

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Recent studies have pinpointed the onset of the Great Ordovician Biodiversification Event (GOBE) to occur within a narrow timespan of a few million years during the early–mid Darriwillian. This onset is, as such, well-constrained with climatic changes suggesting that cooling climate facilitated an earth-state shift that again led to the radiations. The Ordovician Baltic Palaeobasin is likely one of the best studied regions with respect to the GOBE interval. Still, little is known about intra-basinal differences across clades and ecological niches, as well as temperature proxies at this time. This is fundamental data that needs to be obtained if one is to understand macroevolutionary trends and ecosystem evolution.

To address this issue, we have built an astrochronological time scale allowing for high-precision correlation across the basin. New ¹⁸O-brachiopod data, collected bed by bed from Öland, further enable direct comparison on a bed-by-bed scale across facies belts and, geographically, across the East Baltic. In addition, new conodont richness data through the Dapingian–Middle Darriwillian from the Steinsodden area, southern Norway, permit a similar scale temporal correlation between the deep-water Norwegian section and that of already published shallow-water brachiopod data from the St. Petersburg Region, Russia. Thus, enabling direct comparison between the sessile benthos and the nekto-benthos across facies belts in absolute time.

Examining the Climate/Tectonic Implications of Sandbian–Katian Environmental Change in the Southern Appalachians Utilizing K-bentonite Apatite Phenocryst Geochemical Correlations

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The stratigraphic record of the late Sandbian to early Katian interval along the southeastern margin of Laurentia contains evidence of significant environmental change. However, opposing interpretations exist regarding environmental conditions during the Late Ordovician. Paramount to developing a clearer understanding of the relative importance of climate or tectonic drivers for these depositional changes is correlation between sections with sufficient resolution to distinguish among alternative explanations for environmentally significant events. To correlate and to test the interregional synchronicity of important events in the Sandbian-Katian interval (which includes the GICE, the M4/M5 sequence boundary, conodont speciation, and changes in carbonate lithologies) we established a K-bentonite framework based on apatite geochemistry. These isochronous tie-points for K-bentonite beds, including the Deicke and Millbrig, were established in four spatially distant sections across the southern Appalachians allowing us to determine the precise stratigraphic position of these events and their stratigraphic relationships in time and space.

Results show that magmatic apatite from beds identified as the Deicke and Millbrig K-bentonites at Fort Payne, AL, Gladeville, TN, Hagan, VA, and Dolly Ridge, WV display similar elemental concentrations to previous analyses of Deicke and Millbrig beds, while beds in the upper Stones River and lower Dolly Ridge formations at Fort Payne and Dolly Ridge display trends similar to previous analyses of the Elkport K-bentonite. The start of the GICE at Fort Payne begins in the upper Stones River Fm. and predates the proposed M4/M5 boundary, while both events are younger than the Elkport K-bentonite. The GICE, M4/M5, and the base of the *Plectodina tenuis* zone at Gladeville are coeval, but predate the Millbrig K-bentonite. The M4/M5 at Hagan and Dolly Ridge is slightly younger than the Millbrig, while tentative first appearance of *Plectodina tenuis* and the base of the GICE are slightly younger than the M4/M5. Additionally, all sections show a shift from peritidal depositional conditions to shallow ramp or deeper ramp conditions across the M4/M5 boundary. The timing of events and their positioning relative to one another suggests a causal relationship between the events. However, the order of events and their positioning relative to K-bentonite stratigraphy differ between sections. This suggests that the stratigraphic positions of the M4/M5 and the initiation of the GICE do not always appear as synchronous events in the stratigraphic record, and that their stratigraphic positions may be influenced by local tectonic forces that can override climate driven eustatic changes.

