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## Special issue

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## Foreword

Tõnu Meidla, David A. T. Harper and Thomas Servais

In 1984 Valdar Jaanusson provided a comprehensive overview of the characteristic features of the Ordovician Period in his introductory paper 'What is so special about the Ordovician' for the Fourth International Symposium on the Ordovician System in Oslo. He highlighted three key aspects: (1) the exceptionally high sea levels that led to the formation of extensive carbonate continental shelves, (2) significant changes in biodiversity, especially in groups that were rare or absent during the Cambrian Period and (3) notable biogeographical and climatic variation. While none of these features are entirely unique to the Phanerozoic eon, their simultaneous occurrence during the Ordovician Period continues to guide research on the Ordovician System, offering a wide array of phenomena to direct and synthesise new observations and theories.

Subsequent symposia have expanded on the list of these main topics, encompassing biodiversity studies on major groups of organisms and investigations of the glaciation event at the end of the period together with one of the 'Big Five' mass extinctions and its consequences; studies of impacts and the stable isotopic geochemistry of various elements, as well as palaeoceanography have advanced rapidly in the last 50 years. The upcoming 14th International Symposium on the Ordovician System, to be held in Tallinn, Estonia, on 15–26 July 2023, will continue to explore these and related aspects of the system. Additionally, the programme for the symposium includes a pre-conference excursion to the most spectacular Ordovician sections in Estonia and a post-conference excursion to the key Ordovician sections in Sweden, further enriching an already exciting programme.

The selection of Estonia as the venue for the upcoming global meeting on the Ordovician is compelling for several reasons. Firstly, approximately one third of Estonia's territory is occupied by outcrops of Ordovician rocks. Furthermore, these rocks are widely distributed throughout the country, encompassing a significant portion of one of the most extensively studied Ordovician palaeobasins, together with Latvia, Lithuania, northwestern Poland, Sweden, as well as parts of Denmark, Norway, and Russia.

The Ordovician rocks of this region have been the subject of intensive studies since the latter half of the 19th century. Over many decades, the sedimentary facies and stratigraphy of the Ordovician rocks in this area have been meticulously documented, providing a wealth of detailed information. Additionally, the extensive available documentation for the principal Ordovician fossil groups, based on superb preservation, further highlights the scientific value of this region. As a result, Estonia along with its neighbouring Baltoscandian countries is considered one of the key areas for global Ordovician studies.

The present volume serves as the proceedings of the 14th Symposium on the Ordovician System, published as a special issue of the *Estonian Journal of Earth Sciences*. This symposium is sponsored by the Subcommittee on Ordovician Stratigraphy of the International Union of Geological Sciences. Comprising 81 contributions, including 28 short papers and 53 abstracts, the volume covers a wide range of research areas such as chronostratigraphy, biostratigraphy, chemostratigraphy, palaeontology, regional geology, correlation issues, impacts, and many more – in fact, displaying a cross-section of contemporary research on the Ordovician System around the world.

This volume continues the long-standing tradition of former symposia arranged by the Ordovician Subcommittee to publish special books devoted to the Ordovician System. This tradition began in 1976 with the publication of the renowned volume 'The Ordovician System' (Cardiff, 1976), edited by M. G. Bassett. Since then, a substantial number of books and conference volumes, referenced in the research papers of this current volume, have been specially dedicated to the Ordovician System, its rocks and its fossils. The present volume includes contributions by authors from 20 countries summarising the results of current research, which will be presented as oral or poster presentations during the symposium.

A significant highlight of the programme for this meeting is an event to unveil the new two-volume opus on the Ordovician System of the world – including a global synthesis of successions in Europe (*Geological Society, London, Special Publications*, 532) and the rest of the world (*Geological Society, London, Special Publications*, 533). This is a monumental work that will remain an essential resource for many years to come. The classic Estonian succession with its detailed biostratigraphy, and its adjacent Baltic correlatives, will remain the core of Ordovician research. Publication of the volumes of the Geological Society has, however, highlighted the great diversity of the Ordovician System now known from virtually all corners of the world, a continued area of focus of the 14th ISOS. In addition, the close links of the Ordovician Subcommittee with IGCP programmes continue with IGCP 735 'Rocks and the Rise of Ordovician Life' focused on widening the global reach of the system and its researchers, and on the issue of de-colonisation of Ordovician data.

The organisers would like to express their gratitude to all contributors who have enriched this meeting with their valuable contributions. Special thanks are extended to the keynote speakers and the members of the Scientific Committee for their essential roles in shaping the event. The organisers would also like to extend their thanks to the institutions that have provided additional support for this gathering: Tallinn University of Technology, the University of Tartu, the Estonian Geological Survey, and the Estonian Museum of Natural History. Their support has been instrumental in making this meeting possible.



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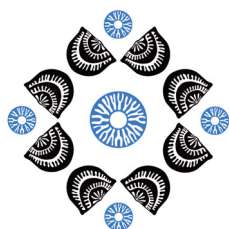
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14<sup>TH</sup> ISOS  
ESTONIA 2023

# Advances in the Lower Ordovician of the western Iberian Chain, NE Spain

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### ABSTRACT

The western Iberian Chain of NE Spain represents a lateral prolongation of the West Asturian-Leonese Zone. As other proximal sectors fringing NW Gondwana, the chain comprises a conformable and continuous Furongian–Tremadocian transition, comprising a thick (3600–4500 m) Lower Ordovician sedimentary succession, exclusively composed of siliciclastic strata and deposited in mid-latitude (temperate) waters. Although the shelly fossil record is not abundant, some key trilobites and brachiopods allow the identification of distinct biogeographic links with the Argentinian margin of West Gondwana, Oaxaca (Mexico), and the neighbouring Montagne Noire (France), with which a common biostratigraphic biozonation can be envisaged. Two phosphoritic interbeds rich in linguliformean brachiopods punctuate the Valconchán and Borrachón formations, and represent event beds related to condensation processes and sedimentation of explosive ignimbritic tuffs, respectively.

### Introduction

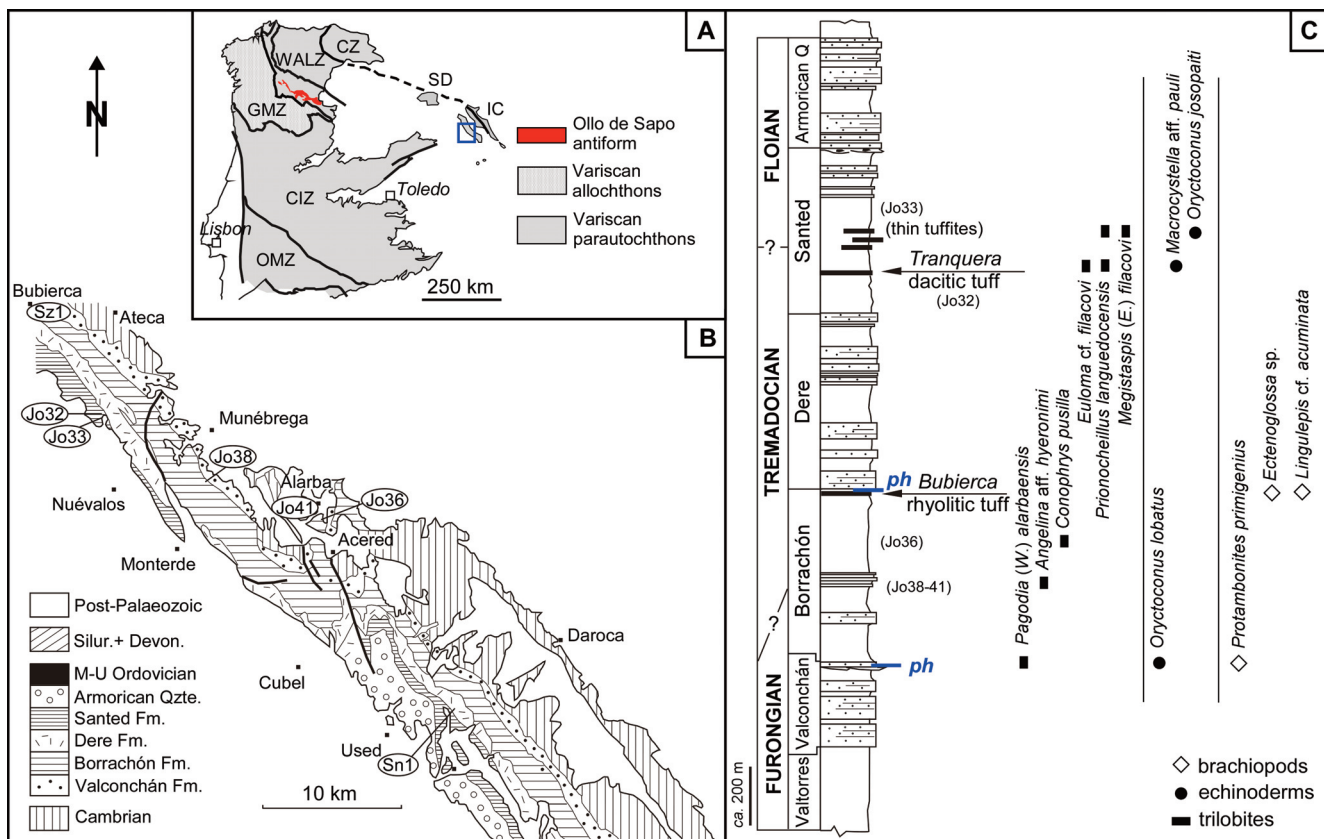
In the Iberian Massif, the Ollo de Sapo (‘toad eye’) magmatism has long been recognized as an enigmatic Furongian–Early Ordovician (495–470 Ma) assemblage of felsic (sub-)volcanic and plutonic rocks. The main exposures of this event crop out along the core of a 600 km long antiform fringing the northeastern edge of the Central Iberian Zone (Fig. 1A). Penecontemporaneous felsic byproducts locally occur in the neighbouring Ossa-Morena Zone and the Armorican and Occitan domains, reflecting the onset of a large igneous province (LIP) of ca 200 000 km<sup>3</sup> (García-Arias et al. 2018). The Ollo de Sapo magmatic event is also contemporaneous with the development of the so-called Toledanian Phase and gap, which place upper Tremadocian–Floian rocks overlapping with the inherited palaeorelief of tilted Ediacaran–Cambrian blocks. Their unconformable contact, ranging from paraconformities to angular discordances, involves a stratigraphic gap of ca 22 m.y. This unconformity can be correlated with the ‘Furongian gap’ of the Ossa-Morena Zone and the Anti-Atlas of Morocco, and the Norman gap of the Central and North Armorican domains (Álvaro et al. 2021). The Toledanian Phase, however, is absent in the most proximal sector of the Iberian margin, i.e. the West Asturian-Leonese and Cantabrian zones, and their lateral prolongations into the Sierra de la Demanda and Iberian Chains (Fig. 1A, B). In the latter, a continuous and conformable Furongian–Lower Ordovician transition has traditionally been documented, unaffected by the Toledanian uplift and erosion. The Furongian–Tremadocian trilobite, echinoderm and brachiopod assemblages of the western Iberian Chain are updated and summarized in this short communication.

### Results and discussion

The Iberian Chains, located in the NE of the Iberian Peninsula (Fig. 1A, B), represent a lateral prolongation of the West Asturian-Leonese and Cantabrian zones. There, the Furongian–Lower Ordovician strata consist of successive alternations of shale- and sandstone-dominated sedimentary units, and comprise, from bottom to top, the Valtorres Formation (Acón Group), the Valconchán, Borrachón, Dere and Santed formations (Ateca Group, broadly coinciding with the ‘Iberian Series’ of Schmitz 1971 and Josopait 1972), and the Armorican Quartzite Formation (Fig. 1C).

The Valtorres Formation, 200–350 m thick, consists of monotonous green shales, locally punctuated by sandstone interbeds and silica concretions. Towards its top, there is a gradual increase in the thickness and abundance of sandstone interbeds.

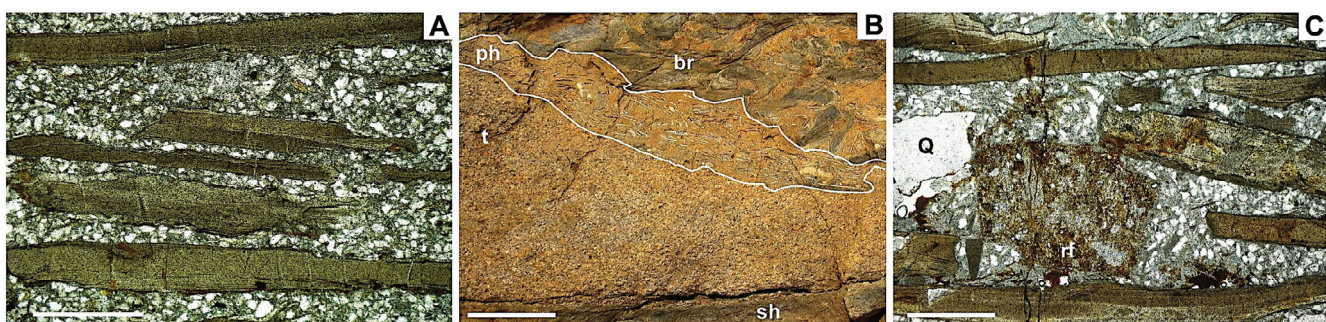




**Fig. 1.** **A** – pre-Variscan exposures of the Iberian Massif. Abbreviations: CIZ – Central Iberian Zone, CZ – Cantabrian Zone, GMZ – Galicia Trás-os-Montes Zone, IC – Iberian Chains, OMZ – Ossa-Morena Zone, SD – Sierra de la Demanda, and WALZ – West Asturian-Leonese Zone; **B** – fossiliferous outcrops of the western Iberian Chain (boxed in Fig. 1A): Jo – Josopait (1972), Sn – Scheuplein (1970), and Sz – Schmitz (1971); **C** – Furongian–Lower Ordovician stratigraphic framework of the Iberian Chains with stratigraphic ranges of reported shelly fossils; *ph* – shelly phosphorites.

The overlying Valconchán Formation, 30–300 m thick, consists of thin- to thick-bedded sandstones and quartzites with shale and conglomerate interbeds. Trilobites of the Valtorres Formation and the lowermost part of the Valconchán Formation (Josopait 1972; Wolf 1980; Shergold and Sdzuy 1991) form a Furongian association, which includes agnostids (*Pseudagnostus* sp.) and trilobites, such as *Aphelaspis* aff. *Aphelaspis* *rara*, *Elegantaspis* cf. *beta*, *Parachangshania*? sp., *Punctaspis*? *schmitzi*, and *Valtorresia* *volkeri* (Shergold and Sdzuy 1991), associated with the brachiopods *Billingsella* *jalonensis* and *B. perarea* (Havlíček and Josopait 1972). According to Shergold and Sdzuy (1991), this fauna may be considered to be approximately equivalent to the *Parabolina*

*spinulosa* Zone of Baltica. In contrast, the upper part of the Valconchán Formation has yielded the trilobite *Pagodia* (*Wittekindia*) *alarbaensis* (Shergold and Sdzuy 1991), the pelmatozoan holdfast *Oryctoconus lobatus* (Álvarez and Colchen 2002; Zamora et al. 2009), and the brachiopod *Protambonites primigenius* (Havlíček and Josopait 1972). Based on the occurrence of their respective genera and subgenera in Afghanistan, Turkey and the Cantabrian Zone, this endemic assemblage has traditionally marked the Furongian–Tremadocian transition in the Iberian Chains. Near Valconchán village, the topmost part of the Valconchán Formation contains a condensation phosphorite level, up to 10 cm thick, composed of disarticulated and broken linguliformean brachiopods (Fig. 2A),



**Fig. 2.** Lower Ordovician phosphorites from the western Iberian Chain. **A** – thin-section photomicrograph of linguliformean brachiopods forming the condensation phosphoritic level of the Valconchán Formation, near Valconchán; **B** – rhyolitic tuff (t) embedded in the shales (sh) of the Borrachón Formation, overlain by a phosphoritic shelly (ph) level and breccia (br) rich in clasts derived from three underlying facies, near Bubierca; **C** – thin-section photomicrograph with linguliformean brachiopods associated with rhyolitic fragments (rf) and engulfed quartz (Q) clasts. Scales = 1 mm (A, C) and 4 cm (B).

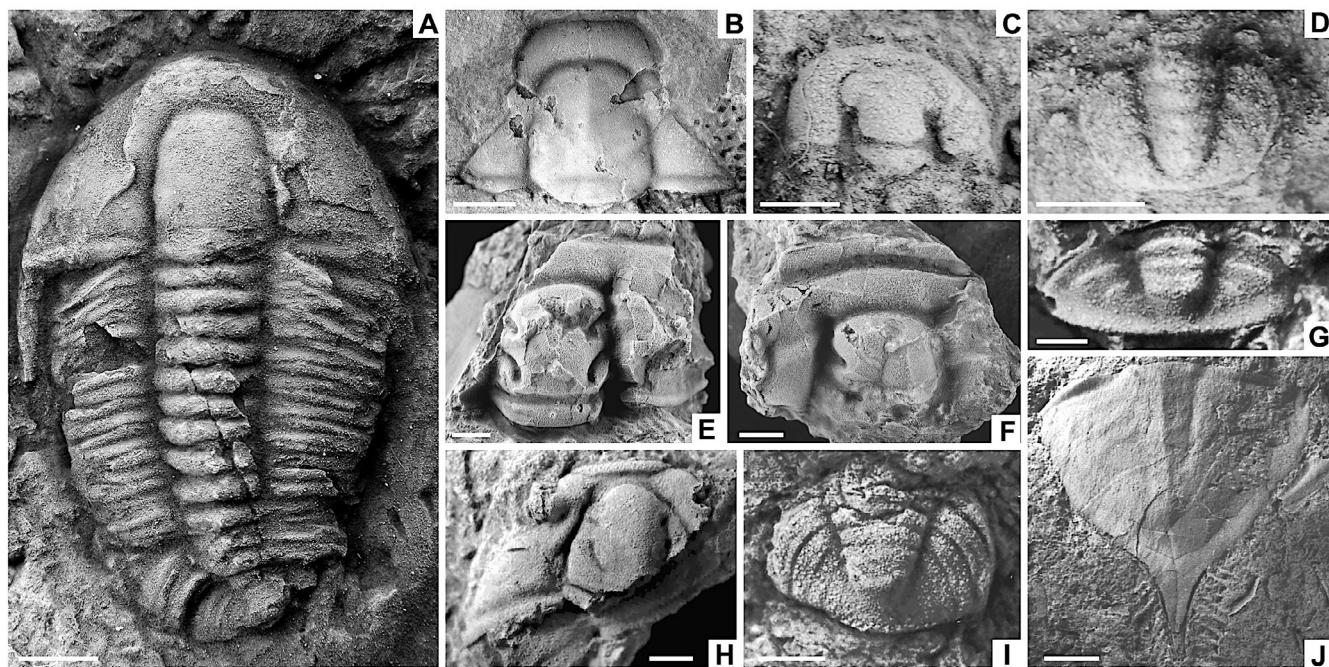
and separating two shallowing-upward shoaling cycles, up to 2.4 m thick.

The overlying Borrachón Formation, 320–900 m thick, comprises mainly green shales with subsidiary sandstone interbeds, which have yielded trilobites (e.g., *Angelina* aff. *hyeronimi*, *Asaphellus* sp., *Conophrys pusilla*, and *Dikelocephalina* sp.), acritarchs and ichnofossils (*Cruziana simplicata*, *C. furcifera* and *C. rugosa*) (Schmitz 1971; Josopait 1972; Kolb and Wolf 1979; Wolf 1980). The occurrence of age-diagnostic acritarchs allows its assignment to the Tremadocian. The presence of the olenid *Angelina* aff. *hyeronimi* (reported by Hammann et al. 1982, 24; and illustrated in Fig. 3A, B) allows taxonomic and biogeographic links with *A. hyeronimi*, a key species crossing the Furongian–Tremadocian boundary interval in Argentina (where the stratigraphic range comprises the *Cordylodus intermedius*, *C. lindstromi* and *C. angulatus* conodont-based zones; Tortello 2003) and the basal Tremadocian of Mexico (Robison and Pantoja-Alor 1968), which would suggest that the Furongian–Tremadocian boundary should be tentatively located within the lowermost part of the Borrachón Formation. *C. pusilla* (Fig. 3C, D) allows correlation with the homonymous Tremadocian biozone from the southern Montagne Noire (Vizcaíno and Álvaro 2003). A rhyolitic tuff located in the vicinity of Bubierca (Figs 1B, 2B, C) has yielded broken linguliformean brachiopods, such as *Ectenoglossa* sp. and *Lingulepis* cf. *acuminata* (Wolf 1980).

The overlying sandstones and quartzites of the Dere Formation are 420–850 m thick and contain ichnofossils (*Cruziana simplicata* and *C. rugosa*), poorly preserved linguliformean brachiopods, trilobites (e.g., *Asaphellus* sp.)

and molluscs, and acritarchs (Scheuplein 1970; Schmitz 1971; Havlíček and Josopait 1972; Wolf 1980).

The shale-dominated Santed Formation, 200–950 m thick, has yielded ichnofossils, trilobites, brachiopods, echinoderms and acritarchs (Schmitz 1971; Josopait 1972; Wolf 1980; Zamora et al. 2009). The Tremadocian – ‘Arenig’ (Floian) boundary interval is currently placed within this formation. Josopait (1972), Wolf (1980) and Hammann et al. (1982) reported the youngest Tremadocian and oldest ‘Arenig’ trilobites in the vicinity of the Tranquera dam (Fig. 1B). The uppermost Tremadocian fossil assemblage occurs within a dacitic tuffitic bed (Josopait’s Fp 32; Álvaro et al. 2008), which has yielded, among others, the trilobites *Euloma* cf. *filacovi* and *Prionocheilus* cf. *languedocensis*, whereas the lowermost ‘Arenig’ assemblage (Josopait’s Fp 33) contains *Prionocheilus* cf. *languedocensis* and *Megistaspis* (*Ekeraspis*) cf. *filacovi* (Fig. 3E–J). Wolf (1980) correlated both levels biostratigraphically with the ‘faunizones’ E and F of the southern Montagne Noire, which were re-evaluated by Vizcaíno and Álvaro (2003) as two different fossil assemblages (not yet found in the same section of the Montagne Noire) belonging to the *Euloma filacovi* Zone, which would include the Tremadocian–Floian boundary interval. Finally, the overlying Armorican Quartzite Formation, 450–650 m thick, consists of two thick-bedded quartzite and sandstone members separated by a shale-dominated middle member. The formation has yielded rare brachiopods, conularids, bivalves and trilobites (Babin and Hammann 2001), and ichnofossils (*Cruziana rugosa* and *C. imbricata*). A recent U–Pb dating of K-bentonites embedded in the Armorican Quartzite (upper Barrios Formation) of the Cantabrian



**Fig. 3.** Representative Early Ordovician trilobites (reported by Hammann et al. 1982, but not previously illustrated) from the western Iberian Chain; all fossils are housed in the Palaeontological Museum of the University of Zaragoza. **A, B** – complete skeleton and cranium of *Angelina* aff. *hyeronimi* from Josopait’s (1972) localities Jo38 and Jo41, south of Munébrega and Alarba villages; **C, D** – cranium and pygidium of *Conophrys pusilla* from Josopait’s locality Jo36, south of Alarba village; **E–G** – two cranidia and one pygidium of *Euloma* cf. *filacovi* from Josopait’s (1972) locality Fp32 (dacitic tuff) at La Tranquera dam; **H, I** – cranium and pygidium of *Prionocheilus* cf. *languedocensis* from Josopait’s (1972) localities Fp32 and Fp33 at La Tranquera dam; **J** – pygidium of *Megistaspis* (*Ekeraspis*) cf. *filacovi* from Josopait’s (1972) locality Fp33 at La Tranquera dam. Scales = 2 mm (E, F, H, I) and 1 mm (A–D, G, J).