Untangling the ecology and fossil preservation knot for Paleozoic biotas

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Fossil deposits are a tangle of multiple signals that make understanding the functioning of past ecosystems a complicated and fraught process. The main difficulty is whether differences between fossil sites show an evolutionary or ecological signal or are influenced by fossil preservation. These processes are not independent as anatomical or behavioral differences can alter preservational pathways. It is particularly important to untangle these interacting processes when examining the animal communities of the Cambrian Explosion and Ordovician Radiation, where exceptional preservation of soft tissues provides relatively complete assemblage data. A novel method of data partitioning based on probabilistic modelling is used to examine these factors with respect to the Walcott Quarry, Burgess Shale, Canada (510Ma) and the Fezouata Shale, Morocco (c. 475Ma). As the prototypical Burgess Shale-type locality, the Walcott Quarry, is usually used as a basis for understanding Cambrian community structure and early ecosystem evolution. The result of probabilistic modelling shows that the Walcott Quarry biota best preserves the endobenthic community whilst systematically under-representing the nekton/plankton. The reverse is true for the Fezouata biota, with under-representation of the endobenthos. Taken in concert with data from a bioturbation index for these sites, a new model of comparative taphonomy is developed based on sedimentary flow timing with respect to organism mortality. These results suggest that during the Cambrian Explosion and Ordovician Radiation the most exceptional fossils sites must still be calibrated against each other to understand the unfolding evolutionary events and ecosystem structures at the transition between the Cambrian Explosion and the Ordovician Radiation.

The breakup of the L-chondrite parent body, its signature in mid-Ordovician sediments in Baltoscandia and the precise timing relative to the Ordovician biodiversity expansion

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The breakup of the L-chondrite parent body (LCPB) in the asteroid belt 465.8 ± 0.3 Ma is a unique event in the late history of the solar system. We know of no other breakup event during the past 3 Gyr of the same magnitude with similar consequences. Even today the most common type of meteorite falling on Earth, the L-chondrites, originate from this event. The majority of these L-chondrites have K-Ar degassing ages of ~ 470 Myr linking them to the breakup of a ~ 150 km parent body in the asteroid belt at that time. There is also ample evidence in Earth's geological record for this event, such as:

- A one-order-of magnitude increase in the flux of asteroids 0.1–2 km large that impacted Earth in the 30 Myr period after the breakup. This is the only confirmed asteroid shower on Earth the past 3 Gyr.
- An extreme abundance of macroscopic (1–21 cm large) fossil L-chondritic meteorites recovered from Baltic Orthoceratite limestone during quarrying.
- A two to three orders of magnitude increase in extraterrestrial ^3He , representing the most fine-grained dust from the breakup, accompanied by a similar increase in relict spinel grains from L-chondritic micrometeorites.

Judging from the distribution of extraterrestrial ^3He in the Hällekis quarry section at Kinnekulle the LCPB breakup took place when sea level began to fall in Baltoscandia, leading to the formation of the prominent Täljsten lowstand deposit. The Occam's razor explanation to this coincidence is that the enormous amounts of dust ejected into the inner solar system by the LCPB event shaded Earth from sunlight. This may have triggered an ice age or accelerated an ice-age trend already underway; water was transferred from the oceans to continental ice. It cannot be ruled out, as an alternative explanation, that the LCPB event and a long-term gradual cooling of the Earth during the Ordovician are both effects of a large-scale astronomical process that disturbed the inner solar system. One argument in favour of this scenario is the anomalous character of the micro-meteorite assemblages of the mid-Ordovician sediments that formed just before the LCPB event, but more research is needed.

There appears to be different views to what extent the great Ordovician biodiversity "expansion" (GOBE) is represented by a step-wise series of events or a more-or-less gradual increase in biodiversity over ~ 30 Myr. This complicates any attempts to relate the effects of the LCPB breakup to the GOBE.

Early Palaeozoic diversifications: ‘explosions’ and ‘events’ or a continuum of change?

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Based on several ‘high impact’ publications and (text-) books aimed at a general and, wider audience, it is currently generally considered that the diversification of early Palaeozoic marine life was established through a number of relatively radical ‘events,’ such as the Cambrian ‘Explosion’ and the Great Ordovician Biodiversification ‘Event’ (GOBE). In particular the first ‘event’, the Cambrian ‘Explosion,’ is the focus for many research projects, because it is considered, by many, a truly spectacular moment in the history of life. In the last four decades, the Ordovician Radiation has also been the subject of numerous studies, and more recently some authors have considered that the Ordovician biodiversification was a relatively brief ‘event.’

Here we present a somewhat different scenario. Our review of biodiversity curves of marine organisms indicates that, despite fluctuations in amplitude (some substantial), a large-scale, long-term radiation of life took place during the early Palaeozoic Era; it was aggregated by a succession of more discrete and regionalized radiations across geographies and within phylogenies. This major biodiversification within the marine biosphere started during the late Precambrian time and was only finally interrupted in the Devonian Period. It includes both the Cambrian ‘Explosion’ and the GOBE.

There are sufficient grounds to indicate that the establishment of modern marine ecosystems took place during a continuous chronology of the successive establishment of organisms and their ecological communities, developed during the ‘Cambrian substrate revolution’, the ‘Ordovician plankton revolution’, the ‘Ordovician substrate revolution’, the ‘Ordovician bioerosion revolution’ and the ‘Devonian nekton revolution’. At smaller scales, different regional but important radiations can be recognized geographically and some have been identified and named (e.g. those associated with the ‘Richmondian Invasion’ during the Late Ordovician in Laurentia and the contemporaneous ‘Boda event’ in parts of Europe and North Africa), in particular from areas that were in or moved towards lower latitudes, allowing high levels of speciation on epicontinental seas.

Most available datasets remain incomplete for many geographical areas, but also for particular time intervals (e.g. the late Cambrian ‘Furongian Gap’).

The early Palaeozoic biodiversification therefore appears to be a long-term process, modulated by bursts of significant diversity and intervals of inadequate data ; its progressive character will become increasingly clearer with the availability of more complete datasets, better global coverage and more advanced analytical techniques.

Ordovician Diversification of calcimicrobes and calcareous algae

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Despite the crucial role of epibenthic primary producers (cyanobacteria, green and red algae), no diversity curves for calcimicrobes and calcareous algae are available to assess the pyramiding paleoecology characterizing the Ordovician biodiversification episode. A total of 24 taxa of calcimicrobes and calcareous algae are identified from a Dapingian to lower Katian succession of carbonate sedimentary rocks exposed at the Leyayilitag ridge, Bachu Uplift, Tarim Basin, northwest China. These are 14 taxa of calcimicrobes, seven taxa of Dasycladales, one taxon of Bryopsidales and two taxa of Cyclocrinales. Within the lower Katian *Belodina confluens* Zone, the diversity increases substantially from around five to more than 20 taxa per 2 Ma. This increase in diversity is based on new calcimicrobes (*Bija*, *Ortonella*, *Garwoodia*, *Hedstroemia*, *Rothpletzella*, *Phacelophyton*, *Rauserina*) and the diversification of Dasycladales and Cyclocrinales. By comparison, the global diversity of calcimicrobes and calcareous algae (derived from literature data) started to increase earlier, namely within the late Darriwilian *Pygodus serra* Zone (offset of about 4 Ma). This offset might be due to the peculiar lithology of the Sandbian Tumuxiuke Formation (condensed section of red nodular limestones bounded by disconformities). However, a similar temporal offset is recorded for calathid sponge mounds. Therefore, the Tarim tectonic microplate (Tarim Block) might display an endemic–anachronistic character. The diversity curves of Ordovician benthic primary producers (calcimicrobes, calcareous algae) are similar to those recorded by some fossil groups, in particular eleutherozoan echinoderms. Global diversification of calcimicrobes, calcareous algae, non-calcified marine microalgae, phytoplankton in association with the landing of plants together cooled and oxygenized the Ordovician and might co-evolve or trigger the Great Ordovician Biodiversification Event.