Zone, northern Spain, has yielded an age of  $477.47 \pm 0.93$  Ma (Gutiérrez-Alonso et al. 2016), a result extremely close to the currently accepted interpolated age for the Tremadocian–Floian boundary GSSP at  $478.6 \pm 1.7$  Ma.

## Conclusions

The western Iberian Chain of NE Spain comprises a thick (3600–4500 m) and conformable Lower Ordovician sedimentary succession, exclusively composed of siliciclastic strata and deposited in mid-latitude (temperate) waters fringing NW Gondwana. The Furongian–Tremadocian boundary interval lies within the Borrachón Formation, where the trilobite *Angelina* aff. *hyeronimi* supports a direct correlation with the Argentinian margin of Gondwana and Oaxaca. The Tremadocian–Floian boundary interval is placed within the Santed Formation, where the trilobites *Euloma* cf. *filacovi*, *Prionocheilus* cf. *languedocensis* and *Megistaspis* (*Ekeraspis*) cf. *filacovi* allow a direct correlation with the southern Montagne Noire, France. Two phosphoritic interbeds rich in linguliformean brachiopods punctuate the Valconchán and Borrachón formations, and represent event beds related to condensation processes and sedimentation of explosive ignimbritic tuffs, respectively.

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# Ordovician collections stored at the National Museum of Natural History of the NAS of Ukraine

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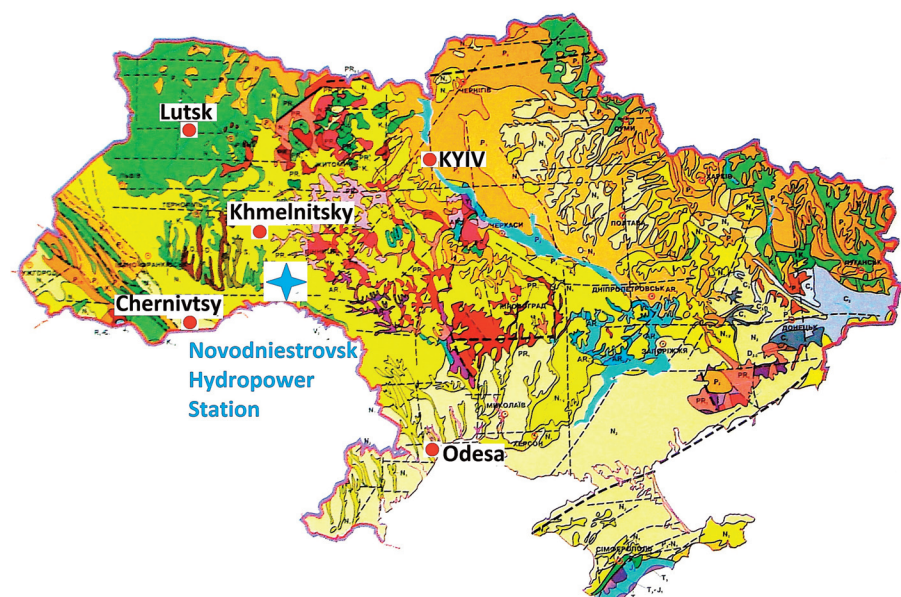
### ABSTRACT

We reviewed our department's collections dealing with the Ordovician System, stored at the National Museum of Natural History of the National Academy of Sciences of Ukraine (NMNH NAS). The first investigation of the Ordovician palaeontology of Ukraine was published by the Romanian researcher T. Vascăușanu before the Second World War. The study of the Ordovician sections during the 1960s was related to geological prospecting. Most outcrops along the Dniester River in the middle of the valley were available for study before the construction of the dam of the Novodniestrovski Hydropower Station, which raised the level of the reservoir near the dam to 60 m. The reservoir is 198 km long and has covered outcrops ranging from the Ediacaran to the Pridoli. Ordovician fossils are represented by diverse remains of brachiopods, molluscs, corals, bryozoans, graptolites, echinoderms, conodonts, and others.

### Introduction

In total, the National Museum of Natural History in Kyiv has only twelve collections containing Ordovician samples, collected from 1874 to 2011. Two of the older collections were transferred from Kyiv University as a result of its reorganisation. The others were given by authors for preservation as monographically described collections. Some samples are displayed in the museum, whereas others are stored in the hall of 'monographic collection', which is only accessible to specialists. These monographic collections were assembled by P. N. Venjukov, V. S. Krandievskiy, P. D. Tsegelnjuk, V. P. Grytsenko, N. V. Zernetskaya, and others.

In Ukraine, the Ordovician sections are largely eroded, with a total thickness of only approximately 10 m. The outcrop sections are located on the banks of the Dniester River (Fig. 1) and represented by two members (Horaivka and Subich formations) divided by an unconformity. More than 400 samples from these sections are



**Fig. 1.** Geological map of Ukraine (after Bragin et al. 2001, 67) showing the locations mentioned in the text.

represented by brachiopods, corals, graptolites, molluscs and bryozoans. Other samples were obtained from the boreholes in Volyn and Podillia, which are located along the western slope of the Ukrainian Shield, extending from Lutsk to Odesa (Fig. 1). Some samples were obtained from boreholes drilled in Moldova.

## Results and discussion

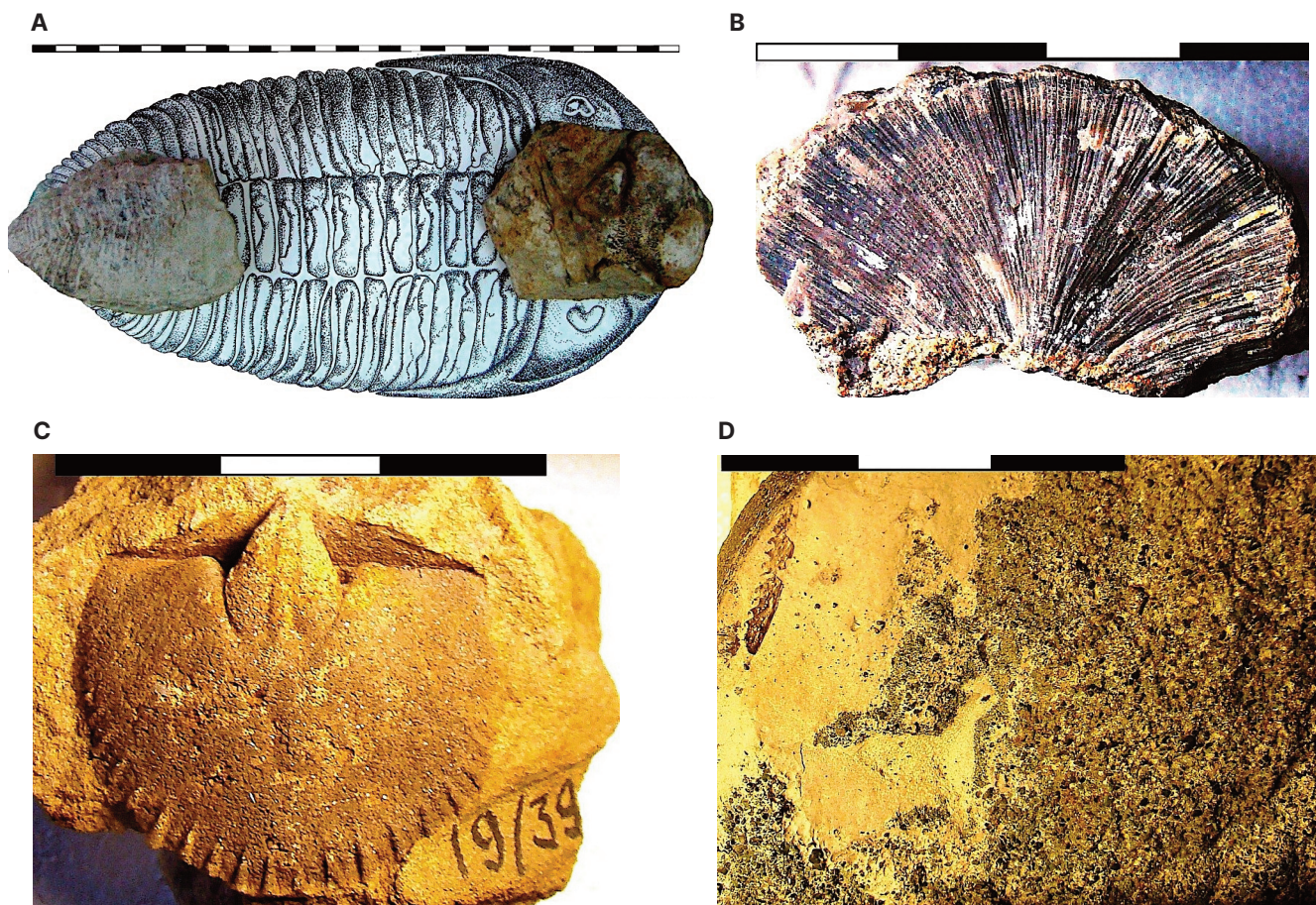
The Middle–Upper Ordovician deposits in the territory of Ukraine were first described in 1931 in the Dniester Valley Basin (Vaskâutsanu 1931). The stratigraphic description and the age of the Ordovician deposits was clarified by T. N. Alikhova (1956). She showed that the Molodove Stage extends into the upper part of the Middle and lower part of the Upper Ordovician. The first palaeogeographic map was created by P. L. Shulga (1960).

The Ordovician strata in the Podillia and Volyn regions of western Ukraine are represented in the lower part by limestone, glauconite-rich and clayey sediments with graptolites (Fig. 2D). These beds are closer in lithology to the Lower Ordovician Leetse Formation.

The Tremadocian Stage with *Obolus apollinis* Eichwald was found in Volyn in cores intersecting the Vyzhivka Formation at the base of the sequence. Stratigraphically overlying units are the Ishev, Nadishev and the Pishcha formations, which are correlated with regional stages such as Hunneberg, Billingen (Lower Ordovician), Volkhov, Kunda, Aseri, Lasnamägi, Uhaku (Middle Ordovician), Kukruse, Haljala, Keila, Oandu, Rakvere, Nabala and Vormsi (Upper Ordovician).

The Ordovician deposits of the Kovel Region (Volyn) were divided into two formations: Petrovichi and Viysk (Tsegelnjuk 1977). Subsequently, these formations were renamed the Smidyn and Rostan formations, respectively, in accordance with the decisions of the Ukrainian Regional Interdepartmental Stratigraphic Committee (Grytsenko 1984).

The Ordovician terrigenous-carbonate deposits of the Middle Transnistria region belong to the Molodove Stage (Alikhova 1956), which is divided into the Horaivka and Subich formations. The Horaivka Formation was correlated with the Oandu and Rakvere stages on the basis of data from a monographic study on brachiopods, and the Subich Formation was correlated with the Vormsi Stage of the regional standard of the Ordovician deposits of Estonia (Nölvak et al.



**Fig. 2.** **A** – *Chasmops extensa* from the Horaivka Formation, reconstructed from fragments; **B** – *Esthonioporella crassimuralis*, Darrivilian, Horaivka Formation, Nadniestrianka village; **C** – *Boreadorthis* cf. *sadewitzensis* (Roemer), No. 1786/4, Nadniestrianka village, Darrivilian, Horaivka Formation; **D** – oolitic sandstone with graptolite gen. et sp. indet., borehole 5443, depth 347 m; Floian, lower part of the Smidyn Formation; **E** – *Subulites* (*Subulites*) *gigas* (Eichwald), No. 1922/196, Nadniestrianka village, left bank of the Dniester River; Middle Ordovician, Horaivka Formation; **F** – *Holopea ampullacea* Eichwald, No. 1922/126, Kytaigorod village, left bank of the Ternava River; Upper Ordovician, Subich Formation; **G** – *Loxoplocus* (*Lophospira*) *esthona* Koken, No. 1922/109, Nadniestrianka village, left bank of the Dniester River; Upper Ordovician, Subich Formation; **H** – limestone with a fragment of *Megistaspis* sp., No. 2210-14, Volyn, borehole 5443, depth 341.5 m, Dapingian Stage, Smidyn Formation. Scale bar is calibrated in 10 mm intervals. (Continued on the next page)

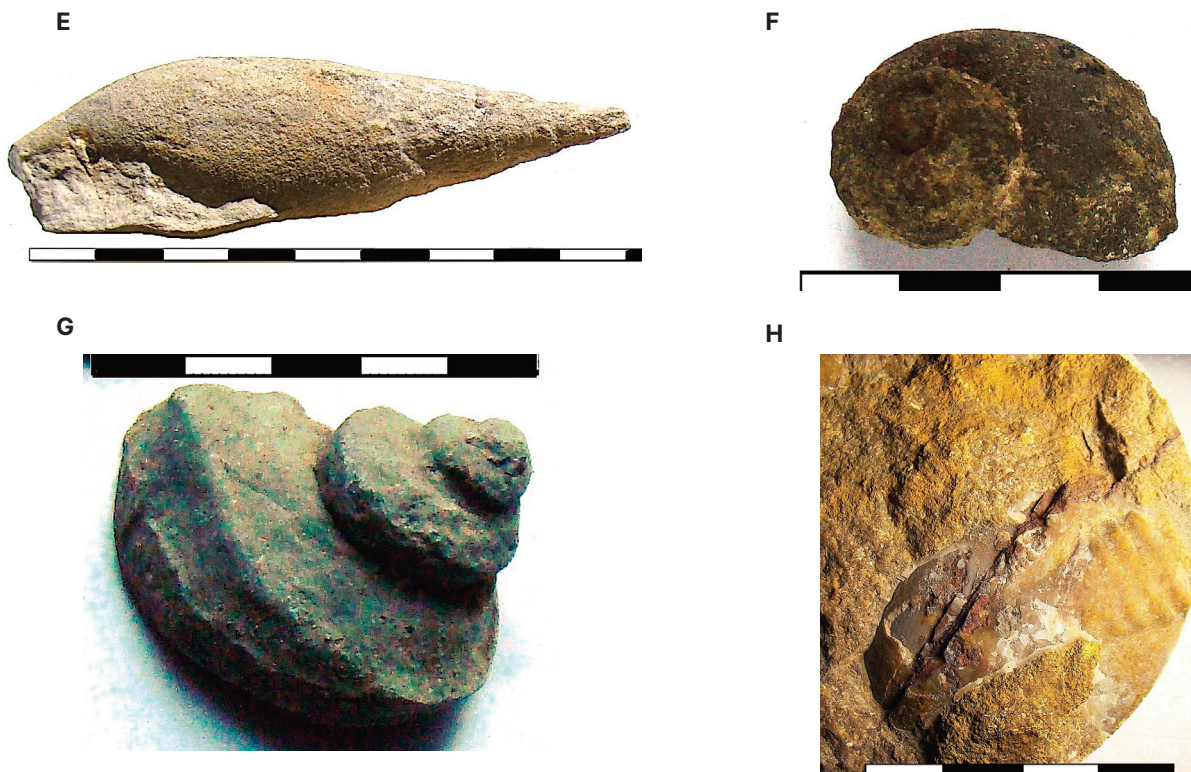


Fig. 2. Continued.

2006). The Horaivka Formation is distributed from north of Podillia to south-east of the Moldova Plate and reaches the Odessa region of Ukraine (Bukatchuk and Tsegelnjuk 1973). In the south-western part of the territory of Moldova, the Baroncha Beds extend into the Middle Ordovician and are overlain by the Molodove Stage, which was attributed to the Upper Ordovician (Bukatchuk 1972).

The limestones of the Upper Ordovician Series within the territory north-west of Moldova and the Chernivtsi region of Ukraine extend into the Moresheshty Beds of the lower Silurian (Trandafilova et al. 1968). In the limestones, P. D. Tsegelnjuk recognized *Triplesia insularis* Roemer, *Pseudolingula quadrata* Sowerby and *Bekkeromena semipartita* (Roemer), which are found in the Subich Formation in the Upper Ordovician (Bukatchuk and Tsegelnjuk 1973). The Upper Ordovician deposits are not known southwards, in the north-western Black Sea region and the southern part of Moldova (Tsegelnjuk 1980).

The Middle Ordovician limestones of the Belichevska Formation (light grey argillites with siltstones) were found in the Lviv Palaeozoic Trough in boreholes Litovizh-1 and Dublyany-4 (Drygant 1976, 1979). In the tectonic blocks of the Ukrainian Carpathians, the remains of conodonts and graptolites were discovered, correlating them with the upper part of the Lower and the lower part of the Upper Ordovician (Drygant and Boichevska 1984). Based on this data, the Ordovician extends along the south-western outskirts of the East European Platform from Volyn to Odesa regions (Krandievskiy and Bukatchuk 1969; Tsegelnjuk 1980, 1993).

Some of the important groups of fossils that were studied include: ostracods – by Krandievskiy (1969) and Abushik and Sarv (1983); brachiopods – by Tsegelnjuk (1976); conodonts – by Drygant (1975, 1979) and Drygant and Boichevska

(1984); gastropods – by Zernetskaya (1976); trilobites – by Konstantinenko (2002, 2005). These studies made it possible to carry out a total biostratigraphic analysis of the Ordovician deposits in Ukraine (Konstantinenko 2011, 2013).

## Conclusions

Ordovician deposits are distributed in Ukraine on the western slope of the Ukrainian Shield. In the Middle Transdnier region, these rocks include sandstone of the Horaivka Formation and limestone of the Subich Formation, correlated with the Middle and Upper Ordovician, respectively. The sections include a rich fossil assemblage, although in many cases preservation is not good due to the influence of recrystallization and weathering. Nevertheless, graptolites, ostracods, conodonts, brachiopods, trilobites, gastropods, and other fossils were found and studied.

The Ordovician deposits and fossils, which were actively investigated in Ukraine in the second half of the 20th century, support a correlation mostly with the Baltic region.

The sedimentation during the Middle Ordovician and the fossils testify to shallow-water conditions and warm water with normal salinity. The Upper Ordovician sediments (mostly limestones) suggest a deeper sea and warmer climate.

The restricted thickness of the Ordovician deposits provides evidence of an almost stable regressive tectonic regime.

Unconformities and conglomerates located in the lower and upper parts of the formation are evidence of erosion of sediments in the outcropping sections of Podillia.

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# Using 3-D mapping to understand an Upper Ordovician buildup and facies complex in the upper Lexington Limestone, central Kentucky, USA

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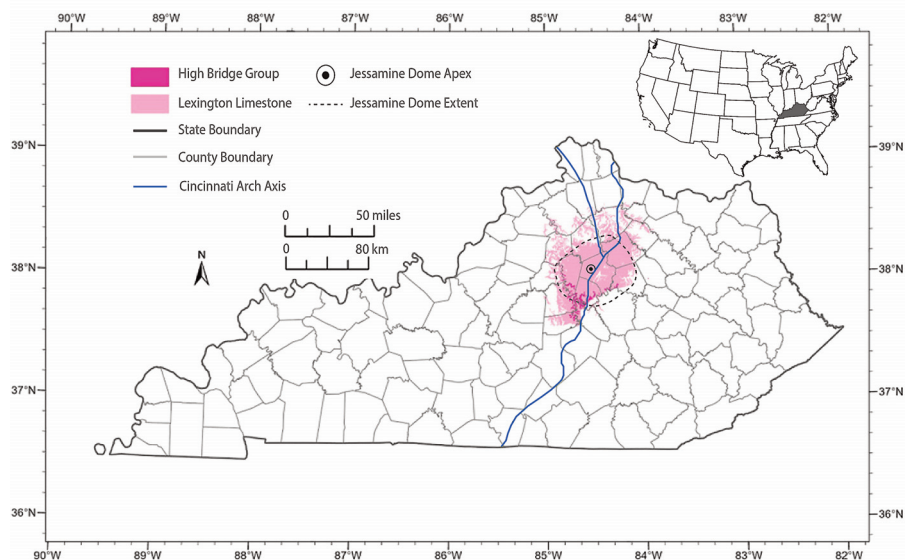
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### ABSTRACT

The upper parts of the Upper Ordovician Lexington Limestone in central Kentucky, USA, are interpreted to reflect a structurally controlled carbonate buildup, represented by a facies mosaic of shoal complexes and interbedded shale units. Facies intertonguing is complex and two-dimensional (2-D) mapping has been difficult. In this project, we converted 2-D maps to 3-D maps to show the extent of various facies and the complex nature of intertonguing. The resulting 3-D maps can be viewed from various vantage points and show the likely influence of basement structures as well as the results of post-depositional structural activity.

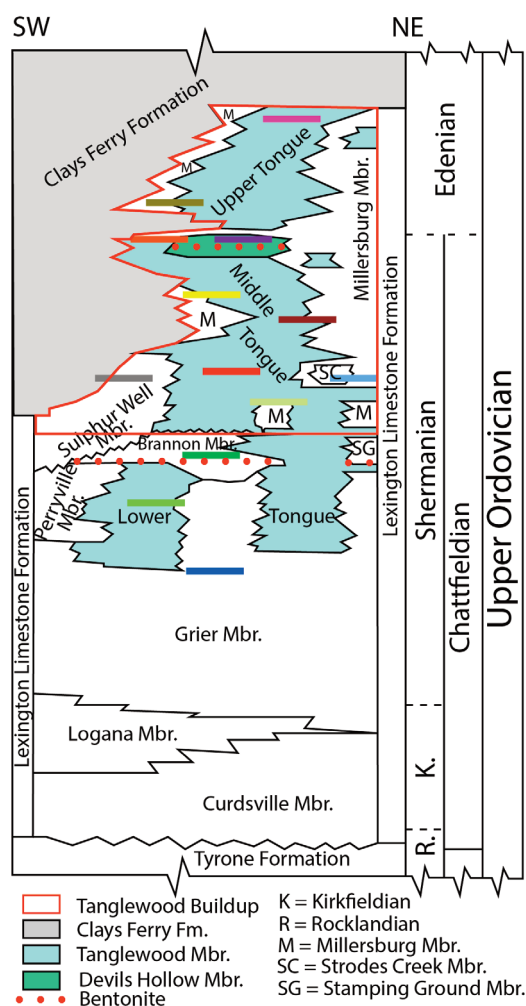
### Introduction

The Lexington Limestone, also known as the Trenton Limestone in the subsurface, is a prominent Upper Ordovician (Sandbian–Katian; Chatfieldian–Edenian) limestone and shale unit that crops out in the Jessamine Dome culmination of the Cincinnati Arch in north-central Kentucky, USA (Fig. 1). It was deposited during the Taconic tectophase of the Taconian orogeny across the Lexington Platform, immediately cratonward of the Taconian foreland basin (e.g., Etensohn et al. 2004). Since the Lexington Limestone was first described in 1898, the formation and its members were interpreted to exhibit relatively tabular, “layer-cake” geometries (e.g., McFarlan 1943), and Lexington only included members up to the level of the Brannon Member (Fig. 2), which are approximately equivalent to the Trenton Series of New York (Brett



**Fig. 1.** Distribution of the Upper Ordovician Lexington Limestone and underlying High Bridge Group, exposed on the Jessamine Dome culmination along the Cincinnati Arch. Much of the unit distribution reflects parts of the post-Trenton upper Lexington Limestone (parts above the Brannon Member; see Fig. 2).