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An exceptional record of early Paleozoic redox change from the Road River Group, Yukon, Canada

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Determining the causal relationship (if any) between biological evolution and changing environmental conditions requires knowledge of the long-term record so that minor fluctuations can be correctly distinguished from major changes. Here we report an expansive record of Paleozoic seafloor redox change from the upper Cambrian to Middle Devonian Road River Group deposited in the Richardson trough of Yukon, Canada. This represents an ideal sedimentary succession to investigate long-term redox change, as it provides a nearly continuous record of deep-water marine sedimentation over ~110 million years of Paleozoic history. More than 1,100 shale samples from the Road River Group and other Paleozoic shale units worldwide were analyzed for major- and trace-element geochemistry, iron speciation, and total organic carbon content. Redox geochemical data indicate that bottom waters were broadly anoxic during the entirety of Road River Group deposition, but independent evidence from iron speciation and Mo/U ratios suggests that the biogeochemical nature of anoxia changed through time. Both in Yukon and in a global dataset, Ordovician through Early Devonian anoxic water columns were broadly ferruginous (non-sulfidic), with a transition towards more euxinic (sulfidic) water columns in the mid-Early Devonian (Pragian). Thus, an ~80 million-year interval of the early Paleozoic was characterized by ferruginous bottom waters, similar to the Neoproterozoic redox geochemical record. Utilizing this new global shale compilation, trace metal-based inferences of the global extent of reducing conditions suggest that dynamic redox conditions characterized the Paleozoic, with relatively more oxygenated conditions in the late Cambrian-Early Ordovician and Mid-Late Devonian. Within the context of this long-term redox record, the shale geochemical record does not provide evidence for oxygenation events temporally associated with the Great Ordovician Biodiversification Event, either locally in the Richardson trough or in global trace metal datasets.

How did invasion events promote evolutionary and ecological change during the Great Ordovician Biodiversification Event?

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The biotic and ecological changes of the Great Ordovician Biodiversification Event fundamentally shifted the marine ecosystem. Understanding ecosystem change across this interval requires detailed consideration of local, regional, and global processes that combined to produce this dramatic change. During the course of IGCP 653 and related projects, considerable progress has been made in terms of quantifying biotic, ecological, and abiotic environmental change during the Ordovician Period. From the datasets developed, it has become clear that the Middle Ordovician, particularly the Darriwilian Stage, was a time of coordinated change in the earth-life system. Abiotic processes, particularly sea level changes and shifting oceanic circulation, resulted in oscillating intervals of biotic immigration events (BIMEs) and isolation. The dispersal—or species invasion—phase of BIME events was critical for facilitating species movement and introduction of clades to new paleocontinents. The complementary process of geographical isolation—due to paleogeography, numerous interoceanic islands, tectonism, glacial-interglacial cycles and newly developed habitat heterogeneity—would have promoted speciation via vicariance. When considered in the context of Stigall's (2019) invasion hierarchy, the GOBE is best categorized as an Interchange Invasion. By explicitly considering the hierarchical structure and biogeographical aspects of evolutionary processes during the GOBE, it is possible to more synthetically consider the factors and processes driving diversity increase during this key interval.

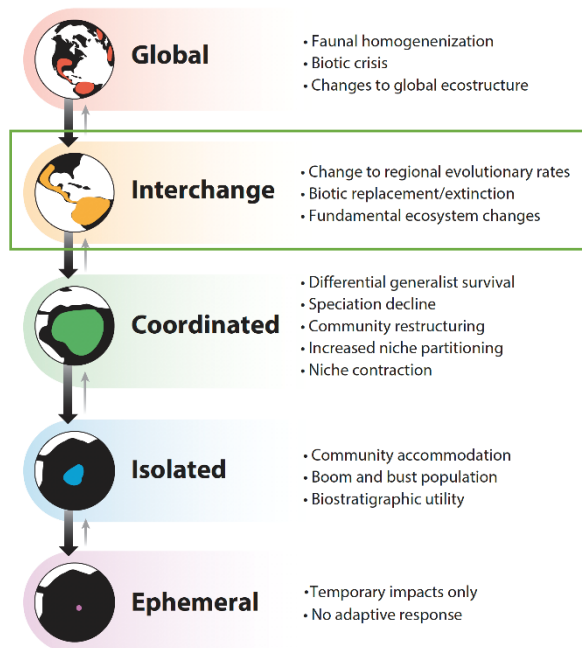


Figure 1. Invasion hierarchy from Stigall (2019). Characteristics of biotic patterns during the GOBE correspond to those of an Interchange Invasion.

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On ocean anoxia and the onset of the Great Ordovician Biodiversification Event

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The Great Ordovician Biodiversification Event (GOBE) is one of the most significant increases in marine biodiversity in Earth's history. The cause(s) of the GOBE remain poorly understood and may include profound changes in external environmental conditions. Marine dissolved O₂ levels specifically could have played a critical role in controlling the physiological viability of marine habitat. Reconstructing Ordovician marine redox conditions is therefore key to evaluating whether environmental factors could have facilitated the expansion of metazoan ecosystems across the GOBE. Here, we provide the first quantitative analyses of the extent of global marine redox chemistry changes in the Early-Middle Ordovician oceans using $\delta^{238}\text{U}$ of marine carbonates. The $\delta^{238}\text{U}$ trends from three widely spaced carbonate sections are remarkably similar, yielding a mean value of -0.49‰ . The nearly invariant and low $\delta^{238}\text{U}$ values over ~ 15 Myr indicate persistent anoxia in the Early-Middle Ordovician oceans. A U isotope mass balance model combined with a Monte Carlo framework suggests $>3\%$ of the global seafloor was overlain by euxinic bottom waters. Using an intermediate complexity Earth system model (cGENIE), we suggest that increases in nutrient supply and primary productivity were likely necessary to maintain persistent oceanic anoxia through the Early-Middle Ordovician in the context of other inferred changes in surface temperature and atmospheric O₂. We present two endmember scenarios for environmental change across the GOBE: 1) a stable marine system with dominantly anoxic deep-waters in which environmental change is unlikely to have driven early increases in biodiversity, 2) a model compatible with existing reconstructions of cooling and atmospheric oxygenation, requiring increased primary productivity to balance the marine redox landscape – potentially playing a key role in the onset of the GOBE.

A cyclostratigraphic analysis of the Late Cambrian Alum Shale

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We report evidence for Milankovitch cycles in two drill cores from the Cambro–Ordovician Alum Shale Formation of Scandinavia. The signal is preserved in elemental abundances recorded at high stratigraphic resolution by core scanning XRF analysis (0.2 mm resolution). The new data enable us to establish a floating timeline calibrated to the stable 405-kyr eccentricity cycle for a ~8.7 Myr interval across the Miaolingian–Furongian boundary. This interval spans the Steptoean Positive Carbon Isotope Excursion (SPICE), which is recorded in the $\delta^{13}\text{C}_{\text{org}}$ in the studied drill cores. We calculate the durations of the *Olenus* Superzone to 3.4 ± 0.2 Myr, the *Parabolina* Superzone to 1.9 ± 0.3 Myr, the *Leptoplastus* Superzone to 0.33 ± 0.18 Myr, the *Protopeltura* Superzone to 0.51 ± 0.20 Myr, and the SPICE event straddling the Paibian and lower main part of the Jiangshanian Stage to 3.0 ± 0.2 Myr. The sedimentation rate shows similar trends at both drilling locations and is inversely correlated to eustatic sea level changes in certain time intervals, opening tantalizing new prospects of using cyclostratigraphic analyses of shales to track eustatic sea level variations. The identification of obliquity cycles enables us to calculate the Cambrian Earth–Moon distance as well as the day length at ~493 Ma to $368.9 \pm 2.3 \cdot 10^6$ m and 21.78 ± 0.29 hr, respectively.