**Fig. 2.** Schematic stratigraphic column of the Lexington Limestone showing the facies mosaic in the upper part of the unit, or Tanglewood buildup, only part of which is shown. The colored horizontal lines represent contact horizons that were mapped as separate layers or feature classes on the final 3-D map. Each color represents a member or a Tanglewood tongue (adapted from Ettensohn et al. 2004).

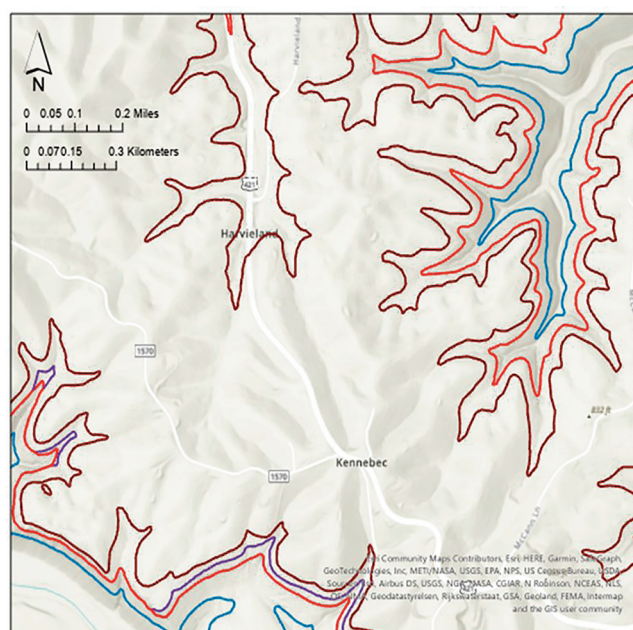
et al. 2004). Hence, the Lexington Limestone is called the “Trenton Limestone” in the subsurface of Kentucky (e.g., Shaver 1985) and adjacent states. However, during the combined U.S. Geological Survey-Kentucky Geological Survey Mapping Program from the 1960s to the early 1990s, detailed mapping in central Kentucky showed that “stray” tongues of bioclastic, calcarenitic limestone interbedded with shales and nodular limestones, which occurred above the Lexington Limestone in the Cynthiana Formation, were lithologically similar and intertongued with parts of the Lexington Limestone below (e.g., Black et al. 1965) (Fig. 2). Hence, the term “Cynthiana” was abandoned, and the various bodies of bioclastic limestone were included as the Tanglewood Member of the Lexington Limestone (Black et al. 1965), which expanded the thickness and concept of the Lexington Limestone to carbonate units younger than the Trenton equivalents in central Kentucky (Fig. 2). These re-interpretations meant that the Lexington Limestone in central Kentucky was about 98 m (320 ft) thick, compared to a more typical thickness of 61 m (200 ft) for the more tabular, subsurface Trenton equivalents, which intertongue on all flanks with the shales and

fine-grained limestones of the Clays Ferry Formation (Black et al. 1965; Cressman 1973) (Fig. 2).

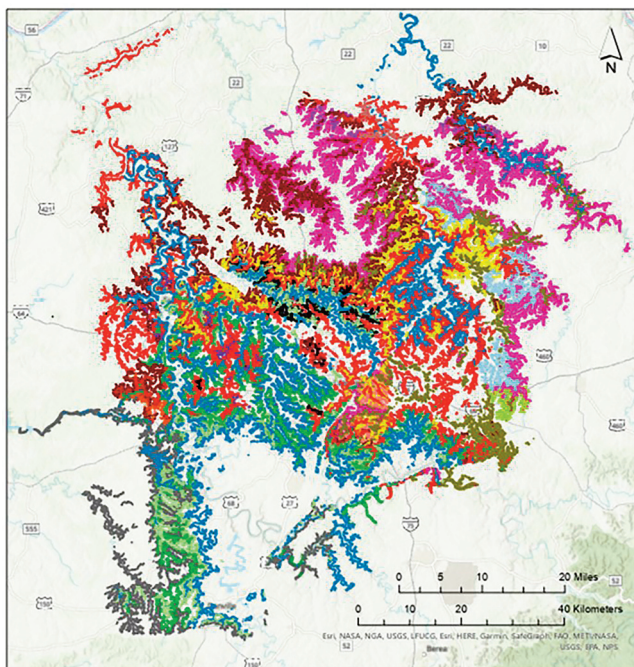
In 1992, Ettensohn examined the distribution of the coarse, bioclastic, Tanglewood limestones and made cross sections through them, suggesting that the extra thickness of the upper Lexington Limestone in the central Kentucky area (37 m, 120 ft) and its roughly triangular outline reflected a carbonate buildup on reactivated basement structures (Ettensohn 1992). The coarse, bioclastic limestones in the buildup (Tanglewood Member; Fig. 2) were interpreted to represent shoal complexes related to periods of uplift, whereas interbedded shales were interpreted to represent eustatic highstands (Ettensohn et al. 2004). The roughly triangular distribution of these shoal complexes was shown to coincide with modern structures that had basement precursors. This coincidence was the impetus for us to generate a 3-dimensional (3-D), compatible geo-framework map to answer two key questions: 1) can 3-D mapping be used to characterize complex geologic surfaces such as those that bound the upper Lexington Limestone and its included members; and 2) can 3-D mapping confirm the likelihood of structural control on the upper Lexington Limestone and its members?

## Procedures

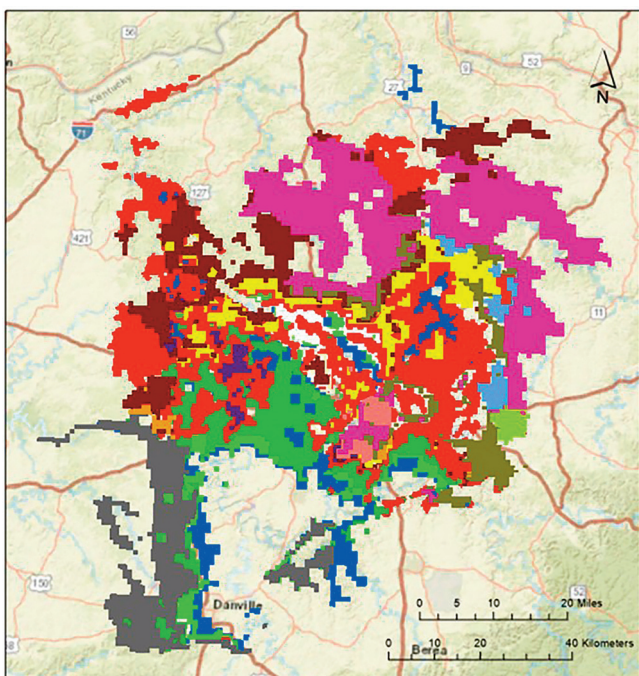
The Lexington members or tongues to be mapped were color-coded (Fig. 2), and those colors were applied to contacts in an already digitized state geologic map. Individual, colorized, contact horizons were then mapped as layers or feature classes (Fig. 3). Point features along each line were subsequently generated and associated with an elevation from the Kentucky Digital Elevation Model. Even though the colored layers appear to be horizontal, they represent a range of elevations. A half-mile buffer zone was then generated around each point



**Fig. 3.** Outcrop contacts for the Grier (blue), Tanglewood (orange and brown) and Devils Hollow (purple) members of the Lexington Limestone shown as specific, color feature classes, as indicated by similarly colored horizontal lines in Fig. 2.

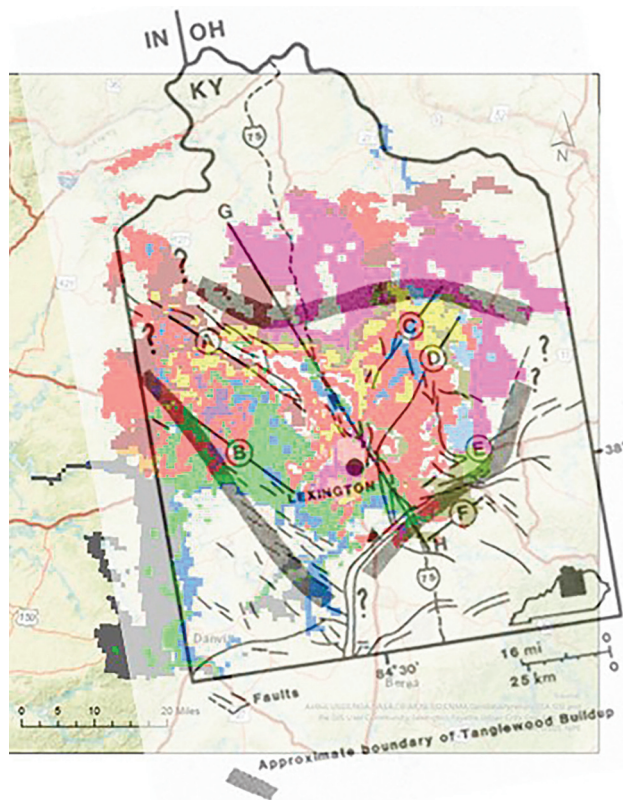


**Fig. 4.** Expanded (buffered) contacts of upper Lexington Limestone units in central Kentucky as 2-D polygons. Contact colors as indicated in Fig. 2.



**Fig. 5.** Aerial view of the 3-D raster file based on the data points in Fig. 4 for units in the upper Lexington Limestone. Colors reflect colored contact lines in Fig. 2.

feature on each color feature or contact so that each contact could be converted into a polygon with contour-like characteristics (Fig. 4). As each point on any one of the color contacts or features has an elevational component associated with it, the two-dimensional (2-D) map files (Fig. 4) can be converted into 3-D raster files, so that each color feature or contact represents a range of elevations (Fig. 5). The polygons in Fig. 5 are now 3-D compatible and presented in a superpositional framework so that colored layers higher in the section in Fig. 2 are superimposed on lower-level, colored layers.



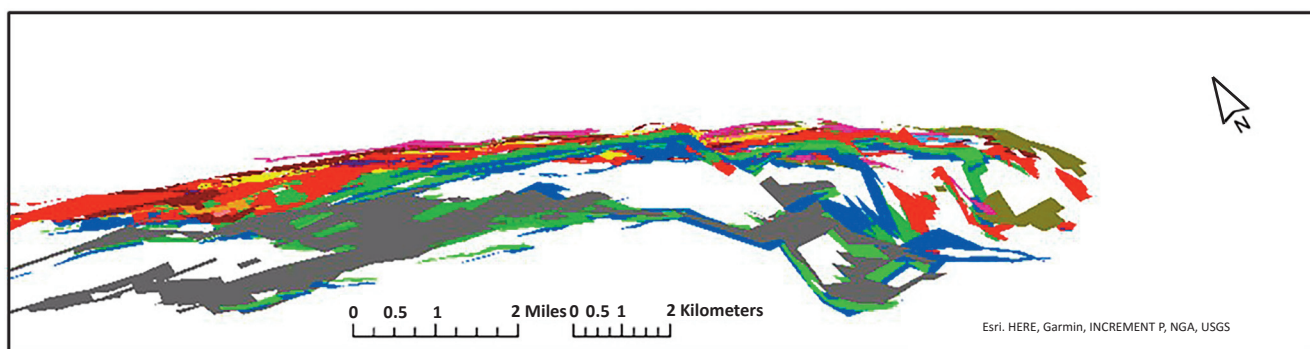
**Fig. 6.** Superposition of the Lexington area structure map from Ettensohn et al. (2004) on a 3-D raster-file map (Fig. 5), showing patterns that correlate with known structures.

Large-scale structural trends also become apparent when a Lexington area structural map (Ettensohn et al. 2004) is superimposed on the 3-D map (Fig. 6). This superpositional framework enables rotation around multiple axes, as shown in Fig. 7. Figure 7 depicts a cross-sectional view from an eastward-looking vantage point. Different rotational views may show varying trends in elevation, facies interrelationships, and the aerial extent of members and tongues.

### Discussion

This study demonstrates the possibility of using 2-D mapping to generate 3-D maps, observable from multiple vantage points. By color-coding important contacts and associating points on the contacts with elevation data, 2-D maps were used to generate 3-D properties, such as stratigraphic and structural trends. Changes in elevation and member distribution align well with the previously mapped 2-D, triangular Tanglewood buildup (Fig. 6), Jessamine Dome, and some major fault zones (Fig. 6). Although mapped structures do reflect reactivated basement faults, and 3-D mapping does suggest facies control by these structures, structural features such as the Jessamine Dome and the sloping beds in Fig. 7 are the product of structural activity during or since the last major orogenic event during Pennsylvanian–Permian time.

The methodology clearly has limitations, including the resolution of the stratigraphic horizons to be mapped, the type of software, and the extent of previous 2-D mapping. Confirming elevation data for contacts in the field is critical for ensuring confidence in the resulting 3-D maps.



**Fig. 7.** Three-dimensional sectional view of the map in Fig. 5, looking eastward, generated by rotation around an axis. The view shows the gently dipping nature of beds on the Jessamine Dome, as well as the sloping nature of the Grier (blue), Sulphur Well (gray), lower Tanglewood (light green) along a declivity in the right foreground that is associated with fault zone B and one side of the Tanglewood buildup (Fig. 6).

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We wish to thank the 3-D Geoframework Team at the Kentucky Geological Survey and the U.S. Geological Survey for their support of the project through the EDMAP program. Svend Stouge and an anonymous reviewer helped improve the quality of the paper. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

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# The Evae transgression: a major event?

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### ABSTRACT

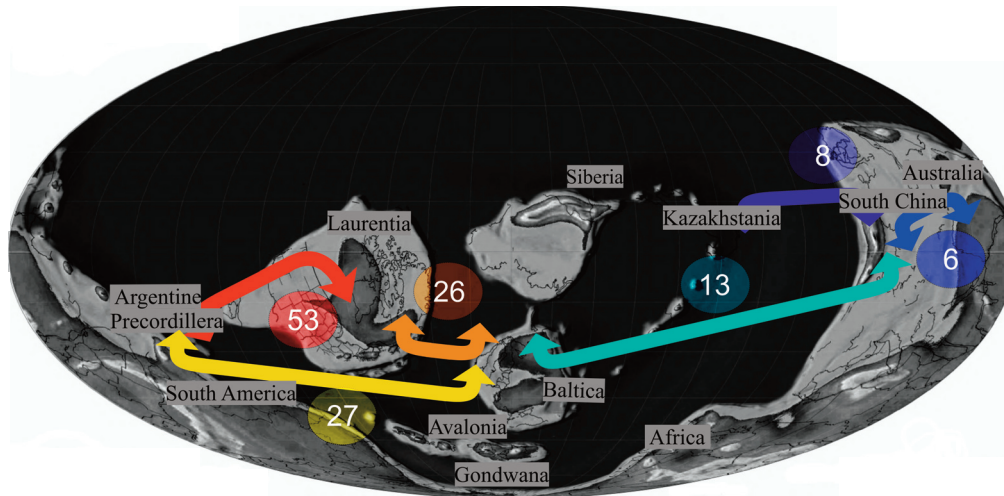
The most extensive sea-level event of the Early Ordovician is known as the Evae transgression. During the highstand of this event, the conodont index species *Oepikodus evae* reached its acme and often coincided with the peak in conodont generic diversity. The main objective of this study is to statistically evaluate the degree of similarity in conodont species composition between the Argentine Precordillera, Laurentia, Baltica, Kazakhstania, South China, and Australia at that time. Cluster analysis shows two main faunal groups moderately to poorly differentiated, indicating that some paleogeographic barriers may not have decreased during the Evae transgression. On the other hand, a paleolatitudinal control over the distribution of species is suspected, considering the occurrence of a higher number of species dwelling in mid-low latitudes than in mid-latitudes. This suggests that this event could have been of a lesser magnitude or duration than previously claimed.

### Introduction

The Evae transgression is considered the most extensive of the Early Ordovician (Bagnoli 1994). This event was explicitly reported in some sections of Laurentia, Baltica, South China, and the Argentine Precordillera (Stouge and Bagnoli 1988; Barnes 2004; Wu et al. 2010a, 2010b; Mango and Albanesi 2021). The index species *Oepikodus evae* reached its acme during the highstand of that transgression (Bagnoli 1994). Moreover, the first peak of conodont generic diversity has been recorded in Baltica (Nielsen 2004; Männik and Viira 2012) and South China (Wu et al. 2010a, 2010b) at that time. During the highest sea-level rises, shelf expansion leads to open-water species colonizing these environments, which occasionally drove some shelf species to extinction (Fortey 1984; Lehnert et al. 2013). At the same time, the appearance of new species by adaptive radiation often coincides with major transgressive events (Bagnoli 1994; Nielsen 2004). Another faunal response is the more fluid exchange of species at a global scale because the paleogeographic barriers tend to decrease, resulting in a provincial breakdown (Fortey 1984; Albanesi and Bergström 2010). The main objective of this study is to statistically evaluate the degree of similarity in conodont species composition between the Argentine Precordillera, Laurentia, Baltica, Kazakhstania, South China, and Australia during the highstand of the Evae transgression.

### Materials and methods

The highstand of the Evae transgression is defined here as the time interval when the conodont index species *Oepikodus evae* reached its acme, often coinciding with the peak in conodont generic diversity (Bagnoli 1994; Wu et al. 2010a, 2010b; Männik and Viira 2012; Mango and Albanesi 2021). Studies that do not fit this definition were excluded. This resulted in some plates, such as North China (e.g. An et al. 1983), Siberia (e.g., Sennikov et al. 2015) and intracratonic basins of Australia (e.g. Stewart and Nicoll 2003) not being represented in the analysis. A total of 35 studies from 28 sections worldwide were selected, located in the Argentine Precordillera, Newfoundland, Baltoscandia, South China, Kazakhstan, and Australia (Fig. 2A and references therein). The degree of similarity in conodont species composition was assessed by cluster analysis using the Jaccard index ( $J_i$ ), which has a range from 0 (no similarity) to 1 (maximum similarity) (Jaccard 1912). Based on the similarity matrix generated, the degree of similarity between the different paleocontinents is defined here as low or poor ( $J_i$  0 to 0.49), intermediate or moderate ( $J_i$  0.50 to 0.70) or high ( $J_i$  0.71 to 1). The analysis was performed with PAST 4.10 software (Hammer



**Fig. 1.** Paleogeographic map showing the possible migration shortcut routes and the number of shared species between the Argentine Precordillera, Laurentia, Baltica, Kazakhstania, South China, and Australia during the Eoalpine transgression (modified after Scotese 2014).

et al. 2001). Undetermined and redeposited conodont elements were excluded and some species were synonymized.

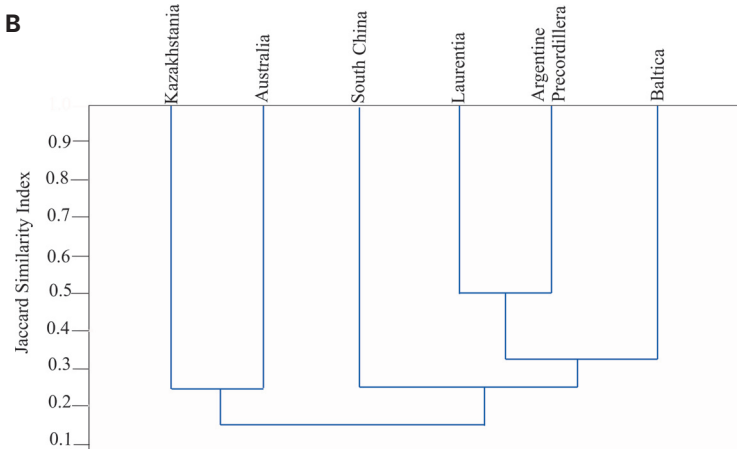
### Results and discussion

Cluster analysis shows two main faunal groups moderately to poorly differentiated (Ji 0.22 to 0.50) during the Eoalpine transgression (Fig. 2B). The first group includes Australia and Kazakhstania with a relatively low faunal similarity (Ji 0.22), which indicates a limited species interchange between these relatively nearby areas at that time. Based on the paleo-latitudinal location of Australia and Kazakhstania (Fig. 1), we

consider that the main barriers that might have restricted the species migration were temperature (convergence of cold-warm waters) and/or paleolatitudinal constraints. The lower number of species found in Australia and Kazakhstania (Fig. 2A) indicates unfavorable environmental conditions for the survival of various species during the Eoalpine transgression. In addition, the presence of a few endemic species in Kazakhstania suggests a certain degree of isolation of this region during that sea-level rise. However, these results could be affected by sampling bias because Australia is represented only by the Lachlan Orogen section and Kazakhstania by the Akzhal suite and Barite quarry sections in the present sta-

A	Paleocontinents	Richness	Sections	Sources of information
	Argentine Precordillera	74	Portezuelo Yanso, Niquivil, Los Gatos Creek, La Silla, Peña Sombria	Albanesi et al. 1998; Albanesi et al. 2006; Mango and Albanesi 2018, 2019, 2020; Authors' unpublished data
	Laurentia	86	Deep Kill, Martin Point, St Pauls Inlet North, Marathon, Wilcox Pass, Profilstranda, South Mayo, N8 9252 (Raven Gill)	Landing 1976; Fåhræus and Nowlan 1978; Johnston 1986; Stouge and Bagnoli 1988; Johnston and Barnes 1999; Izold 1993; Armstrong et al. 2001; Pyle and Barnes 2002; Pyle et al. 2003; Lehnert et al. 2013; Stouge et al. 2015
	Baltica	30	Furuhäll, Horns Udde, Andersön A, Section A (Jämtland), Finngrundet core, Gymninge, Sjurberg, Orreholmen, Mäekalda, Saka	Bagnoli et al. 1988; Bagnoli and Stouge 1997; Ahnesjö 1998; Löfgren 1978, 1985, 1993, 1994, 1996; Viira et al. 2001; Viira et al. 2006
	Kazakhstania	20	Akzhal suite, Barite quarry	Tolmacheva 2014; Tolmacheva et al. 2021
	South China	34	Huanghuachang, Liushuting	Wang et al. 2005, 2009; Wu et al. 2010a, 2010b; Li et al. 2010
	Australia	8	Lachlan Orogen	Zhen et al. 2021

**Fig. 2A** – table of data sets used in this study; **2B** – dendrogram from the cluster analysis based on the Jaccard index showing the similarity in conodont species of the lower *Oepikodus evae* interval between the Argentine Precordillera, Laurentia, Baltica, Kazakhstania, South China, and Australia.



istical analysis (Fig. 2A). Moreover, these sections represent siliciclastic depositional environments, which are poorer for the preservation of conodonts than carbonate-dominated settings (Zhen et al. 2021).

The second group consists of two subgroups, one exclusively with South China, and another formed by Laurentia, the Argentine Precordillera and Baltica. South China shares a relatively low proportion of species with Laurentia (Ji 0.19) and the Argentine Precordillera (Ji 0.26), probably due to the existence of a paleolatitudinal control over the distribution of species during the Evae transgression. In addition, the land areas of Kazakhstan could have functioned as barriers to the dispersal of species from South China to other paleocontinents. A few species are shared exclusively between South China and Australia, showing some exchange between those nearby plates. Moreover, some species were reported exclusively in South China, supporting the idea of a certain degree of isolation of this plate at that time. Although South China is represented by two sections (Fig. 2A), only the Huanghuachang section was heavily sampled as a candidate section for the GSSP of the Dapingian Stage (e.g. Wang et al. 2009). Consequently, it can be assumed that the results are not significantly affected by sampling bias, and probably most of the species that occurred in South China at that time were recorded. Laurentia and the Argentine Precordillera share a higher proportion of species (Ji 0.50), probably due to their close paleogeographic proximity and similar paleolatitudinal position. This probably allowed a more significant exchange of species than with other paleocontinents (Fig. 1). Baltica has less faunal similarity with Laurentia (Ji 0.29) and the Argentine Precordillera (Ji 0.35), perhaps because its location at mid-high latitudes resulted in latitudinal and oceanic constraints, which limited the migration of species there. On the other hand, Laurentia and the Argentine Precordillera show the highest species richness (Fig. 2A), indicating that these areas were the most suitable for the survival of most species under the prevailing conditions. This suggests a latitudinal gradient, with a higher number of species dwelling in mid-low latitudes than in mid-latitudes. Although some degree of exchange between relatively close paleocontinents was identified, it would be less than expected for an event of major magnitude or duration (Fortey 1984). In addition, Kazakhstan, Australia and South China were somewhat isolated, indicating that many paleogeographic barriers may not have decreased during the Evae transgression (Albanesi and Bergström 2010), contrary to what would be expected for a greater transgression.

## Conclusions

In the present study, a limited exchange of species between most of the paleocontinents was identified indicating that some barriers may not have been decreased at that time. On the other hand, a possible paleolatitudinal control over the distribution of species during the Evae transgression is suspected. This suggests that this event could have been of a lesser magnitude or duration than previously claimed. Nevertheless, these interpretations are based exclusively on the

statistical distribution of species in selected sections from the Argentine Precordillera, Baltica, Laurentia, South China, Kazakhstan and Australia, which fit the definition of the Evae transgression considered here. Additionally, the siliciclastic depositional environments and low representation of some sections could have biased the results.

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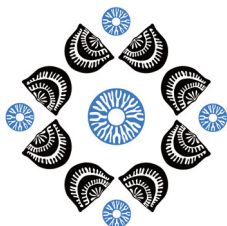
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# Darriwilian (Middle Ordovician) graptolites from the northern margin of the Qaidam Basin (Qinghai, China)

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### ABSTRACT

A restudy of the early Darriwilian graptolites from the Dameigou section in the Qaidam Basin provides some new information for graptolite biostratigraphy. The section contains a number of biserial faunas and easily identifiable *Holmograptus* Kozłowski, 1957, which are the marked faunas of the early Darriwilian. According to the biostratigraphic occurrences of the species, the *Levisograptus dentatus* Zone and the *Holmograptus lentus* Zone are identified from the Qaidam Basin. At the same time, the identification of these two graptolite zones provides materials for replacing the old, long-ranging *Amplexograptus confertus* Zone.

### Introduction

The northern margin of the Qaidam Basin (southern slope of Qilian Mountains) is one of the classic study areas for Middle Ordovician graptolitic strata in northwest China. Of the several sections in this area, the Shihuigou section contains a rich assemblage of Middle Ordovician graptolites.

The graptolites from this region were first studied by Hsü (1959), Mu et al. (1962) and Mu (1963). In 1959, Hsü identified the *Amplexograptus confertus* Zone in this region. Subsequently, Mu et al. (1962) and Mu (1963) identified the *Pterograptus elegans* Zone and the *Amplexograptus confertus* Zone, the latter zone was subdivided into the *Cardiograptus yini* Subzone and the *Paraglossograptus typicalis* Subzone. Chen et al. (2001) restudied the Ordovician graptolites collected from this region and suggested that the *C. yini* Subzone and the *P. typicalis* Subzone should be replaced by the *Archiclimacograptus confertus* Zone and the *Undulograptus austrodentatus* Zone, respectively. In addition, Ge et al. (1990) identified *Tylograptus* Subzone and the *Paraglossograptus typicalis* Subzone from the Miboshan Formation in Tongxin, Ningxia. These strata all belong to the Darriwilian.

### Materials and methods

The Shihuigou Formation originated from the ‘Shihuigou Shale’ redefined by Sun (1997). The strata are rich in graptolites, which are only distributed in Shihuigou and Oulongbuluk areas. The Shihuigou Formation is characterized by black shale with thin limestone, which conformably overlies the Duoquanshan Formation. The graptolite specimens were collected from poorly consolidated black or dark grey shales (Fig. 1). The section belongs to the lower part of the Shihuigou Formation (total thickness is 22.72 m), and the graptolite specimens were collected bed by bed, starting from the base of the section. Most specimens were photographed directly. The materials are deposited in the collections of the Institute of Geology, Chinese Academy of Geological Sciences. The electronic documentation of the study on fossils and strata is deposited in the Geological Survey Stratigraphy and Palaeontology Database of China at <http://8.140.107.20:8080/navigator/index.aspx>.



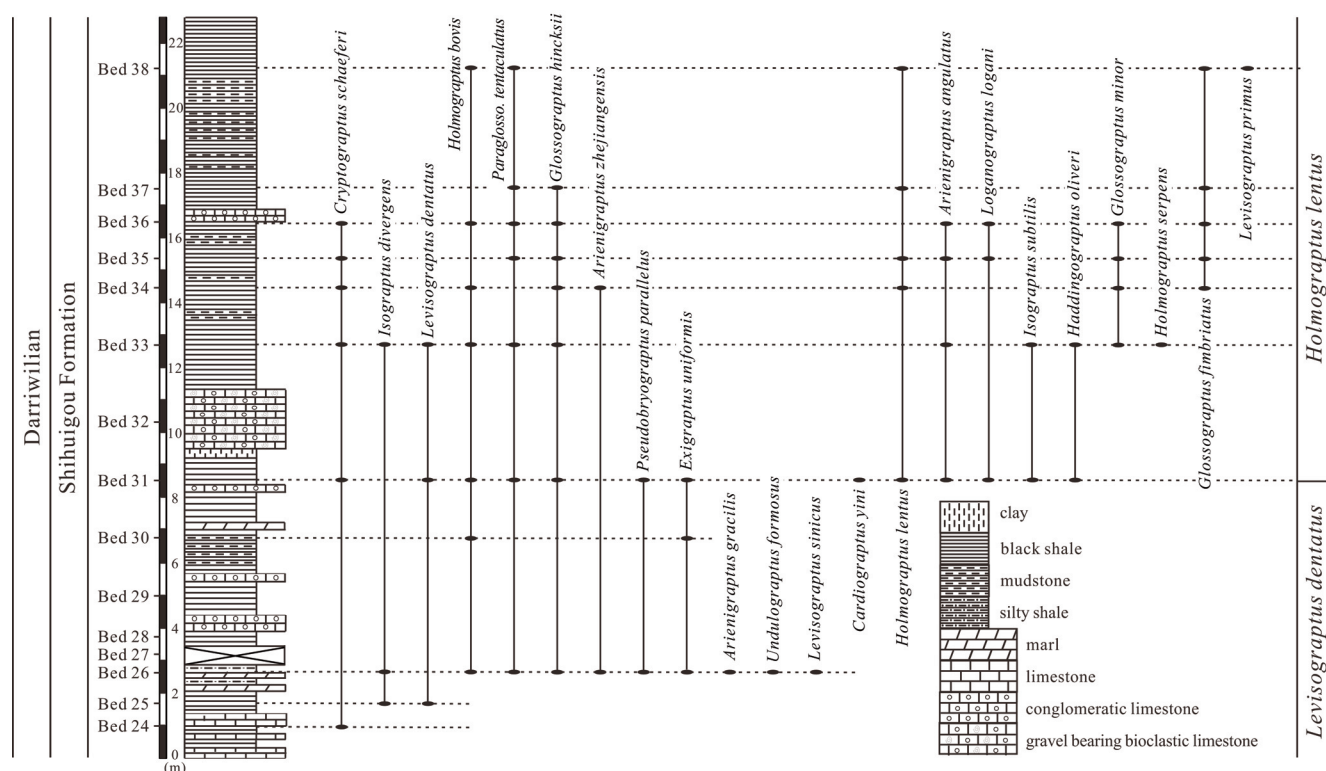


Fig. 1. Graptolite biostratigraphy of the Dameigou section, Qaidam Basin.

### The faunal succession

In the Qaidam Basin, the early Darriwilian was identified by *Levisograptus dentatus* Brongniart. In this study, we recognized *L. dentatus* Brongniart, *L. sinicus* Mu and Lee, *Holmograpus lentus* Törnquist (Fig. 2). Since *H. lentus* is the zone fossil of the *Holmograpus lentus* Zone, we identified two zones in the study area: the *Levisograptus dentatus* Zone and the *Holmograpus lentus* Zone.

#### The *Levisograptus dentatus* Zone

The bottom boundary of the *Levisograptus dentatus* Zone is defined by the first appearance strata (FAD) of *Levisograptus dentatus* Brongniart. In the Qilian Mountains, the FAD of *Levisograptus dentatus* is recognized in Bed 25 (see Fig. 1). The graptolite fauna in this zone is very diverse, with many biserial faunas (e.g. *Levisograptus dentatus* Brongniart, *Levisograptus sinicus* Mu and Lee, *Levisograptus primus* Legg and *Undulograptus formosus* Mu and Lee). In our section, *L. dentatus* is associated with *L. sinicus* and *Holmograpus bovis*, and this fossil assembly in the *L. dentatus* Zone is similar to that in Canada and Argentina (Ortega and Albanesi 2003; Maletz 2009; Serra et al. 2017).

*Levisograptus dentatus* Brongniart (= *Glyptograptus dentatus* (Brongniart)) is a species indicated in the early studies on graptolitic strata in the southern slope of Qilian Mountains. Mu et al. (1962) and Mu (1963) identified the *Amplexograptus confertus* Zone (Fig. 3), including the *Cardiograptus yini* Subzone and the *Paraglossograptus typicalis* Subzone in the Shihuigou section (south of our section). There, in the *Paraglossograptus typicalis* Subzone, *Pseudoclimacograptus formosus* Mu and Lee (= *Undulograptus formosus* Mu and Lee) and *Glyptograptus dentatus* (Brongniart) occur, which are

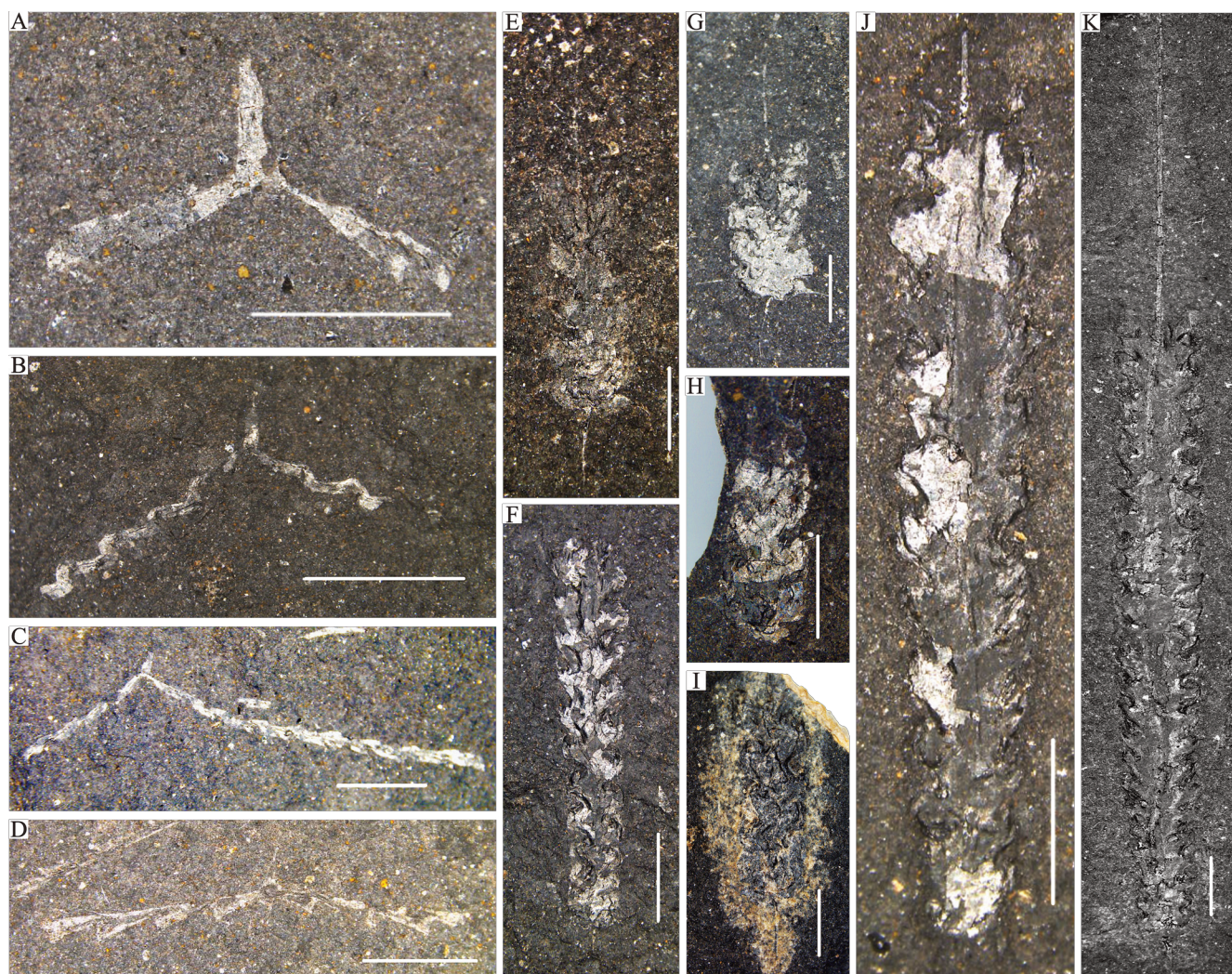
common fossils of the *L. dentatus* Zone from our Dameigou section. The *Paraglossograptus typicalis* Subzone in the Shihuigou section is generally correlated with the *L. dentatus* Zone from the study section.

#### The *Holmograpus lentus* Zone

The bottom boundary of the *Holmograpus lentus* Zone is defined by the FAD of *Holmograpus lentus*. In the Qilian Mountains, the FAD of *Holmograpus lentus* is recognized in Bed 31 (Fig. 1). This unit is rich in *Holmograpus* Kozłowski, the *Holmograpus lentus* Zone of the Dameigou section has different species of *Holmograpus* Kozłowski, including *Holmograpus lentus* Törnquist, *H. bovis* Williams and Stevens, *H. serpens* Brussa (Fig. 2), which is similar to that in Precordillera, Argentina (Ortega and Albanesi 2003).

The relationship between *Holmograpus* Kozłowski and *Tylograptus* Mu is still controversial. Some researchers suggest that these two genera are similar (Jaanusson 1965; Skevington 1965; Maletz 2009). Referring to the aperture and prothecal folds, Zhang and Fortey (2001) suggested that these two genera are still valid. According to the materials in our section and the supplementary figures in Zhang and Fortey (2001, TEXT-FIG. 3.c) and Mu et al. (1962), we found that *Tylograptus geniculiformis* Mu and *Holmograpus lentus* Törnquist share similar aperture features and prothecal folds, and we advocate that these two species are the same.

The *Amplexograptus confertus* Zone is identified in the Miboshan Formation in Tongxin, Ningxia, it includes the *Tylograptus* Subzone and the *Paraglossograptus typicalis* Subzone (Ge et al. 1990). Chen et al. (2001) restudied this formation and revised the *Tylograptus* Subzone to the *Tylograptus* Zone, the *Paraglossograptus typicalis* Subzone to the



**Fig. 2.** **A** – *Holmograpthus bovis* Williams and Stevens, 8.25–8.45 m; **B** – *Holmograpthus serpens* Brussa, 12.11–12.31; **C** – *Holmograpthus lentus* Törnquist, 8.25–8.45 m; **D** – *Xiphograptus lofuensis* Lee, 8.25–8.45 m; **E** – *Levisograptus sinicus* Mu and Lee, 1.50–1.70 m; **F** – *Levisograptus sinicus* Mu and Lee, 8.25–8.45 m; **G** – *Undulograptus primus* Legg, 20.54–20.74 m; **H** – *Undulograptus primus* Legg, 16.68–16.88 m; **I** – *Undulograptus formosus* Mu and Lee, 12.11–12.31 m; **J, K** – *Levisograptus dentatus* Brongniart, 8.25–8.45 m, 8.25–8.45 m. Specimen numbers: **A** – QHDM 31-116-05; **B** – QHDM 33-27-07; **C** – QHDM 31-70-03; **D** – QHDM 31-09-02; **E** – QHDM 26-60-01; **F** – QHDM 31-05-01-02; **G** – QHDM 38-23-01; **H** – QHDM 37-10-03; **I** – QHDM 33-14-06; **J** – QHDM 31-02-01; **K** – QHDM 31-65-01. **B, D, E, F, H, I** were photographed under water. The white bar = 2 mm.

China				Canada	Argentina
Shihuigou section, Qaidam Basin		Tongxin section, Ningxia	Dameigou section, Qaidam Basin	Maletz 2009	Ortega and Albanesi 2003; Serra et al. 2017
Hsü 1959	Mu et al. 1962; Mu 1963	Ge et al. 1990; Chen et al. 2001	This paper		
<i>Amplexograptus confertus</i> Zone	<i>Amplexograptus confertus</i> Zone	<i>Cardiograptus yini</i> Subzone	<i>Tylograptus</i> Zone	<i>Holmograpthus spinosus</i> Zone	<i>Holmograpthus spinosus</i> Zone
				<i>Holmograpthus lentus</i> Zone	<i>Holmograpthus lentus</i> Zone
		<i>Paraglossograptus typicalis</i> Subzone	<i>Undulograptus austrodentatus</i> Zone	<i>Levisograptus dentatus</i> Zone	<i>Levisograptus dentatus</i> Zone
				<i>Levisograptus austrodentatus</i> Zone	<i>Levisograptus austrodentatus</i> Zone

**Fig. 3.** Correlation chart for China, Canada and Argentina.

*Undulograptus austrodentatus* Zone, respectively (Fig. 3). In this section, the *Tylograptus* Zone includes *Tylograptus* sp., *T. spinatus* Mu, *T. regularismus* Mu and *T. globiformis* Mu. There, *T. globiformis* Mu is related to *Holmograpthus lentus*.

Thus, the *Tylograptus* Zone in the Miboshan Formation of Ningxia is comparable to the *Holmograpthus lentus* Zone in our section. Mu et al. (1962) recognized that *Cardiograptus yini* M., G. and Y. are associated with *L. dentatus* and *H. lentus*

(*H. lentus* was named *Tylograptus geniculiformistong* in Mu et al. 1962) in the *Cardiograptus yini* Subzone of the *Amplexograptus confertus* Zone. The FAD of *H. lentus* is at the base level of the *Cardiograptus yini* Subzone (Mu et al. 1962). In our study area, *Cardiograptus yini* M., G. and Y., *H. lentus* Törnquist also appeared in the same layer, whereas the *Cardiograptus yini* Subzone was including *Cardiograptus yini*, *H. lentus* and *L. dentatus* in the Shihuigou section. Therefore, we supposed that the *Cardiograptus yini* Subzone in the Shihuigou section is comparable to the *Holmograptus lentus* Zone in the Dameigou section.

## Conclusions

The Dameigou section in the northern margin of the Qaidam Basin represents early Darriwilian stratigraphic successions in the lowest portion of the Shihuigou Formation. The Darriwilian graptolite fauna includes biserial elements (e.g. *Undulograptus* Bouček and *Levisograptus* Maletz). Referring to our collections, two zones (the *Levisograptus dentatus* Zone and the *Holmograptus lentus* Zone) have been identified. Nowadays, the Darriwilian stratigraphic successions identified in the northern margin of the Qaidam Basin include the *Undulograptus austrodentatus* Zone, the *Levisograptus dentatus* Zone, the *Holmograptus lentus* Zone, the *Pterograptus elegans* Zone (from bottom to top).

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# Solutan echinoderms from the Lower Ordovician of the Montagne Noire (France): new data and palaeobiogeographic implications

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### ABSTRACT

Solutans are relatively common members of echinoderm assemblages in the Saint-Chinian Formation (upper Tremadocian) of the Montagne Noire (France). The revision of all available material confirms that most specimens can be assigned to *Minervae cystis vidali*, which is here reconstructed for the first time. The occurrence of *Plasiacystis mobilis* is evidenced based on a single, well-preserved dististele. The interpretation of the small-sized individual as a putative dendrocystitid is rejected: it corresponds to a juvenile specimen of *M. vidali*. Early Ordovician solutans from the Montagne Noire partly fill the gap between Laurentian mid-late Cambrian syringocrinids and Avalonian-Gondwanan Early-Middle Ordovician taxa.

### Introduction

In spite of some recent reports (e.g. Zhu et al. 2016), very few Furongian–Early Ordovician echinoderm faunas are known worldwide from this critical interval at the transition between the Cambrian explosion and the Great Ordovician Biodiversification Event (Smith 1988). Along with the Fillmore Formation in western Utah, USA (Sprinkle and Guensburg 1995), and the lower part of the Fezouata Formation in the Central Anti-Atlas, Morocco (Lefebvre et al. 2016), the Saint-Chinian Formation in the Montagne Noire, France, is one of the few lithostratigraphic units yielding abundant and diverse Tremadocian echinoderm remains (Thoral 1935; Vizcaïno and Lefebvre 1999; Vizcaïno et al. 2001). This situation probably results from their remarkable three-dimensional preservation in alumino-siliceous concretions and also from nearly 150 years of intensive, continuous sampling (Vizcaïno et al. 2001 and references therein). Echinoderm assemblages from the Saint-Chinian Formation comprise over 30 taxa belonging to eight classes. In terms of abundance and diversity, stylophorans (cornutes and mitrates) are the dominant group. The Saint-Chinian Formation also comprises some of the earliest representatives of the subphylum Asterozoa and of the class Crinoidea. This unit also yielded edrioasteroids, eocrinoids, rhombiferans and solutans (see Vizcaïno and Lefebvre 1999; Vizcaïno et al. 2001 and references therein).

Along with eocrinoids, glyptocystitid rhombiferans and stylophorans, solutans are typical members of the cosmopolitan, low-diversity, Furongian–Early Ordovician echinoderm assemblages (Sumrall et al. 1997; Lefebvre et al. 2013; Zhu et al. 2016). Late Cambrian and younger solutans were vagile members of benthos, generally interpreted as probable detritus-feeders, sweeping soft substrates with their unique feeding appendage (e.g. Kolata 1973; Noailles et al. 2014; Nohejlová and Lefebvre 2022). From Lower Ordovician sediments of the Montagne Noire, a single species of solutans has been described so far (*Minervae cystis vidali*) from the concretion-bearing shales of the Saint-Chinian Formation (Thoral 1935; Ubaghs 1970). Based on the examination of all available material (historical collections and additional specimens collected since Ubaghs' 1970 seminal description of *M. vidali*), the aims of this paper are (1) to revise the morphology and produce the first reconstruction of *Minervae cystis*; (2) to describe and document the first occurrence of *Plasiacystis mobilis* in the Lower Ordovician strata of southern France; and (3) to discuss the palaeobiogeographic affinities of the Montagne Noire solutans.