Ordovician Bioerosion Revolution on Baltica

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Macroboring organisms have evolved and changed through the Phanerozoic. The major rise in the diversity of macroboring ichnofossils took place during the Middle and Late Ordovician. When the term "Ordovician Bioerosion Revolution" was coined by Wilson and Palmer in 2006, seven bioerosional ichnogenera were listed from the Ordovician. A decade later 11 Ordovician bioerosional ichnogenera were reported by Mángano and co-authors. The Ordovician succession of the Baltic region, however, hosts no less than 13 macroboring ichnogenera: *Trypanites*, *Oichnus*, *Tremichnus*, *Gastrochaenolites*, *Sulcolithos*, *Pinaceocladichnus*, *Dendrina*, *Sanctum*, *Osprioneides*, *Petroxestes*, *Bicrescomanducator*, *Rogerella*, and *Entobia*. Moreover, several undescribed macroborings, different bite marks, as well as microborings have been recovered from the Baltic Ordovician in recent years. It is noteworthy that the oldest representatives of eight bioerosional ichnogenera come from Baltoscandia. The earliest bioerosional traces in the Baltic region – *Trypanites* and *Oichnus* – appeared in the Cambrian. Carbonate sedimentation commenced during latest Floian in the region, and bioerosional traces *Trypanites* and *Gastrochaenolites* appear below the Early/Middle Ordovician boundary. A rich assemblage of macrobioerosional traces occur on Dapingian hardgrounds, consisting of *Trypanites*, *Gastrochaenolites* and *Sulcolithus*. Also, the tracemaker of *Balanoglossites* demonstrated the ability to bioerode. Only few Dapingian finds, assigned to *Tremichnus* and *Pinaceocladichnus*, are related to biogenic substrates. In the Darriwilian, three new ichnogenera associated with biogenic substrates appeared: *Sanctum*, *Bicrescomanducator* and *Dendrina*. From the Sandbian, already eight ichnogenera are known and six have been recorded from the Katian. The majority of Upper Ordovician bioerosional ichnogenera in the Baltic region are related to various shelly fossils. *Trypanites* is an exception to this occurring in both organic and inorganic substrates.

Mikuláš and Dronov (2004) expressed the opinion that the Baltic region was the birthplace of bioerosion. Our data corroborate to this idea and show that the Ordovician Bioerosion Revolution might have begun in Baltica. The rapid diversification of bioerosional traces in the region was probably a coincidence of multiple global and regional factors. The major global factors were the seawater chemistry and oxygenation, stability of the sea level and increasing phytoplankton availability. The main regional drivers supporting the diversity of bioerosional organisms were the unusually long "colonisation window", a warming climate and a nutrient-rich, well-oxygenated epeiric sea.

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GOBE and escalation in symbiosis between large colonial animals and their endobionts

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Ordovician large colonial animals with calcareous skeletons (i.e. bryozoans, corals, stromatoporoids) were often inhabited by soft-bodied wormlike organisms, conulariids, rugose corals, cornulitids, and more rarely by gastropods. One can speculate that symbiotic relationships may have influenced the diversification of animals in the Ordovician. However, we did not find any increase in symbiotic relationships before the increase in diversity of the host group.

It seems that the evolution of symbiotic relationships did not contribute much to the Great Ordovician Biodiversity Event (GOBE), but the GOBE may have been the catalyst that started the evolution of symbiotic relationships between large colonial animals and their endobionts, likely as a result of the increased space competition among sessile benthic invertebrates. In addition, increased biodiversity resulting from the GOBE generated more diverse behaviors and physiologies, which in turn made the appearance of symbiotic relationships more likely than in the less diverse pre-GOBE biosphere. There was a progressive escalation in symbiotic relationships in the Ordovician starting from the Darriwilian. Large colonial animals in the Sandbian were more symbiotic than in the Darriwilian, and the Katian ones were more symbiotic than during the preceding stage.

This escalation in symbiotic relationships in the Ordovician can be explained by several hypotheses. Species with mutualistic relationships may have outcompeted species without mutualistic relationships, leading to an increase in mutualistic species. Infestation strategies of parasites likely improved with time, possibly at a faster pace than the anti-parasite strategies of their potential hosts, leading to an increase in parasite-infested species. Finally, those invertebrates that sought refuge from predators may have reacted to an increase in predation pressure with a more intense search for substrates suitable for endobiotic life mode. It is likely that all the factors listed above operated together and caused the escalation in symbiotic relationships between large colonial animals and their endobionts in the Ordovician.