## Materials and methods

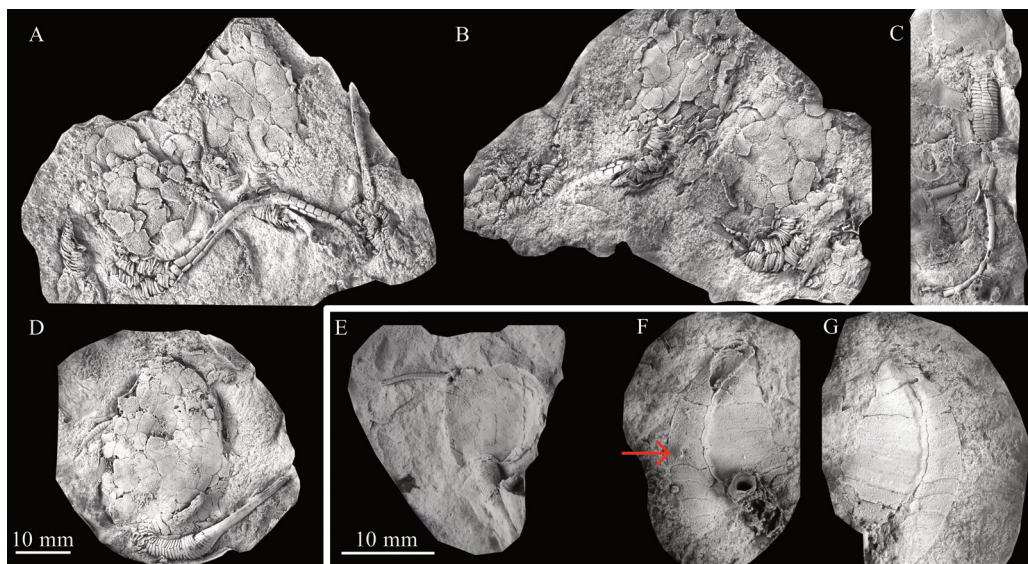
The study material includes 42 solutan specimens collected from the Lower Ordovician of the Montagne Noire (southern France) and catalogued in the following public collections: Natural History Museum, London (BMNHUK: Miquel collection), Musée du Biterrois, Béziers (MBB: Griffé collection), Muséum National d'Histoire Naturelle, Paris (MNHN: Courtessole-Griffé collection), Lyon 1 University, Villeurbanne (UCBL.FSL: Lignières, Kundura, Villebrun, and Vizcaïno collections), and Montpellier University, Montpellier (UM: Azaïs, Roquefort, Thoral, and Villebrun collections). All specimens are from the Saint-Chinian Formation (late Tremadocian, *Euloma filacovi* Zone; see Vizcaïno and Álvaro 2003). In the Saint-Chinian area, this 500 m thick formation consists of relatively monotonous dark concretion-bearing siltstones with fine sandstone intercalations (Vizcaïno et al. 2001; Vizcaïno and Álvaro 2003). The Saint-Chinian Formation has yielded a particularly diverse fossiliferous assemblage typical of moderately deep, well-oxygenated shelf environments, below storm wave base, and comprising bivalves, brachiopods, cephalopods, conulariids, echinoderms, gastropods, graptolites, hyolithids, machaeridians, and trilobites (Thoral 1935; Vizcaïno et al. 2001).

All fossils are preserved three-dimensionally, as empty negative moulds, in aluminosiliceous concretions. So as to reveal their original aspect, solutans were cast with latex and coated with ammonium chloride (NH<sub>4</sub>Cl) for drawing and photographic purposes. Observations and camera lucida drawings were made with a Zeiss SteREO Discovery.V8 binocular stereomicroscope, and photographs with a Canon 5DSR camera equipped with a MP-E 65 mm macro lens. Digital drawings were made with the help of the software Krita 5.0.2.

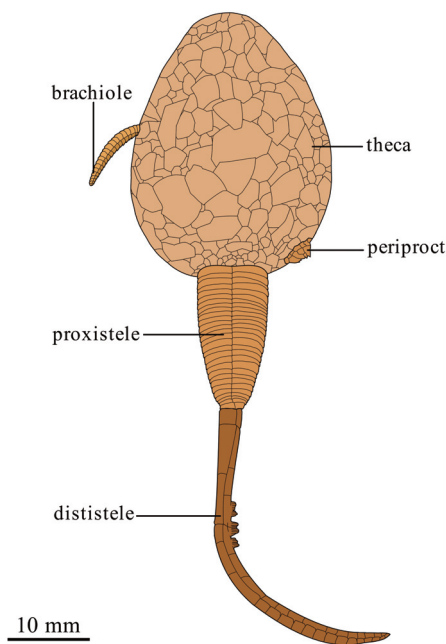
## Results

The re-examination of Thoral's (1935) original type series and over 30 additional specimens (Fig. 1A–E) did not give any significant additional morphological information to the very detailed description of *Minervaecystis vidali* provided by Ubaghs (1970). However, this abundant material made it possible to elaborate on the first detailed, specimen-based reconstruction of this solutan (Fig. 2). Tentative reconstructions of *M. vidali* were already provided by Lefebvre et al. (2012, fig. 2.1) and Rozhnov (2022, fig. 4h), but they were simply combining two original camera lucida drawings figured in Ubaghs (1970, figs 39.1 and 41.1). Moreover, the observation of all available individuals of *M. vidali* indicates that, when preserved, their twisted dististele is not straight but consistently curved to the right (Fig. 1A, C). *Minervaecystis* shares with *Pahvanticystis* and *Plasiacystis* the possession of a non-apical, laterally inserted brachiole, a relatively large, inflated, ovoid theca, and a flattened, twisted dististele (Lefebvre and Lerosey-Aubril 2018). *Minervaecystis* differs from *Pahvanticystis* in the more posterior insertion of its brachiole, a proportionately longer proxistele (comprising over 20 tetramerous rings), and the morphology of its dististele (narrower, and with lateral comb-like spikes). *Minervaecystis* mostly differs from *Plasiacystis* in having a proxistele consisting of numerous, regularly arranged tetramerous rings (this region is composed of numerous, unorganized, imbricate, scale-like plates in *P. mobilis*), and an elongate, stem-like dististele, instead of a short, broad, paddle-like distal structure (Prokop and Petr 2003; Lefebvre et al. 2012).

Lefebvre and Lerosey-Aubril (2018) questioned the possibility that the smallest known individual assigned to *Minervaecystis* (UM.AC1.636) and figured by both Thoral



**Fig. 1.** Solutans from the Saint-Chinian Formation (upper Tremadocian), Montagne Noire (Hérault, France); latex casts of original specimens. **A–E** – *Minervaecystis vidali* (Thoral, 1935); **A–B** – cluster of four individuals (part and counterpart); BMNHUK.E.23695 (Miquel coll.), locality Cassagnoles; **A** – nearly complete individual (in lower aspect) in the centre of the cluster, with a fully articulated brachiole and a long, strongly curved, twisted dististele; **B** – same individuals (in upper aspect); **C** – well-preserved individual (in lower aspect) with a strongly curved, twisted dististele; UCBL.FSL.713595 (Kundura coll.), locality Prades-sur-Vernazobre; **D** – fully articulated theca (in upper aspect) with a brachiole and a well-preserved anal pyramid, to the right of homoio스테 insertion; lectotype, UM.AC1.634 (Villebrun coll.), locality Saint-Chinian; **E** – juvenile individual; UM.AC1.636 (Thoral coll.), locality Prades-sur-Vernazobre; **F–G** – *Plasiacystis mobilis* Prokop and Petr, 2003; latex casts of the dististele (part and counterpart) of the single known specimen (MBB.GG.6, Griffé coll.), locality Saint-Chinian; note the presence of a well-defined spike-shaped tubercle on one of the two sides (**F**, red arrow).



**Fig. 2.** Reconstruction of *Minervaeocystis vidali* (Thoral, 1935), Saint-Chinian Formation (upper Tremadocian), Montagne Noire (France).

(1935, pl. 11, fig. 2) and Ubaghs (1970, pl. 16, fig. 5) could represent one of the oldest known dendrocystitid solutans. Their suggestion relied on the quadrangular aspect of the theca and, mostly, on the location and morphology of the periproct (relatively large, rounded, low structure formed of several elongate tapered plates forming a well-defined anal rosette). However, the re-examination of the original specimen (Fig. 1E) does not support this interpretation but confirms its identification as a juvenile individual of *M. vidali* (Thoral, 1935; Ubaghs 1970). Its unusual aspect results from the combination of a theca preserved as a hollow internal mould, with two appendages (brachiole and homoiostele) occurring as three-dimensional external moulds. Consequently, contrary to most other specimens of *Minervaeocystis*, the periproct of UM.ACI.636 is visible in internal view. Its regular arrangement into a well-defined, closed rosette suggests that the prominent, cone-shaped (external) morphology of the periproct observed in most individuals is possibly preservational and/or results from its ability to open outwards (valvular structure). As in all other specimens of *Minervaeocystis*, the brachiole of UM.ACI.636 is inserted laterally, away from the apex and on the antanal side of the theca (i.e. opposite the periproct).

Although the occurrence of *Plasiacystis mobilis* in the Lower Ordovician of the Montagne Noire was regularly mentioned (e.g. Lefebvre et al. 2012, 2016), no remains of this solutan have been formally described or illustrated from this region so far. The detailed re-examination of the historical collections made it possible to confirm the presence of *P. mobilis*, based on a single, well-preserved, isolated dististele (MBB.GG.6, part and counterpart) collected from the Saint-Chinian Formation. Its short and broad, bean-shaped, flattened morphology (Fig. 1F–G) is typical of *Plasiacystis* and identical to the dististele in Czech specimens of *P. mobilis* (see Prokop and Petr 2003; Lefebvre et al. 2012). The distally

incomplete paddle-like appendage of MBB.GG.6 consists of two unequal series of wide, flattened plates, with those forming the concave lateral edge about twice as long as those on the opposite, convex margin. The dististele slightly increases in thickness along the longitudinal suture running along the opposite sets of plates, left and right. In MBB.GG.6, a well-defined tubercle (spike) occurs on one side of the dististele. It cannot be formally excluded that some poorly preserved solutan thecae traditionally assigned to *Minervaeocystis* may indeed belong to *Plasiacystis*.

## Discussion

Their abundant and almost continuous fossil record from the lower Drumian to the upper Floian of (modern) North America (Alabama, Nevada and Utah) suggests that solutans very likely originated in Laurentia (Zamora et al. 2013a; Lefebvre and Lerosey-Aubril 2018), possibly from a gogiid-like ancestor (Parsley 1997). The yet undescribed solutans from the Sandu Formation (Jiangshanian) of South China represent the earliest known occurrence of this clade outside Laurentia (Zamora et al. 2013b; Zhu et al. 2016). In this context, the late Tremadocian solutans from the Montagne Noire correspond, along with coeval occurrences from the Central Anti-Atlas (Morocco), to the earliest known record of this class in high-latitude Gondwanan regions (Lefebvre et al. 2013, 2016). The two taxa occurring in the Lower Ordovician of southern France (*Minervaeocystis* and *Plasiacystis*) are closely related to Cambrian syringocrinids from Laurentia (*Castericystis*, and mostly *Pahvanticystis*; see Lefebvre and Lerosey-Aubril 2018). Although *Minervaeocystis vidali* is so far considered endemic to the Montagne Noire, very similar isolated homoiosteles sp. from the Whipple Cave Formation (upper Furongian) of Nevada (Ubaghs 1963; Sumrall et al. 1997) have been tentatively assigned to this genus (*Minervaeocystis?* sp.), and the yet undescribed remains of minervaeocystids are also known from the Wah Wah Formation (late Floian) of Utah (Sprinkle and Guensburg 1993). In sharp contrast to the Montagne Noire, where it is extremely rare, *Plasiacystis mobilis* is particularly abundant and widespread in the Lower Ordovician of Morocco, with occurrences ranging from the late Tremadocian to the late Floian (Lefebvre et al. 2016; Saleh et al. 2022; Dupichaud and Lefebvre 2022). The latter solutan has a remarkably long temporal range, as it is also present in the Darriwilian of Shropshire, UK (Hope Shale; Lefebvre et al. 2012), and of the Prague Basin, Czech Republic (Šarka Formation; Prokop and Petr 2003; Lefebvre et al. 2012).

## Conclusions

Solutans were relatively common members of late Tremadocian benthic communities in the southern Montagne Noire (France). The revision of all available specimens from the Saint-Chinian Formation made it possible to confirm the occurrence of two distinct taxa: (1) the most abundant one, *Minervaeocystis vidali*, is here reconstructed for the first time, with new information on the morphology of its periproct;

(2) *Plasiacystis mobilis*, which is particularly rare in the Lower Ordovician of the Montagne Noire, is described and figured for the first time; and (3) the occurrence of putative dendrocystitids is not confirmed. The Montagne Noire solutan assemblage documents a key evolutionary transition, with a mixture of plesiomorphic morphologies inherited from the worldwide expansion of syringocrinids outside Laurentia in the late Cambrian (*Minervaecystis*), and the onset of new, highly derived morphotypes in Avalonia and Gondwana (*Plasiacystis*) in the Early and Middle Ordovician. During the Darrwilian, the persistence and diversification of solutans in the latter two geographic areas fuelled their expansion to Baltica and Laurentia (where they had disappeared at the end of the Floian) in the Late Ordovician.

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# Tectonic, foreland-basin origins of Upper Ordovician black gas shales in the Appalachian Basin of eastern United States

Frank R. Etensohn and Gustavo Martins

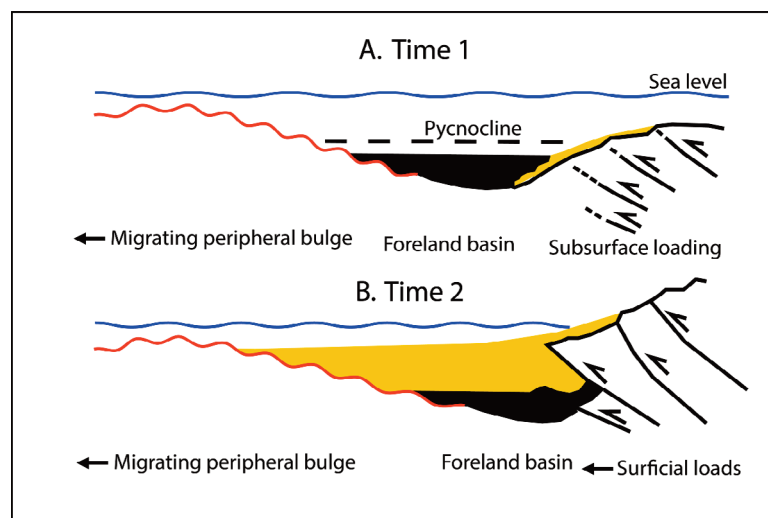
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### ABSTRACT

Black gas shales are major parts of many foreland-basin sequences and comprise important components of unconformity-bound tectophase cycles, which reflect sedimentary/stratigraphic, flexural responses to deformational loading and relaxation in an orogen. Using as examples Upper Ordovician black gas shales, deposited during the Taconian orogeny in the Appalachian Basin of the eastern United States, black-shale origins and their importance in understanding the tectonic framework are discussed. Foreland-basin black shales are clearly the product of distinctive tectonic frameworks and histories, and aside from economic value, may provide important controls on the timing and location of tectonic events.

### Introduction

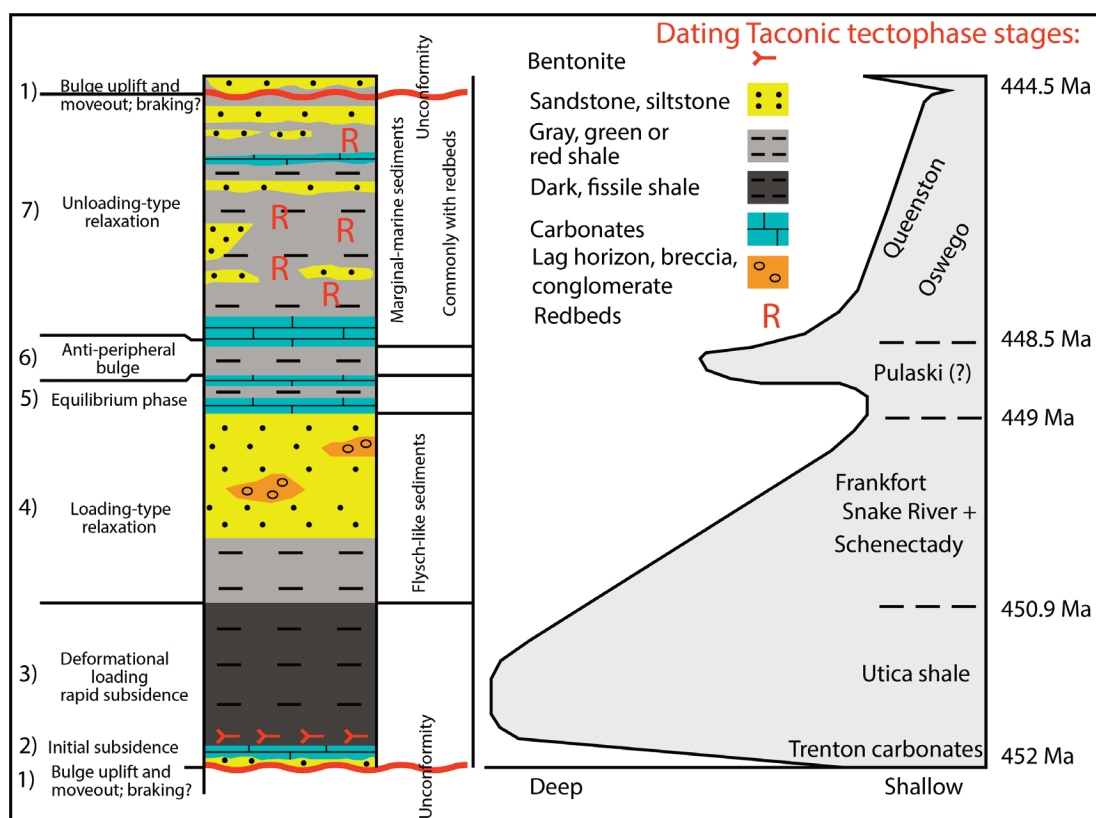
In the Appalachian Basin, gas-prone black shales are major parts of most flexural, foreland-basin sequences and reflect the timing of major loading-related, foreland subsidence. The Upper Ordovician Utica black shales, for example, are some of the most productive gas shales in the United States, and they represent early foreland-basin deposits during the Taconic tectophase of the Taconian orogeny (Etensohn 1991). In fact, black shales are among the earliest deposits in foreland basins (Fig. 1A) and are parts of cycles showing a consistent sequence of lithologies, called tectophase cycles (Fig. 2). Overlying a bulge-related unconformity, marine black



**Fig. 1.** Schematic diagrams showing the timing and relationships between foreland-basin generation, bulge moveout, sediment infill and deformational loading in the orogen.

**A** – basin-bulge formation during early, subsurface, subaqueous deformational loading with little sediment influx during the first three phases of a typical tectophase cycle (Fig. 2). With major subsidence and little clastic input, organic-rich muds accumulate in the deep, stratified basin. **B** – “loading-type relaxation” (Fig. 2, phase 4), during which a now-static surficial load and drainage net develops, supplying coarser clastic sediments to the subsiding foreland basin. A pycnocline is a zone of thermohaline density stratification in a deepening basin with decreasing O<sub>2</sub> content (adapted from Etensohn 1997). Orange color – coarser clastic sediments, black color – black, organic-rich muds.





**Fig. 2.** A typical unconformity-bound tectophase cycle from the northern Appalachian Basin. Unit names are examples from the Late Ordovician Taconic tectophase of the Taconian orogeny (see Figs 3b, 4) in New York State. Dates are derived from the radiometric dating of bentonites and biostratigraphy. The Upper Ordovician Utica Shale Group and its equivalents at the base of the tectophase sequence are major sources of unconventional gas in the eastern United States (Kirschbaum et al. 2012) (adapted from Ettensohn et al. 2019).

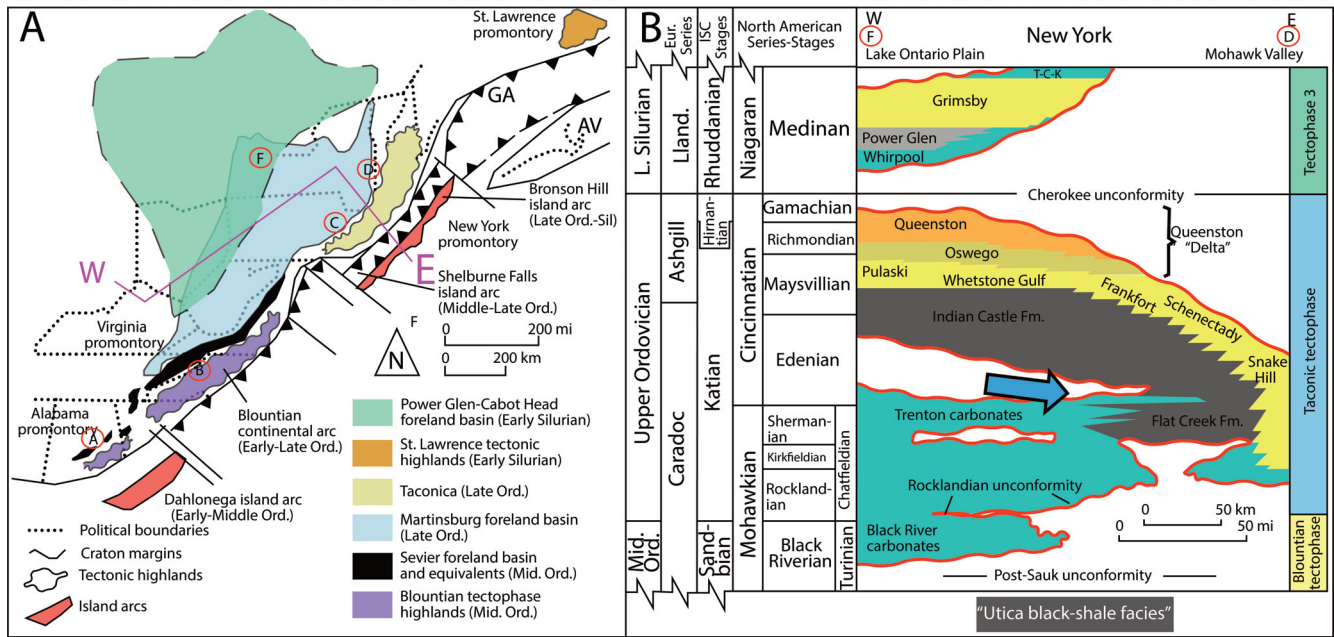
shales initiate most cycles and mark the time of maximum deformational loading and flexural subsidence. However, they are deposited when most deformation is subaqueous and produces little clastic influx (Fig. 1A). In the absence of major clastic input, organic matter with suspended clay and silt comprises most of the sedimentation in the early foreland basins. With rapid subsidence and low sedimentation rates, the basins quickly became stratified, facilitating the preservation of the organic-rich sediments (Fig. 1A). The shales in each cycle are overlain by a series of relaxational clastics, including deeper-water, flysch-like clastics followed by more shallow, marginal-marine, molasse-like clastics. These thick clastic deposits may preserve underlying organic-rich sediments from weathering and erosion and provide potential reservoirs for conventional hydrocarbons derived from the underlying organic-rich muds.

### Tectonic implications

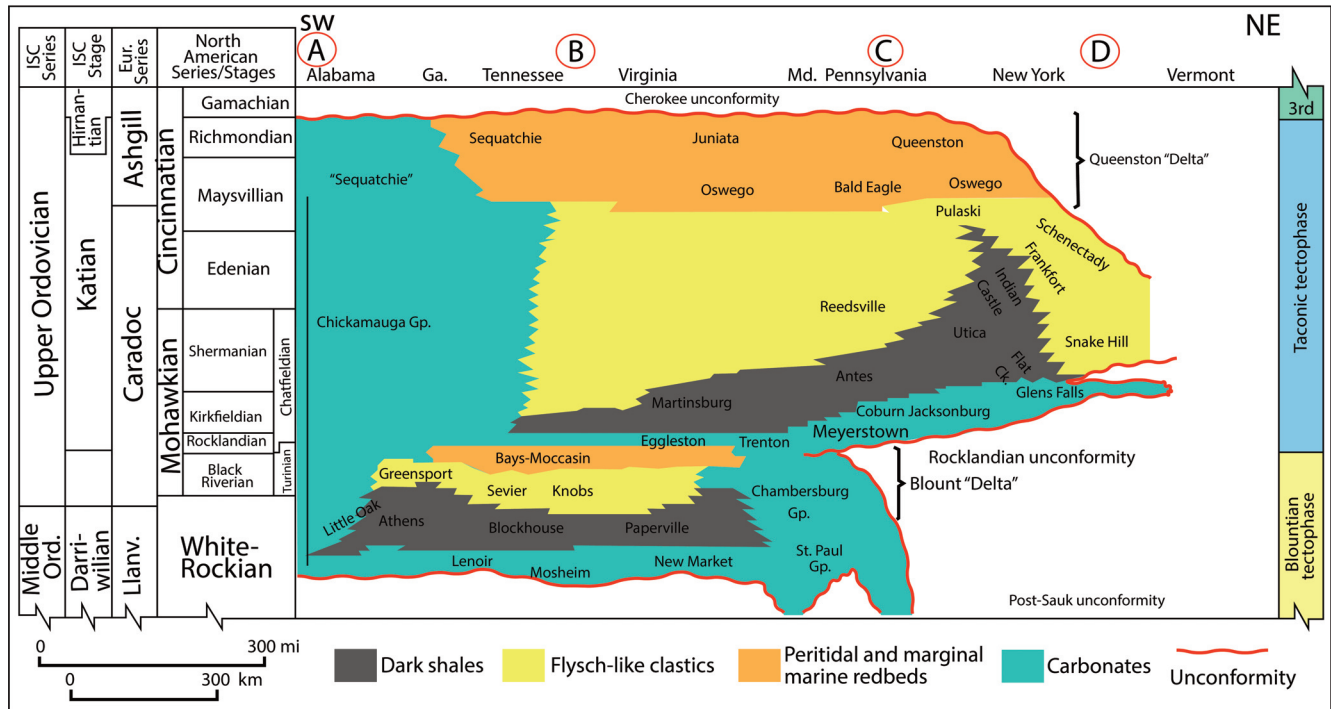
Moreover, because of the distinctive character of black shales in the surface and subsurface, mapping their distribution (Fig. 3A) supports the role of tectonism in their origin and may even help track the progression of orogeny in space and time. In the Appalachian area of the United States, the distribution of Middle to Upper Ordovician black shales suggests that the Taconian orogeny proceeded in a diachronous fashion from south to north along the eastern Laurentian margin, and that tectophases were mediated by convergence

at successive continental promontories. Hence, based on black-shale distribution, the Taconian orogeny was apparently a “transgressive” orogeny in that the locus of convergence shifted northeastwardly parallel to the strike of the Appalachian Basin during Mohawkian (Sandbian–Katian, Blackriverian–Chatfieldian) time. By the end of Blackriverian time, the Blountian tectophase of the Taconian orogeny largely focussed on the Virginia promontory, had expended itself, while by the Blackriverian–Chatfieldian (early Katian) transition, the focus of orogeny had shifted to the New York promontory in what has been called the Taconic tectophase. This transition between tectophases and black-shale foreland basins is illustrated along section line A-B-C-D in Figs 3A and 4 and was mediated by successive southwest-northeast collisions at continental promontories (Fig. 3A).

Abrupt changes in the distribution of black shales in time and space, as noted at the arrow in Fig. 3B, may also indicate major changes in the nature of the orogeny. For example, during the Late Ordovician (Mohawkian–Cincinnatian, Katian–Hirnantian) Taconic tectophase, changes in the distribution of the Martinsburg and Utica black shales (Figs 3A, 4) support a reversal of subduction polarity that effected the reactivation of basement structures and basin migration (Fig. 5). Shale distribution suggests that early Chatfieldian (early Katian), east-verging subduction early in the tectophase generated a cratonic extensional regime that resulted in a relatively narrow foreland basin along reactivated Iapetan basement structures (Fig. 5A). Abruptly, however, in late



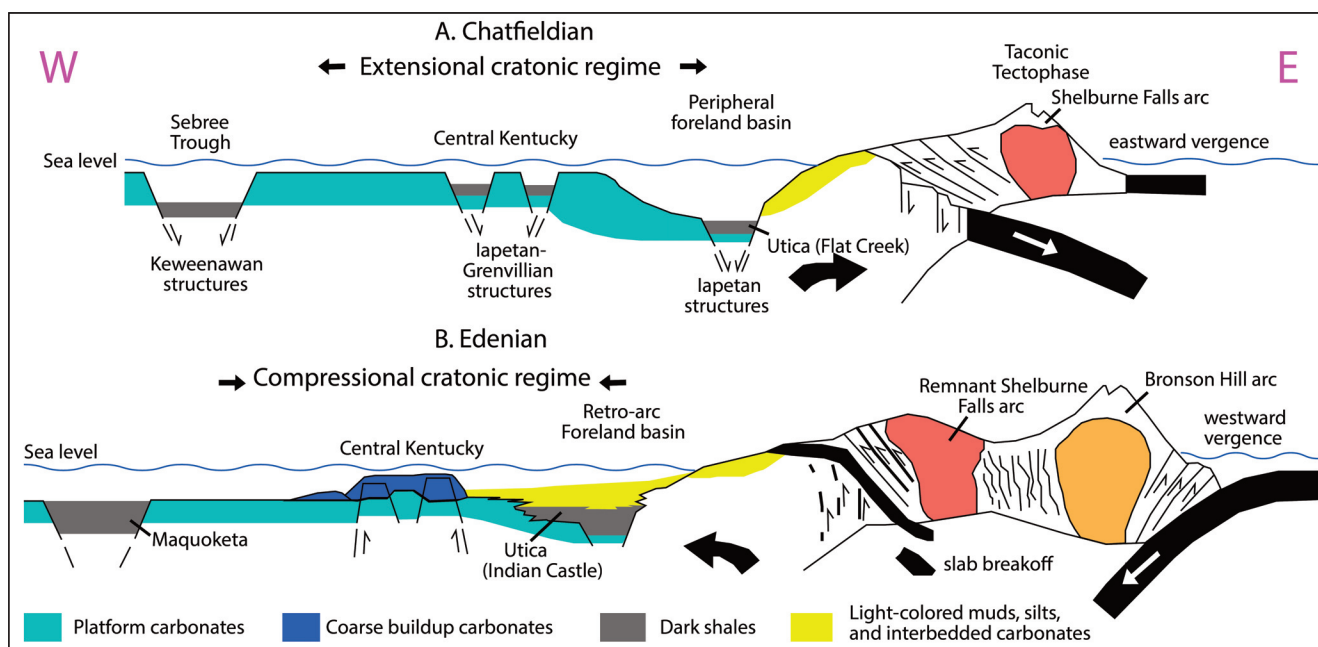
**Fig. 3. A** – tectonic framework for tectophases of the Middle–Late Ordovician Taconian orogeny along the southeastern margin of Laurentia. The mapped, blue, black-shale basin is the Late Ordovician Martinsburg–Utica foreland basin, representing collision at the New York promontory. Cross section A-B-C-D is shown in Fig. 4 and schematic section W-E in Fig. 5. **B** – cross section F-D in Fig. 3A, showing an abrupt change in the nature and development of black shales at the arrow. At the arrow, foreland-basin black shales and an underlying unconformity migrate westward in space and time into the Michigan Basin (not shown). This abrupt change probably represents a change in subduction polarity near the Chatfieldian–Edenian (mid-Katian) transition (see Fig. 5) (adapted from Ettensohn et al. 2019).



**Fig. 4.** SW-NE cross section A-B-C-D in Fig. 3A. Note the presence of two, complete, unconformity-bound, tectophase sequences (Blountian and Taconic) and how the sequences migrate northeastward in time, indicating the diachronous nature of the Taconian orogeny. In the Taconic tectophase, northeastward migration of the foreland basin is shown by the migration and “younging” of dark shales in that direction (adapted from Ettensohn et al. 2019).

Chatfieldian–early Edenian (early Katian) time, subduction vergence apparently changed to the west (Fig. 5B), generating a regionally compressional regime that was accompanied by subsidence and change in regional dip, such that black shales and an underlying unconformity migrated westwardly (Figs 3B, 5B). By Maysvillian (late Katian) time, the distribution

of Utica and Utica-equivalent black shales shows that the Appalachian and Michigan basins merged into one large, fully yoked basin. The coincidence of changes in basin shape and migration with the shift in subduction polarity suggests a causal relationship (Figs 3B, 5). The approximate time of polarity change is well-known from other sources but is also



**Fig. 5.** Schematic diagrams showing craton-wide consequences of change in subduction polarity in the orogen, along section line W-E in Fig. 3A. **A** – Chatfieldian extensional regime with eastward subduction and Utica black shales (Flat Creek) filling an extension-related foreland basin. **B** – Edenian compressional regime with westward subduction and westwardly migrating Utica black shales (Indian Castle; see Fig. 3B) (adapted from Ettensohn and Lierman 2015).

well-constrained by the biostratigraphic ages of and changes in the distribution of the related black shales (Figs 2, 3B).

## Conclusions

Black, organic-rich, unconventional gas shales are common in many foreland basins and owe their origin there to flexural tectonic mechanisms related to deformational loading in the adjacent orogen. Ordovician black-shale units in the Appalachian Basin of the eastern United States demonstrate that black shales are early parts of unconformity-bound tectophase cycles and are responses to active deformational loading, which is the shortest part of an orogeny.

Subsequent coarser clastic deposition, in contrast, is a relaxational response to earlier deformation and reflects the greater part of an orogeny. These cycles suggest that black shales as hydrocarbon source and reservoir rocks are clearly the product of distinctive tectonic frameworks and histories, and aside from economic value, may provide important controls on the timing and location of tectonic events.

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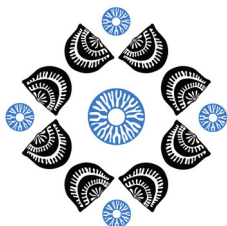
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brachiopods, carbonate fluorapatite,  
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# Early diagenetic transformation stages revealed by micro-analytical studies of shelly phosphorites, Rakvere region

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## ABSTRACT

Furongian–Tremadocian phosphorites of Estonia are sandstone rich in biogenic apatite, represented by brachiopod detritus. The study focuses on the mineralogical and micro-analytical characterisation of phosphorites from the Aseri, Toolse, and Kabala deposits based on FE-SEM and EPMA analyses. The shell fragments are composed of alternating compact and porous laminae, but with considerably poor preservation of pristine textures, superseded by the formation of authigenic CAF-apatite during the early diagenesis. In all settings, the shells showed preferential uptake of Sr into the porous cryptocrystalline laminae. The altered areas are composed of massive apatite crystallites with Mn-enriched layers. They are frequently covered with pyrite, indicating progressive recrystallisation under the influence of interstitial fluids and fluctuations in redox gradients in coastal environments.

## Introduction

In sedimentary phosphorites, P<sub>2</sub>O<sub>5</sub> can occur in several forms, such as fossilised bones, nodules, or other biochemogenic phosphates (Godet and Föllmi 2021). The precipitation of biochemogenic phosphates in marine sediments is restricted to the transition zone between oxic and suboxic environments close to the sediment-water interface. The most common phosphate encountered belongs to the apatite mineral group, with cryptocrystalline carbonate fluorapatite (CAF-apatite), also referred to as ‘francolite’, dominating in the occurrence of cryptocrystalline grains (Lécuyer et al. 1998; Ptáček 2016). Francolites are non-stoichiometric minerals with the generalised formula (Ca<sub>10-a-b</sub>Na<sub>a</sub>Mg<sub>b</sub>(PO<sub>4</sub>)<sub>6-x</sub>(CO<sub>3</sub>)<sub>x-y-z</sub>(CO<sub>3</sub>F)<sub>y</sub>(SO<sub>4</sub>)<sub>z</sub>F<sub>2</sub>) and numerous structural and chemical variations. Chemical substitutions can occur in all its lattice sites (the two Ca<sup>2+</sup> sites, PO<sub>4</sub><sup>3-</sup> and F<sup>-</sup>) (McLennan 2001; Veiderma et al. 2005). Bioapatites, another sedimentary apatite source, originate from phosphate biomineralisation of the hard skeleton of vertebrates and some invertebrates. For the precipitation of vertebrate bones and teeth, the nucleation by proteins and macromolecular matrices provides casts that control crystal growth. Such processes presumably also control the segregation of the skeleton of invertebrates (Trappe 1998). In inarticulate brachiopods, direct biomineralisation occurs as precipitation of phosphate to stabilise the exoskeletons. Their shells are initially composed of hard tissues, amorphous hydrogels, phosphate precipitates, and organic matter (Lowenstam and Weiner 1989). Post-mortem, during the diagenesis, the biogenic phosphatic matter chemically evolves toward CAF-apatite composition through various substitutions, together with an increase in crystallite size and formation of authigenic apatite phases (Trappe 1998). However, such alteration pathways are still only fragmentally understood (Ferretti et al. 2021).

The shelly phosphorites found in northern Estonia were deposited during the Cambrian–Ordovician transition in the coastal zone of a shallow, epicontinental sea (Heinsalu and Viira 1997; Nielsen and Schovsbo 2011). They belong to the Kallavere Formation, which spreads over most of northern Estonia and parts of the Leningrad region in northwestern Russia (Fig. 1; Kaljo et al. 1988). The Kallavere Formation in the study area has low thermal maturity. It exhibits no evidence of hydrothermal influence due to overall tectonic stability and shallow burial of the region (Kirsimäe

et al. 1999). The mineral matter of loosely cemented rock comprises quartz and phosphatic detritus, composed of lingulid remnants, and is enriched in rare earth elements (REE) and Sr. The abundance of phosphatic detritus and the presence of organic-rich mudstones have been interpreted to reflect a nutrient-rich palaeoenvironment with high primary productivity (Artyushkov et al. 2000; Baturin and Ilyin 2013). Previous studies have shown that shelly phosphorite deposits are highly variable in the mineralisation characteristics of phosphates, the type of accessory phases, the state of preservation, and consequently are likely to reflect alteration under somewhat different diagenetic environments (Nemliher and Puura 1996; Lang et al. 2015; Lumiste et al. 2021; Vinn et al. 2021).

This contribution aims to decipher the diagenetic transformation pathways in shelly phosphorites by combining textural analyses and geochemical mapping with a field emission scanning electron microscopy (FE-SEM) and a field emission electron probe micro-analyser (EPMA). We focus on distributions of P, Mn, Fe, and Sr to trace diagenetic variations in brachiopod fragments, along with the microstructures of the shells and associated carbonate cement. All selected minor compounds could fit into  $\text{Ca}^{2+}$  sites of apatite. Due to the same ionic charge and the close radii of  $\text{Sr}^{2+}$  to  $\text{Ca}^{2+}$ , such uptake is expected to take place readily, starting in vivo and continuing during post-deposition together with  $\text{F}^-$  uptake to bioapatite lattice (Trueman and Tuross 2002; Martin and Scher 2004). Mn and Fe (oxy)hydroxides are known to be major carrier phases transporting P to the sea bottom and releasing bounded P to sediments in the course of reduction and thus supporting diagenetic phosphatisation.

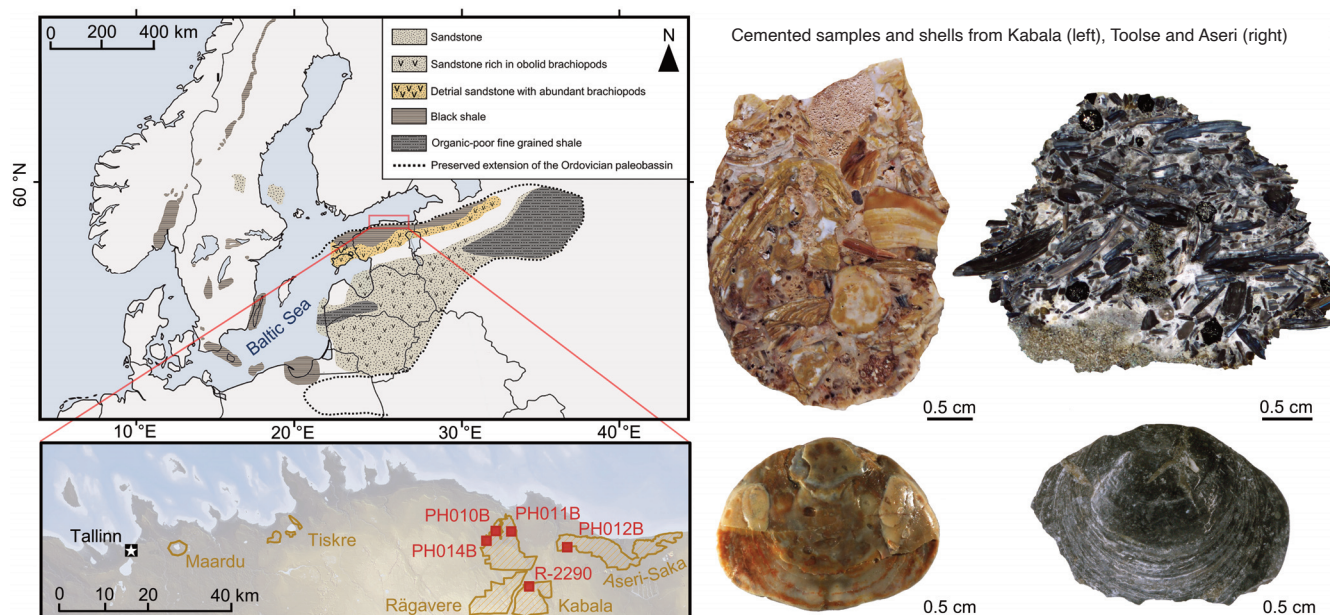
## Materials and methods

The 21 studied samples originate from five drill cores within the Toolse, Kabala, and Aseri deposits (Fig. 1). The Kallavere Formation was sampled across its entire section in the new

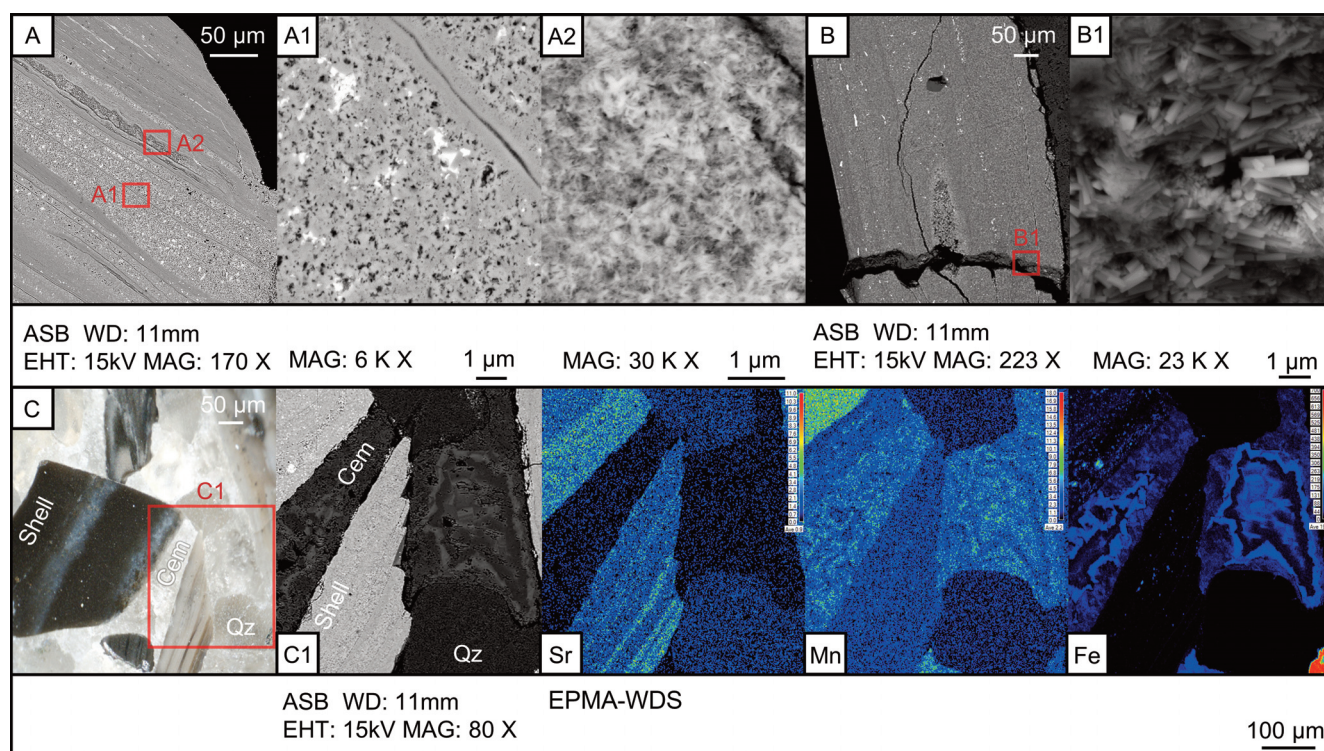
cores of Toolse and Aseri, in the framework of broader geochemical research on REE resources of phosphorites (Graul et al. in press). Additional spot samples from previous studies were included from the Kabala deposit. The materials were prepared as thick sections for micro-analytical investigations using cold-curing resin. The textural analysis was performed at the Center for Material Analysis, University of Oulu. FE-SEM investigations of selected carbon-coated polished thick sections were conducted on a Zeiss ULTRA plus instrument using a backscattered electron detector (AsB). Quantitative wavelength dispersive spectrometer (WDS) analysis of major and trace elements was performed with a JEOL JXA-8530F Plus (EPMA). The following analytical conditions were used for the WDS point analyses: a beam size of 5–10  $\mu\text{m}$ , an acceleration voltage of 15 kV, and a current of 15 nA. The peak counting time was set at 10 seconds for the element peaks and at 5 seconds for the background measurements. The following elemental lines and standards were analysed: Fe ( $\text{K}\alpha$ , magnetite), Mn ( $\text{K}\alpha$ , Mn), P ( $\text{K}\alpha$ , apatite), Sr ( $\text{L}\alpha$ ,  $\text{SrF}_2$ ). Matrix correction with the ZAF iterative method was applied to all analyses. This correction considers three effects influencing the X-ray characteristics: atomic number (Z), absorption (A), and fluorescence excitation (F). For the analysis of the WDS elemental map, the following elemental lines were used: Mn ( $\text{K}\alpha$ ), P ( $\text{K}\alpha$ ), Fe ( $\text{K}\alpha$ ), and Sr ( $\text{L}\alpha$ ). A focused spot, an accelerating voltage of 20 kV, a current of 20 nA and a dwell time of 50 ms were used for measurements.