Conodonts from siliciclastic rocks: a case study from the Portezuelo del Tontal Formation, Ordovician of the Western Argentine Precordillera

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During the past three decades, conodont investigations in the Ordovician of the Argentine Precordillera included major developments in taxonomy, biostratigraphy, palaeoecology, palaeogeography and paleothermometry. Conodont studies flourished within the fossiliferous limestones of the San Juan Formation and the overlying calcareous units of the central and eastern Precordilleran domains. In contrast, conodont reports from the deeper siliciclastic sedimentary successions of the Western Precordillera, which involve slope to ocean floor sedimentary rocks including pillow lavas and mafic-ultramafic bodies in its westernmost sections, are noticeably scarce, and are essentially restricted to the mixed clastic-calcareous turbidites of the Yerba Loca Formation. Thus, the general absence of appropriate facies for sampling conodonts, along with the laboratory difficulties in recovering conodonts from siliciclastic rocks, hinders the assessment of the conodont biostratigraphic framework of the Precordilleran basin.

In an attempt to precisely date of deposition of the ca. 2 km-thick siliciclastic Portezuelo del Tontal Formation, we thoroughly searched for rocks samples with calcareous reaction in the Telégrafo Creek and the Cerro Cóndores stratigraphic sections, on the western and eastern slopes of the Sierra del Tontal, respectively. After processing 10 rock samples in total (2-3 kg each) following standard laboratory procedures, only 2 samples from Cerro Cóndores were productive, yielding merely 50 conodont elements. The recovered assemblage includes *Ansella jemtlandica* (Löfgren), *Costiconus costatus* (Dzik), *Drepanodus arcuatus* Pander, *Parapaltodus simplicissimus* Stouge, *Paroistodus originalis* (Sergeeva), *P. h. horridus* (Barnes & Poplawski), *P. h. secundus* Albanesi, *Periodon macrodentatus* (Graves y Ellison), *Protopanderodus graei* (Hamar), and *Spinodus spinatus* (Hadding), which typically coexist in the Darriwilian (Middle Ordovician) *Yangtzeplacognathus crassus* Zone (Dw1–Dw2), a critical interval in the tectonostratigraphic history of the Precordillera. This zone has wide geographical distribution, involving most of the transitional interval from the San Juan Formation to the overlying Las Aguaditas, Las Chacritas, Los Azules, and Gualcamayo formations at the eastern and central domains of the Precordillera. Recognition of the *Y. crassus* Zone in the Portezuelo del Tontal Formation also allows for a tight intercontinental correlation with South China and Baltoscandia. In view of our results, the great importance of conducting conodont investigations in siliciclastic sedimentary deposits is reaffirmed.

Preliminary report on $\delta^{13}\text{C}_{\text{carb}}$ isotope excursion through the Silurian of Jočionys-299 borehole, Eastern Lithuania

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Lithuania is located in the eastern part of the Silurian Baltic Basin which was located near the equator during the Silurian. Jočionys-299 borehole is located in the Eastern Lithuania. The Silurian geological section of Jočionys-299 borehole is composed of siliciclastic, carbonate and sulfatic deposits and represents shallow-marine; lagoonal and sabkha environments.

Samples for $\delta^{13}\text{C}_{\text{carb}}$ isotope analysis were collected from the interval between 234.35 – 90.3 m approximately every 1 m. The stable carbon isotope values from carbonates were measured using Thermo Gasbench II coupled with a Thermo Delta V isotope ratio mass spectrometer.