## Results and discussion

The typical original valve structure of these inarticulate brachiopods displays an alternation of thin, compact laminae and thicker, baculate laminae (Fig. 2A; Cusack et al. 1999; Nemliher 2006). Baculate laminae are interpreted as remnants of the organic matrix of brachiopods, while compact laminae are interpreted as densely mineralised apatite structures (Lang



**Fig. 1.** Preserved extension of the Ordovician Palaeobasin, after Popov et al. (2019). Location of analysed drill cores and phosphorite deposits. Examples of analysed materials from the Kabala, Toolse, and Aseri deposits.



**Fig. 2.** SEM-AsB texture examples of shelly phosphorites. **A** – brachiopod section from the Kabala deposit. **A1** – crystallised compact laminae by phosphogenisation and diagenetic alteration. **A2** – porous baculate lamina with fibrous aggregates; **B** – fractured brachiopod section from the Toolse deposit. **B1** – tabular crystallites of CAF-apatite in a fresh fracture; **C** – optical microscopy image of an altered coquina section in carbonated cement from the Toolse deposit. Abbreviations: Qz – quartz grain, Cem – carbonated cement, Shell – shell fragments. **C1** – EPMA-WDS quantitative analysis of Sr, Mn, and Fe.

et al. 2015). However, in Toolse and Aseri, massive shell structures are abundant, indicating homogenisation of the laminae due to secondary apatite formation, with little preservation of the original material (Holmer 1989; Nemliher 2006). The presence of hydroxyapatite and authigenic CAF-apatite was reported by Nemliher et al. (2004) in Estonian lingulate shells based on X-ray diffraction analyses. The secondarily formed authigenic CAF-apatite is interpreted as the product of post-mortem phosphatisation of organic matter in the shells, combined with a later diagenetic alteration. The altered structures could be commonly identified via dark laminae with a high pyrite content in shell fragments from the Toolse and Aseri settings. Pyrite is predominantly present as microcrystals aligned along the laminae of the valve, with occasional occurrences of aggregates encasing brachiopod detritus. In some cases, secondary apatite has filled the original porosity to such an extent that it is complex to distinguish crystallites, apart from fresh fracture surfaces (Fig. 2B), indicating significant diagenetic recrystallisation. In contrast, in the Kabala deposit, Fe has been preserved in the form of goethite ( $\text{Fe}^{3+}\text{O}(\text{OH})$ ) and brachiopod laminae tend to be considerably more porous with needle-shaped or fibrous aggregates, or compact laminates exhibiting remaining porosity (Fig. 2A). This suggests various degrees of precipitation and recrystallisation according to different rates and diagenetic conditions.

EPMA-WDS analyses demonstrate variations in the abundances of Fe, Mn, and Sr. In the Aseri and Toolse deposits, Fe is found either as microcrystalline pyrite along the shell

laminae or in concentric rims in secondary apatites formed along the edges of the quartz grains, and in carbonate cements that occur in the basal part of the Kallavere Formation (Fig. 2C). In the latter, iron presents zonal distribution. Compared to Fe, the Mn distribution appears to be more complex. Mn is also contained in zonal distribution in the phosphatic rims and the carbonate cement, but Mn also appears in significant concentrations in the dark, more altered areas of the valves. These discrepancies could indicate local variations in the degree of sulphidic conditions and the composition of the interstitial, early diagenetic pore water.

Regardless of locality, Sr is highly concentrated in the porous laminae of the brachiopod detritus and minimally distributed in other parts of shells or carbonate cement. This most likely suggests a major early uptake by poorly crystalline bioapatite with a high surface area controlled by Sr:Ca ratio of the seawater and adsorption onto crystallite surfaces (Trueman et al. 2002). As Sr uptake has shown to considerably strengthen hydroxyapatite-type phases, this process might have been significant for the preservation of originally organic-rich laminae in brachiopod valves.

## Conclusions

The brachiopod fragments of Estonian phosphorites from the Rakvere phosphorite region are dominated by packed structures, with little preservation of original laminae textures overprinted by the formation of secondary CAF-apatite. The degree of diagenetic alteration varies between localities, as

well as the distribution patterns of Sr, Fe, and Mn, which are subject to local redox conditions. The high primary productivity and steep redox gradient close to the sediment-water interface allowed extensive authigenic apatite growth and extensive recrystallisation upon deposition and early diagenesis.

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# The Irish Ordovician brachiopod fauna: A taxonomic renaissance

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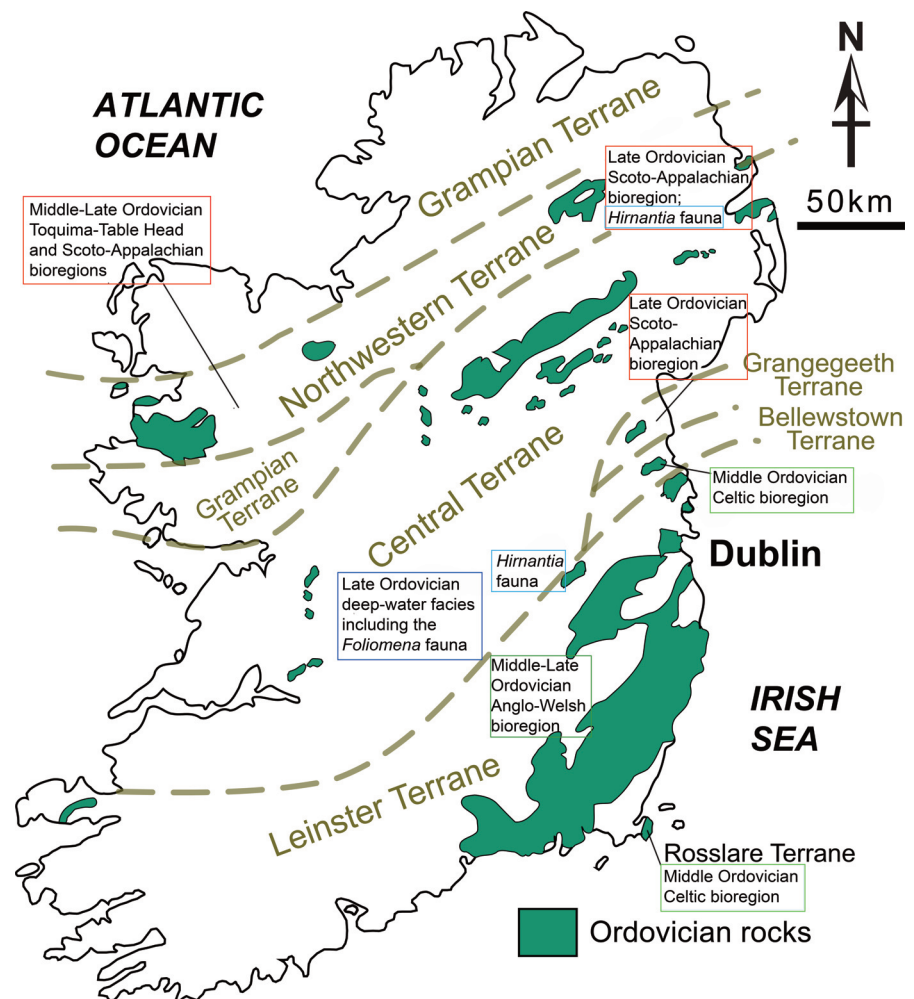
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### ABSTRACT

Despite its small areal extent, the island of Ireland exposes eight Caledonian tectonic terranes; six of them contain Ordovician brachiopod assemblages. These terranes record the early phases and destruction of the Iapetus Ocean through the occurrence of latitude-sensitive brachiopod faunas during the Middle Ordovician and early Late Ordovician; more cosmopolitan faunas characterized the later Ordovician.

### Introduction

The island of Ireland is relatively small, around 85 000 km<sup>2</sup>, but has a unique position on the edge of the European continent, where it was an integral part of the Caledonian mountain chain. Ireland is composed of eight Precambrian and Early Paleozoic terranes (Murphy et al. 1991; Fig. 1), six of which contain key Ordovician brachiopod assemblages (Harper and Parkes 1989). Brachiopods are variably preserved; with the exception of the rich silicified faunas of the Tourmakeady and Portrane limestones, shells are preserved as moulds in siliciclastic facies.



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**Fig. 1.** The eight Irish palaeotectonic terranes, six of which have brachiopod faunas and the bioregionality of these faunas is indicated in boxes. Template courtesy of Annalise Ferretti.



Although brachiopods were collected during the initial geological surveys of the island in the 19th century, and some taxa were described by Thomas Davidson and Frederick M'Coy, the description of the Ordovician fauna was initiated by Alwyn Williams following his arrival as Professor of Geology at Queen's University of Belfast in the mid-1950s. He and his students engaged in a vigorous programme, reviving the importance of the Irish Ordovician brachiopod fauna, specifically its taxonomy, biogeography and ecology. The Irish assemblages were a key part of early provincial studies of the phylum (Williams 1969, 1973). In addition to the taxonomic revisions of the faunas, the successions are now better constrained stratigraphically following the detailed reviews by Harper and Parkes (2000) and Molyneux et al. (2023); all the successions are now correlated with the global stages for the Ordovician System. This short contribution reviews the current knowledge of the Irish Ordovician brachiopod faunas.

### Northwestern terrane

The mountainous terranes of northwest Ireland expose a succession of Ordovician brachiopod faunas ranging from the diverse silicified Dapingian faunas of the Tourmakeady Limestone (Williams and Curry 1985) through the three slate units in the Mweelrea Formation; the first of these, the Lough Shee Mudrocks (Harper et al. 1988) in the Partry Mountains, contains a sparse middle Darriwilian fauna, the second has a late Darriwilian assemblage dominated by *Rhysostrophia* and other Whiterock taxa (Williams 1972) near the mouth of Killary Harbour, and the top slate band contains Sandbian brachiopods on Mweelrea Mountain (Harper et al. 2010). All the faunas developed on the Laurentian margins in a variety of settings. Those associated with volcanic environments, such as the Dapingian carbonates of the Tourmakeady Limestone that capped rhyolitic edifices, are particularly diverse. Those from the lower slate bands belong to the low-latitude Toquima-Table Head realm, whereas those higher up in the top slate band have affinities with the Scoto-Appalachian assemblages.

Farther northeast along strike, the Pomeroy inlier records the later Ordovician faunal developments on the Northwestern terrane (Mitchell 1977). Diverse Katian (Caradoc–Ashgill) brachiopod faunas are similar to those in the classic Girvan succession east on the Scottish mainland. The Sandbian faunas have been revised in detail by Candela (2003), who established a series of ecological associations within the Bardahessiagh Formation (Candela 2001, 2006) evolving on the margins of Laurentia. The Katian faunas are diverse and a deep-water equivalent of the *Hirnantia* brachiopod fauna (Harper et al. 1994) marks the summit of the Ordovician.

### Central terrane

The deep-water facies exposed in the Central Terrane contain few brachiopod assemblages, usually dominated by lingu-lates. Notable, however, is the *Foliomena* brachiopod fauna

in the Katian rocks of the Slieve Bernagh inlier (Harper 1980), which had a widespread distribution from the Darriwilian to the Katian (Rong et al. 1999).

### Grangegeeth terrane

This is one of two small but distinctive terranes in eastern Ireland. The diverse Sandbian brachiopod faunas are dominated by Scoto-Appalachian taxa (Owen et al. 1992), although Williams (1956) noted the presence of the Baltic genus *Productorthis*, which also occurs in the Celtic bioregion (see below). Higher in the succession, a variant of the *Foliomena* fauna is recorded in middle Katian strata (Harper and Mitchell 1982).

### Bellewstown terrane

The second of the small terranes exposes a brachiopod assemblage with affinities with the Celtic group of faunas (Harper et al. 1990). Its association with volcanogenic rocks suggests an intra-Iapetus insular origin. Younger faunas are not well documented but contain both Gondwanan and Anglo-Welsh taxa in ascending succession (Harper and Parkes 1989).

### Leinster terrane

This large and diverse terrane dominates southeast Ireland and has been associated with the Ganderia Terrane. Parkes (1994) monographed Sandbian and Katian brachiopods from the central part of the Leinster Massif and related these to the evolving Iapetus Ocean (Parkes and Harper 1996). In the southern part of the terrane, the Dunbrattin and Tramore Limestone formations of the Duncannon Group, in Co. Waterford, have diverse faunas of late Darriwilian–early Sandbian age, associated with equivalents of the eastern part of the Ganderia Terrane. (Liljeroth et al. 2017). Higher in the succession, the Katian brachiopod fauna of Raheen, Co. Waterford (Harper et al. 2017), is a deep-water assemblage with much in common with the widespread *Onniella-Sericoidea* associations of the later Ordovician.

In the northern parts of the Leinster Massif, Sandbian brachiopods have been described from Herbertstown (Harper et al. 1985), whereas the younger and well-known silicified Katian brachiopod fauna from the Portrane Limestone includes about 100 taxa (Wright 1963, 1964; Wright et al. 2022), possibly a downslope equivalent of the Chair of Kildare Limestone, dominating the Kildare inlier (Parkes and Palmer 1994), where a typical member of the widespread terminal Ordovician *Hirnantia* brachiopod fauna also occurs (Wright 1968; Rong et al. 2020).

### Rosslare terrane

The brachiopods from the hamlet of Tagoat in Co. Wexford (Harper and Bates 2023) and their counterparts on the island of Anglesey and southwest Wales formed the basis for Williams's (1969) Celtic province. During the intervening years, the

concept of the province has been modified to be associated with a string of marginal and island terranes within the higher-latitude belts of the Iapetus Ocean (Harper et al. 2013). The Celtic assemblages, having many endemic taxa and a mixture of genera from the platform provinces, may have acted as both cradles and refugia during the Middle Ordovician.

### Concluding remarks

The six Irish Caledonian terranes, containing brachiopod data, ranged across the Iapetus Ocean. Their faunas record the early phases and destruction of the Iapetus Ocean with contrasting assemblages from the margins of and within the Iapetus Ocean during the early Middle Ordovician. More cosmopolitan faunas such as the *Foliomena* associations populated Ireland during the Late Ordovician, culminating in varieties of the wide-spread *Hirnantia* brachiopod fauna on both Laurentia and Ganderia and associated terranes.

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This study is a contribution to the IGCP Project 735 ‘Rocks and the Rise of Ordovician Life’ and was supported by the Leverhulme Trust (UK). I thank my many collaborators and former research students for their advice and companionship over many years. Linda Hints and Renbin Zhan provided careful and helpful reviews. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

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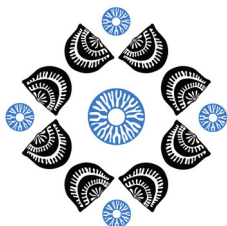
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# Latest Sandbian brachiopods and chitinozoan biostratigraphy in North Estonia

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### ABSTRACT

The latest Sandbian brachiopods and chitinozoans were studied in the Kõrgessaare and Haapsalu drill cores of Estonia. The brachiopod fauna shows a gradual renewal through the Keila Regional Stage (RS), differently from the rather persistent association of chitinozoans. An exception is the uppermost part of the stage, which differs in two sections in the taxonomic composition of chitinozoans and the occurrence of two species-level taxa of the *Dalmanella kegelensis* brachiopod group. *D. kegelensis sensu lato* has been considered an index taxon of the biozone in the Keila RS. It links the brachiopod faunas of North Estonia to those in NW Russia. In the latter region, the dolomitic and siliciclastic lagoonal and peritidal deposits overlying the strata with brachiopods of the *D. kegelensis* group are considered the youngest part of the Keila RS.

### Introduction

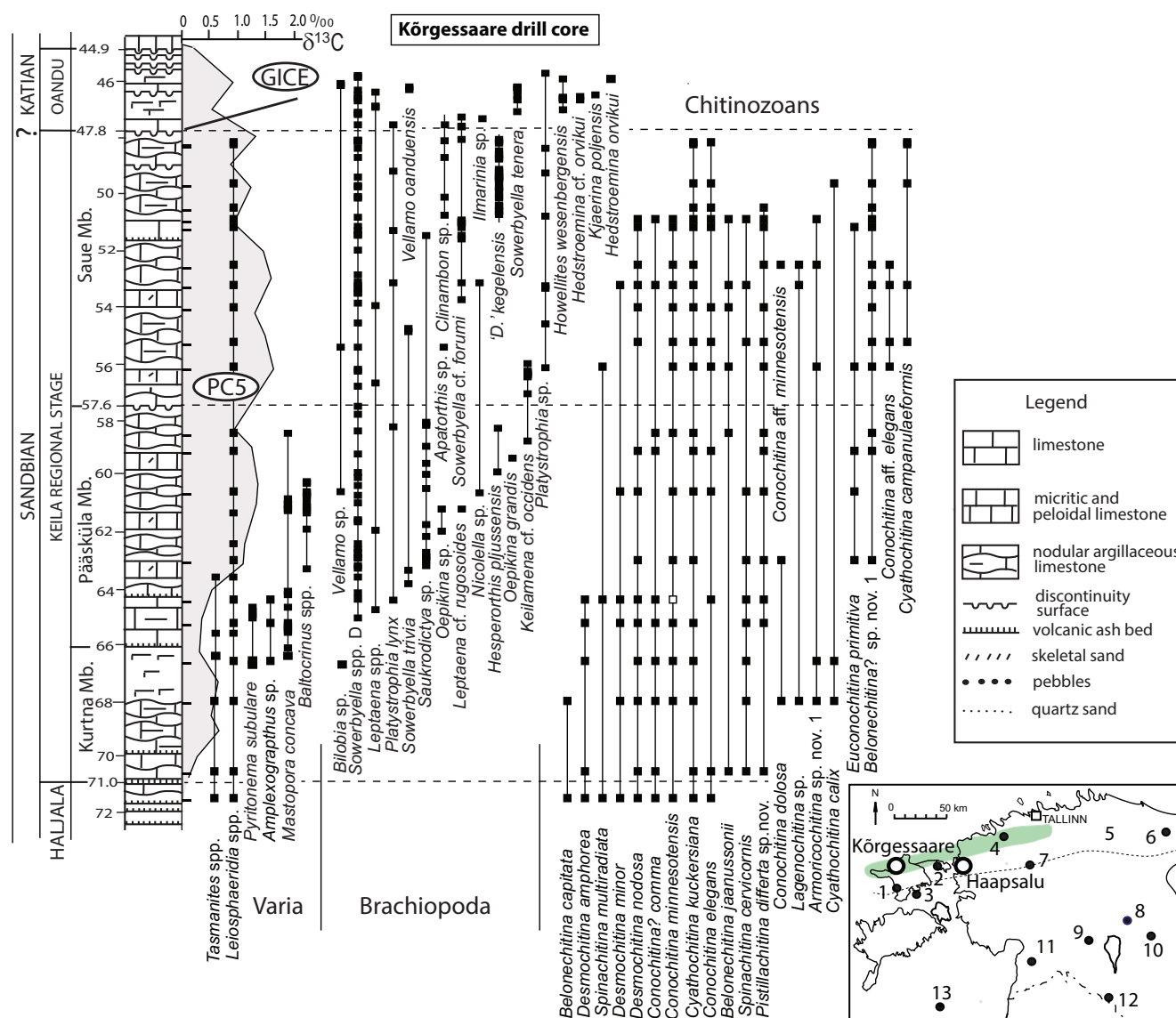
In the East Baltic, the Keila Regional Stage (RS) corresponds to the latest Sandbian and the Sandbian–Katian transition. It has been the subject of special studies on faunas, facies, environments and stratigraphy (Põlma et al. 1988; Ainsaar et al. 1996; Hints and Nõlvak 1999; Ainsaar and Meidla 2001; Kröger et al. 2014). The occurrence of reefs in a narrow belt (Kröger et al. 2014) and the greatest thicknesses over 30 m, instead of 12–15 m in NE Estonia, characterise the Keila RS in NW Estonia. In several sections in West Estonia, the globally identified Guttenberg Carbon Isotope Excursion (GICE) interval falls into a gap at the boundary between the Keila and Oandu RSs (Fig. 1; Ainsaar et al. 2010). However, the GICE is identified in the reefs and related facies (Kröger et al. 2014), as well as in South Estonian sections (Ainsaar et al. 2010).

Alichova (1953, 1960) identified a regional biozone with nominal species *Dalmanella kegelensis* in the Keila RS. This brachiopod has a wide distribution in shallow shelf environments from West Estonia to the western periphery of the Moscow syncline. In Estonia, *D. kegelensis* Alichova, 1953 occurs in the upper part of the Keila RS and is represented by two subspecies (Hints 1975) with different distribution areas. In this study, the subspecies of the *Dalmanella kegelensis* brachiopod group are interpreted as separate species of different genera, marked here tentatively as ‘*D.*’ *kegelensis* and ‘*D.*’ *oanduensis*.

The aim of this report is to document the distribution of brachiopods and chitinozoans in NW Estonia, to characterise the latest Sandbian biotic turnover and find new regional correlation criteria with NW Russia. In the latter region, the Keila RS is represented by the lithologically variable Jelizavetino Formation (Fm).

### Materials and methods

The latest Sandbian rhynchonelliformean brachiopods, chitinozoans and selected other fossils were studied in two sections of NW Estonia (Figs 1–2). The Kõrgessaare and Haapsalu GS3 sections are located on the island of Hiiumaa and on the western mainland of Estonia, ca 60 km apart from each other (Fig. 1). Chitinozoans were studied in 57 samples (ca 150 to 300 grams) using standard processing techniques and hand-picking (Nõlvak et al. 2019). The lithological description of the Kõrgessaare and Haapsalu cores is represented by Rõõmusoks (1970) and Vingisaar (1971), respectively. The collection of brachiopods (GIT 207) and preparates of microfossils are housed at the Department of Geology, Tallinn University of Technology.



**Fig. 1.** Distribution of brachiopods, chitinozoans and selected associated fossils in the Kõrgessaare core section. The empty markers denote doubtful identification (cf.). The carbon isotope curve is marked after Kaljo et al. (2004). GICE corresponds to a gap, the PC5 isotopic zone is presented after Ainsaar et al. (2001). The map (bottom right) shows the sections mentioned in the text: 1 – Männamaa, 2 – Söderby, 3 – Orjaku, 4 – Vasalemma district, 5 – Kerguta, 6 – Oandu, 7 – Rapla, 8 – Laeva, 9 – Viljandi, 10 – Tartu, 11 – Ristiküla, 12 – Valga, 13 – Ruhnu. The green belt marks the distribution area of *'D.'* kegelensis, the dotted line marks the supposed southern boundary of the distribution of *'D.'* oanduensis.

## Results and discussion

The earliest benthic faunas of the Keila age were stressed by a volcanic ash fall forming the Kinnekulle K-bentonite Bed at the base of the stage (Hints and Nõlvak 1999). Several new brachiopod and trilobite taxa appear somewhat above that level. In the Kõrgessaare and Haapsalu sections, spicules of *Pyritionema*, fragments of *Mastopora concava* and the trace fossil *Conichnus* are transitional from the underlying strata. The brachiopod *Sowerbyella* is represented by *S. trivialis* in the lower part and *S. forumi* in the upper part of the stage. The columnals of *Baltocrinus* sp. occur in several succeeding samples in the Kurtina and Pääsküla members. The upper part of the Pääsküla Member (Mb) is characterised by the strophomenid *Keilamena occidens*. The upper part of the Keila RS corresponds to the Saue Mb and is characterised by *S. forumi* and *Clinambon anomalous* (Figs 1–2). Notable is the occurrence of *'D.'* kegelensis and *'D.'* oanduensis in the Kõrgessaare and Haapsalu sections of the Saue Mb, respect-

ively. *'D.'* oanduensis was previously known mainly from NE Estonia, and its stratigraphic position in comparison with *'D.'* kegelensis was unclear. In the Kõrgessaare section, *'D.'* kegelensis also occurs in the upper part of the Saue Mb (Fig. 2), disappearing together with *S. forumi* and *Clinambon* sp. below a discontinuity surface at 47.8 m core depth. Above that level, the Katian species *Sowerbyella tenera*, *Kjaerina poljensis* and *Howellites wesenbergensis* first appear.