According to preliminary $\delta^{13}\text{C}_{\text{carb}}$ isotope results, Silurian can be subdivided in five intervals in the Jočionys-299 borehole. The first interval spans from 234.25 to 211.8 m, here the $\delta^{13}\text{C}_{\text{carb}}$ values were close to +1 ‰ with some minor fluctuations and varied from 0.39 ‰ to 1.44 ‰. In this interval conodont *Pterospirifer am. amorphognathoides* which mark the upper part of Llandovery was found. The $\delta^{13}\text{C}_{\text{carb}}$ values rise gradually from 0.44 ‰ (depth 211.8 m) to 6.4 ‰ (depth 188 m) and gradually fall to –2.29 ‰ (depth 162 m). This positive $\delta^{13}\text{C}_{\text{carb}}$ excursion can be linked to the Ireviken Event of the lower Wenlock. Additionally, *Kockelella ranuliformis* is documented in this interval of Jočionys-299 well core. $\delta^{13}\text{C}_{\text{carb}}$ values are moderately stable in 162 m – 146 m depth and vary from – 2.53 ‰ to – 0.39 ‰. Then, $\delta^{13}\text{C}_{\text{carb}}$ values fall rapidly to – 8.1 ‰ at 145 m depth and rise to – 0.9 ‰ at 141 m depth. The fluctuations of $\delta^{13}\text{C}_{\text{carb}}$ values are rapid in 141 m to 90 m interval. Values vary from – 5.41 ‰ to – 0.92 ‰. There are no major excursions of $\delta^{13}\text{C}_{\text{carb}}$ in the last interval. In the upper part of Jočionys-299 borehole section, *Ozarkodina crispa* (uppermost Ludlow) and *Ozarkodina eosteinhornensis* biozones (lower Pridoli) were distinguished.

In summary, the $\delta^{13}\text{C}_{\text{carb}}$ values varied from – 8.1 ‰ up to 6.4 ‰ in the Silurian section of Jočionys-299 well core. Such a large range of $\delta^{13}\text{C}_{\text{carb}}$ values can be related to shallow marine environments and local peculiarities of sedimentation rates. A more detailed biostratigraphic and lithological study is needed to better understand stratigraphy of Silurian geological section in Jočionys-299 borehole in the future.

Recognizing pulses of extinction from clusters of last occurrences: A Late Ordovician case study

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The Late Ordovician mass extinction is commonly expressed as two clusters of last occurrences in the Hirnantian fossil record. These clusters appear to coincide with sequence-stratigraphic surfaces and facies shifts generated by the glaciation and the deglaciation of the supercontinent Gondwana. Consequently, glacioeustatic changes have been proposed as a principal driver of the Late Ordovician mass extinction, with each cluster of last occurrences interpreted as a pulse of extinction. However, stratigraphic architecture can produce clusters of last occurrences that can be misinterpreted as extinction pulses. These clusters typically occur at abrupt changes in facies or sequence-stratigraphic surfaces. Misinterpreting these clusters of last occurrences as pulses of extinction can lead to a misunderstanding of the pattern (number of extinction pulses), timing (age), and tempo (rapidity) of the extinction, which would result in a misunderstanding of possible causes of the extinction.

It has been proposed that a basin-wide analysis of the fossil record within a sequence-stratigraphic framework can be used to distinguish between clusters of last occurrences caused solely by extinction pulses from those generated by sequence-stratigraphic architecture. A basin-wide approach makes it possible to take into account lateral facies shifts in response to sea-level change and thus to determine the extent to which patterns of last occurrences reflect extinction dynamics versus stratigraphic architecture.

Here, we use a modelling approach to test how glacioeustatic changes would affect the expression of a variety of possible Late Ordovician mass extinction scenarios. Using the sedimentary basin model Sedflux 2.1, we simulate stratigraphic columns based on an inferred Late Ordovician sea-level curve. We combine these with a branching model of evolution and extinction, as well as water-depth preferences for each taxon, to simulate several Late Ordovician mass extinction scenarios.

We first show that stratigraphically-generated clusters of last occurrences are observed even in a basin-wide analysis of the fossil record because for some taxa there is a basin-wide loss of their preferred facies. However, by coarsening the stratigraphic resolution to the systems-tract level and removing taxa whose last occurrences coincide with a basin-wide loss of their preferred facies, we can consistently and correctly identify the pattern of extinction for a variety of extinction scenarios. We are undertaking the field work to determine whether this approach will enable the identification of the extinction pattern across the Ordovician/Silurian boundary on Anticosti Island, Canada.



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