A rich and well-preserved assemblage of chitinozoans in both sections (Figs 1–2) corresponds to the middle part of the *Spinachitina cervicornis* Biozone (Nõlvak et al. 2006). Furthermore, the distribution and diversity of chitinozoans and rare graptolites (such as *Amplexograptus maxwelli*) are generally in good accordance with previous data from Estonia and Latvia (e.g., Goldman et al. 2015).

In the Haapsalu core, *Angochitina multiplex* and *Hercichitina spinetum* appear immediately above the Kinnekulle K-bentonite, providing additional criteria for the stage bound-

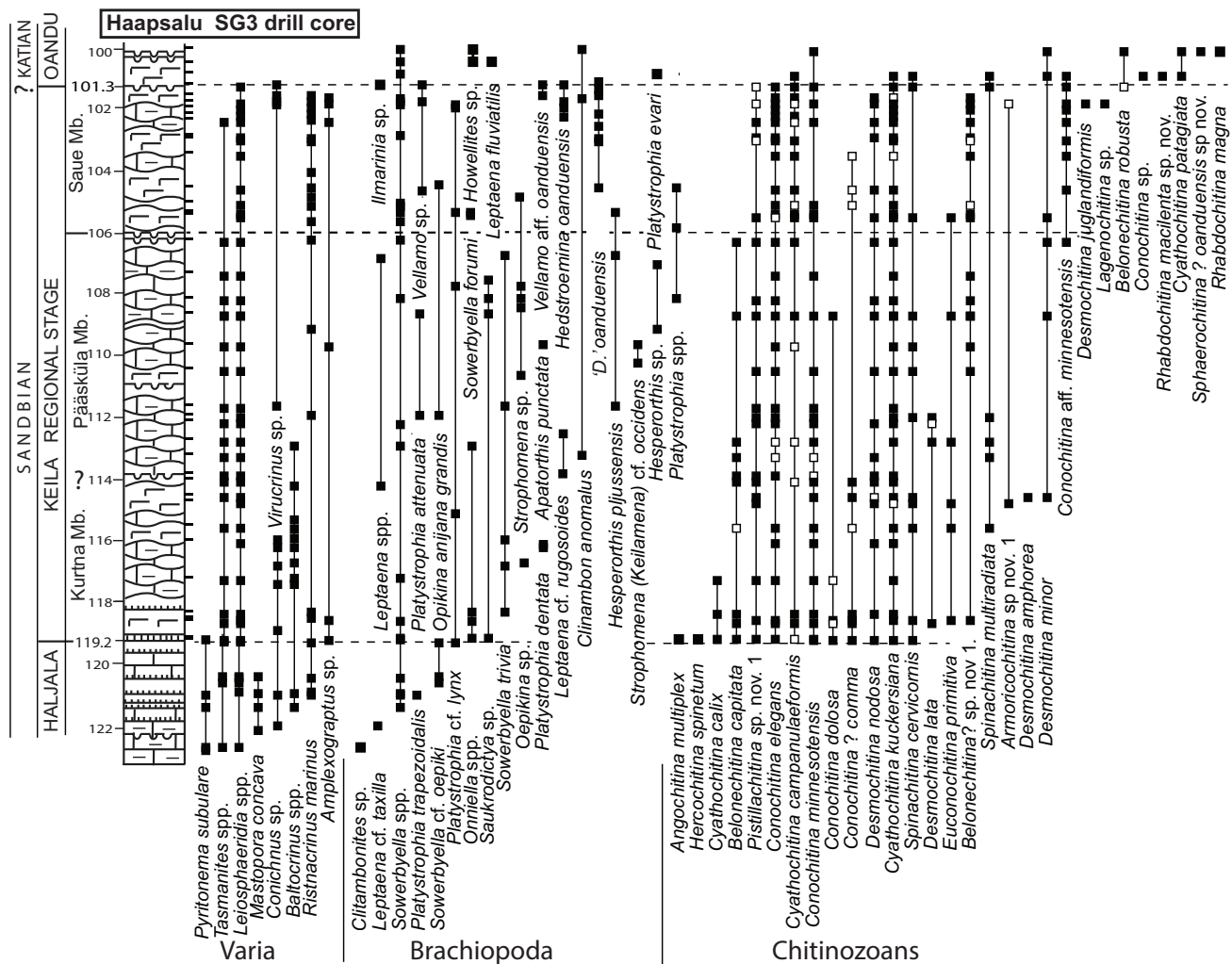


Fig. 2. Distribution of the latest Sandbian brachiopods, chitinozoans and selected other fossils in the Haapsalu GS3 core. For the legend, see Fig. 1.

ary (Hints and Nölvak 1999). In the Kõrgessaare section, the lowermost part of the Keila RS is sparsely sampled, and the two marker species were probably overlooked. In both sections, the taxonomic composition of the chitinozoan fauna is very similar to that of the underlying Haljala RS; however, *Belonechitina?* sp. n. 1, *Conochitina* aff. *minnesotensis*, *C.* aff. *elegans* are only characteristic of the Keila RS. A notable change in the chitinozoan assemblage occurred in the Kõrgessaare section within the upper part of the Saue Mb, on the level of ca 51 m (Fig. 1), where several species disappeared. The impoverished chitinozoan fauna may represent the youngest part of the Keila RS, corresponding to the weakly falling limb of the carbon isotope curve (Fig. 1) and the occurrence of '*D.*' *kegelensis*. In the Haapsalu core, a similar low-diversity fauna was not recovered from the uppermost Keila RS. This suggests a more significant gap at the Keila–Oandu boundary in this section (Fig. 2), marked by a hard-ground and the disappearance of many chitinozoans (*Pistillachitina* sp. nov. 1, *Conochitina elegans*, *Desmochitina nodosa*) and prasinophyceans (*Leiosphaeridia* spp.) characteristic of the Keila RS. However, the overlying Oandu RS contains several new chitinozoan species (*Cyathochitina patagiata*, *Sphaerochitina?* *oanduisis* sp. nov.) (Fig. 2).

Based on these new data, the Saue Mb seems to have a somewhat different age in the two sections studied. The in-

terval with low diversity of chitinozoans and the occurrence of '*D.*' *kegelensis* may be missing in the Haapsalu section.

The combined study of chitinozoans and brachiopods in association with selected other fossils in the Kõrgessaare and Haapsalu sections revealed continuous renewal of the shelly fauna. At the same time, a relatively invariable composition of the chitinozoan fauna is helpful for correlation across facies boundaries. An exception is the uppermost part of the Keila RS, represented by the Saue Mb. In NW Estonia, the Saue Mb follows the period of deposition of nearshore peloidal limestones of the Pääsküla Mb, grades into the grainstones of the Vasalemma Fm with reefs, and marks a new cycle in sedimentation. The stratigraphic extent of the Saue Mb possibly differs to some degree in different localities. Moreover, the brachiopods conspecific with the holotype of '*D.*' *kegelensis*, defined by Alichova from the Saue locality, occur mainly in the north-western part, including in the reef-related settings. The other group of shells ('*D.*' *oanduisis*) was adapted in offshore more muddy-bottom environments. Its distribution area possibly extends from NW Estonia to NW Russia. Due to the inappropriate choice of holotype among the specimens with restricted distribution in westernmost Estonia, the biostratigraphic significance of *Dalmanella kegelensis* sensu Alichova should be reconsidered. The uppermost Keila RS with '*D.*' *kegelensis* brachiopod group in

Estonia differs notably from those in NW Russia, where the stage is represented by a variety of lithologies of the Jelizavetino Fm, including lagoonal, peritidal dolomitic carbonates and sandstones (Dronov 2005). The occurrence of kukersite-rich beds in the upper half of the Keila RS is unusual for Estonian sections, where only a few kukersite interlayers are known. The relatively high content of siliciclastic material in carbonates of the uppermost Keila RS in NW Russia makes this interval similar to the Variku Fm in Estonia, which forms a belt in the transitional facies zone in the Baltic Basin (Ainsaar and Meidla 2001). Based on ostracod biostratigraphy, the Variku Fm is of Keila–Rakvere age (Ainsaar et al. 1999). The main positive shift on the carbon isotope curve belongs to the lowermost part of the silty deposits of the Variku Fm (Bauert et al. 2017), which should correspond to the youngest part of the Keila RS. Based on chemostratigraphic data, this part of the Keila RS is missing in the studied Kõrgessaare and Haapsalu sections. However, the positive isotope shift (GICE) characterises the reefs in northern Estonia (Kaljo et al. 2001; Kröger et al. 2014). The exact age of the siliciclastic deposits in NW Russia is unknown; however, this region could be the source area of siliciclastic material in the Estonian sections. The siliciclastic deposits in the basin supposedly represent the terminal episode of the deposition during the Keila age.

## Conclusions

The combined study of shelly faunas and microfossils ensures more reliable correlations and a better understanding of facies patterns during rapid environmental changes. New data showed that biostratigraphic usage of *Dalmanella kegelensis* s. l. should be disregarded due to the existence of two separate species. However, both ‘*D.*’ *kegelensis* and ‘*D.*’ *oanduensis* occur in the uppermost Sandbian below the GICE. They are associated with somewhat different chitinozoan assemblages, possibly indicating different stratigraphic ranges. The latest Keila sequences in Estonia and NW Russia deserve further high-resolution studies in order to decipher the sequence of events, climate shifts, sedimentation patterns and stratigraphic gaps across the Keila–Oandu transition in Baltoscandia.

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# A diverse Hirnantian scolecodont assemblage from northern Estonia and resilience of polychaetes to the end-Ordovician mass extinction

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## ABSTRACT

We report the discovery of a rich assemblage of latest Katian and Hirnantian scolecodonts (polychaete jaws) from a new Ordovician–Silurian boundary outcrop in the Reinu quarry, northern Estonia. The recovered polychaete fauna contains at least 40 species attributed to 11 families. Many common taxa appear to range from the latest Katian to the Hirnantian and into the Rhuddanian, indicating the resilience of jawed polychaetes to the end-Ordovician mass extinction. The Reinu assemblage is similar to the coeval faunas known from other Baltic sections, as well as from Anticosti Island, Canada, although with some specific features. The study revealed the highest abundance of scolecodonts in the Ordovician of Baltica, with ca 5400 maxillae per kilogram of rock recorded in the Siuge Member of the Ärina Formation, Porkuni Regional Stage, early Hirnantian.

## Introduction

Jaw-bearing polychaete worms were abundant and diverse inhabitants of Ordovician and Silurian shallow-marine environments, and their resistant jaws constitute a common group of organic-walled microfossils – scolecodonts. The end-Ordovician mass extinction that caused a significant diversity decline among most groups of organisms (Harper et al. 2020) is considered to have had a relatively minor effect on polychaetes (Hints 2000; Hints and Eriksson 2007; Eriksson et al. 2013). However, this notion is mainly based on a broad-scale comparison of Ordovician and Silurian faunas rather than on first-hand studies spanning the extinction interval. The precise response of polychaete worms to rapid changes in climate, environments, and ecosystems has thus far remained poorly understood.

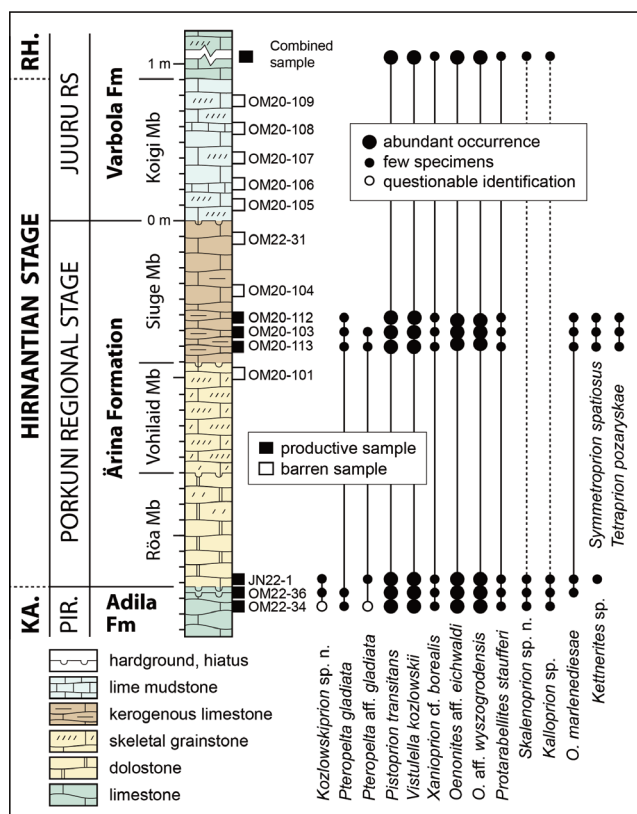
The aim of this paper is to report a recent discovery of a rich fauna of latest Katian and Hirnantian jawed polychaetes from a new Ordovician–Silurian boundary succession in the Reinu quarry, northern Estonia. It provides new insights into the turnover patterns and biogeography of jaw-bearing polychaetes during the end-Ordovician mass extinction.

## Locality and materials

The Reinu quarry is located in northern Estonia, 40 km south of Tallinn (59.08768, 24.74044). The early Silurian limestone of the Varbola Formation (Fm), Juuru Regional Stage (RS), has been quarried for crushed stone production since 2007. The Ordovician–Silurian boundary interval was first exposed in the quarry in 2020. As of 2022, the topmost Pirgu (latest Katian) and the entire Porkuni (Hirnantian) regional stages have been accessible. The Porkuni RS is represented by shallow-marine carbonates of the Ärina Fm, divided into dolostone (Röa Member (Mb)), skeletal grainstone (Vohilaid Mb) and kerogenous limestone (Siuge Mb) and, in places, reef limestone (Tõrevere Mb). The thickness of the formation varies across the quarry, being ca 2.3 m in the main section sampled (Fig. 1). The Ärina Fm is distributed in northern and central Estonia and considered to be primarily early Hirnantian in age, bound by stratigraphic gaps (Meidla et al. 2023). Whereas the basal part of the 11-m-thick Varbola Fm, the Koigi Mb, is likely of late Hirnantian age, the main part of the formation is Rhuddanian (Gul et al. 2021; Meidla et al. 2023).

The lower part of the Reinu section (Fig. 1) was sampled for microfossils in 2020 and 2022, and a total of 25 samples were collected. Additionally, three older conodont samples from the Varbola Fm were examined and the data combined to collectively represent the lowermost Silurian fauna. Acid-resistant microfossils were extracted





**Fig. 1.** Generalised stratigraphy of the Reinu quarry and distribution of selected late Katian and Hirnantian jawed polychaetes. The uppermost combined sample represents collectively three individual samples from the ca 11-m-thick Varbola Formation. Abbreviations: Pir. – Pirgu Regional Stage; KA. – Katian; RH. – Rhuddanian.

using acetic and hydrochloric acids. Productive samples contained scolecodonts, melanoscleritoids, foraminiferans and rare chitinozoans. The yield of scolecodonts was highly variable: the grainstone intervals turned barren, but the Siuge Mb provided the richest scolecodont sample from the Baltic Ordovician so far, with ca 5400 posterior maxillae per kilogram of rock in sample OM20-113 (3700 specimens/kg according to the counting method explained by Hints 2000). The entire collection from the Reinu quarry contains tens of thousands of scolecodonts. The material is housed at the Department of Geology, Tallinn University of Technology (abbr. GIT).

## Results and discussion

The latest Ordovician polychaete fauna from the Reinu quarry contains at least 40 species attributed to 17 genera and 11 families, and up to 21 species have been identified in a single sample. Quantitative data are available for few samples only, showing high diversity and a relatively even distribution of dominant taxa. For instance, in sample OM20-113, where the highest abundance was recorded, the dominance index (D) is 0.13, the Simpson Diversity index is 0.87, and the Shannon index is 2.3.

Similarly to most other Baltic Ordovician jawed polychaete assemblages studied so far, the Reinu fauna is dominated by polychaetaspids and mochtlyellids, followed by polychaeturids, xanioprionids, ramphoprionids and atraktoprionids (Figs 1–2).

**Polychaetaspids** may account for more than half of the specimens and are represented by no less than ten species.

*Oeononites* aff. *eichwaldi* (Fig. 2P) and *O.* cf. *wyszogrodensis* (Fig. 2L, M) are the most common ones, occurring in the latest Katian and Hirnantian strata but also ranging into the Silurian. *O. marlenediesae* (Fig. 2N, O) is less abundant but recorded in most samples of Katian and Hirnantian age. A few specimens of *O. zappae* (Fig. 2Q) and *Oeononites* aff. *jennyensis* (Fig. 2K), previously known from the Silurian (Eriksson 1997), were recovered, and several other morphologically distinct species of *Oeononites* are present in the collection, awaiting a systematic description. Polychaetaspids also include rare specimens of a new *Kozlowskiprion* species from the late Katian samples and a questionable find from the Hirnantian.

**Mochtlyellids** are strongly dominated by two long-ranging species, *Pistoprion transitans* (Fig. 2A) and *Vistulella kozlowskii* (Fig. 2B, C), which occur in all the productive samples studied. Other mochtlyellids are represented by rare specimens of *Mochtlyella* ex gr. *fragilis*, *M.* ex gr. *trapezoidea* and *M.* aff. *duplicidentata* (Fig. 2i). Additionally, a few jaws of new mochtlyellid genera (Fig. 2H) are present in the collection. Surprisingly, the typical forms of the genus *Mochtlyella* common in other latest Ordovician sections of Baltoscandia and Laurentia (such as *M.* ex gr. *crystata* and *M.* ex gr. *polonica*) are missing in the studied collection.

**Polychaeturids** are represented by the genus *Pteropelta*, with the typical *P. gladiata* form and a different form, here tentatively assigned to *P.* aff. *gladiata* (Fig. 2U, V, W). It is usually larger, more elongated and has a narrow, pointed ramus on the right MI. Both forms occur in the late Katian as well as Hirnantian samples, but the elongated form is more typical of the Hirnantian samples. The genus is unknown from the Silurian part of the Reinu succession, but polychaeturids possibly occur in basal Llandovery (Hints and Eriksson 2010; authors' unpublished observations).

**Xanioprionids** are represented in most samples by *Xanioprion* cf. *borealis* (Fig. 2D, E). Additionally, a few jaws of an undescribed xanioprionid were encountered (Fig. 2F). Both types of xanioprionid jaws also occur in the Silurian part of the Reinu succession.

**Ramphoprionids** are rare in all samples, represented by two genera and probably three or four species. *Protarabellites* is present in most samples. The latest Katian samples include typical *P. staufferi*, but in the Hirnantian, most specimens resemble *P. rectangularis* (Fig. 2R). However, transitional forms between the two species have been found. A rare but distinct ramphoprionid in the collection is *P.* aff. *triangularis* (Fig. 2S), with a prominent double fang in the right MI. A single recovered specimen probably belongs to a new species, ancestral to the typical *P. triangularis* found in the Silurian (Eriksson 2001). However, some of the left MI elements illustrated by Eriksson (2001, fig. 8:19, 8:23) may represent the same species. In two Katian samples, *Ramphoprion* cf. *gotlandensis* was also identified, and closely similar forms are known from the Silurian (see Eriksson 2001).

**Atraktoprionids** occur in most samples and are represented by at least three different species, of which *Atraktoprion* cf. *major* (Fig. 2Z) is the most common one.

Other taxa include *Skalenoprion* sp. and *Kallopriion* sp. (Fig. 2Y), which are found only in the three oldest samples, but both genera range into the Silurian. Further material is needed for species-level comparison. Paulinitids are rare, probably represented by a single species that also occurs in the Silurian part of the Reinu succession (Fig. 2T).



**Fig. 2.** Selected latest Katian and Hirnantian scolecodonts from the Reinu quarry, northern Estonia. All scale bars correspond to 100  $\mu\text{m}$ . **E, Y** – from sample OM22-36 (Adila Formation, Katian); **G** – from sample OM22-34 (Adila Formation, Katian); **H, S, T** – from sample JN22-1 (Katian/Hirnantian); **Q** – from sample OM20-113 (Siuge Member, Hirnantian); **R, X, Z** – from sample OM20-112 (Siuge Member, Hirnantian); all others are from sample OM20-103 (Siuge Member, Hirnantian). **A** – *Pistoprion transitans*, left MI, GIT 888-1; **B** – *Vistulella kozlowskii*, left MI, GIT 888-2; **C** – *Vistulella kozlowskii*, right MI, GIT 888-3; **D** – *Xanioprion* cf. *borealis*, anterior part of MI, GIT 888-4; **E** – *Xanioprion* cf. *borealis*, posterior part of MI, GIT 888-5; **F** – *Xanioprion* sp., MI, GIT 888-6; **G** – Mochtyellidae gen. nov., left MI, GIT 888-7; **H** – Mochtyellidae gen. nov., left MI, GIT 888-8; **i** – *Mochtyella* aff. *duplicidentata*, right MI, GIT 888-9; **J** – *Lunoprionella?* sp., posterior jaw, GIT 888-10; **K** – *Oeononites* aff. *jennyensis*, left MI, GIT 888-11; **L** – *Oeononites* aff. *wyszogrodensis*, left MI, GIT 888-12; **M** – *Oeononites* aff. *wyszogrodensis*, right MI, GIT 888-13; **N** – *Oeononites marlenediesae*, left MI, GIT 888-14; **O** – *Oeononites marlenediesae*, right MI, GIT 888-15; **P** – *Oeononites* aff. *eichwaldi*, right MI, GIT 888-16; **Q** – *Oeononites zappae*, right MI, GIT 888-17; **R** – *Protarabellites rectangularis*, left MI, GIT 888-18; **S** – *Protarabellites* aff. *triangularis*, right MI, GIT 888-19; **T** – *Kettnerites* sp., right MI, GIT 888-20; **U** – *Pteropelta* aff. *gladiata*, basal plate, GIT 888-21; **V** – *Pteropelta* aff. *gladiata*, left MI, GIT 888-22; **W** – *Pteropelta* aff. *gladiata*, right MI, GIT 888-23; **X** – *Symmetrion spatiozus*, right MI, GIT 888-24; **Y** – *Kalloprion* sp., left MI, GIT 888-25; **Z** – *Atraktoprion* cf. *major*, right MI, GIT 888-26.

Additionally, sporadic specimens of *Symmetrion spatiozus* (Fig. 2X) and *Tetraprion pozaryskae*, as well as a few other taxa, have been recovered in the Siuge Mb.

The stratigraphic succession of the Reinu polychaete fauna suggests that turnovers near the base of the Hirnantian were relatively small. Several species that are common in the Adila assemblage (*P. transitans*, *V. kozlowskii*, *O.* aff. *eichwaldi*, *O.* aff. *wyszogrodensis*, *O. marlenediesae*, *P. gladiata*) continue into the Siuge Mb. Even though the lithology of the two units is rather different, the high abundance, taxonomic composition and diversity indicate similarly optimal conditions

for many polychaete taxa. Still, certain differences can be outlined. For instance, *Kalloprion* sp., *Skalenoprion* sp., *R.* cf. *gotlandensis* and some mochttyellids are confined to the older assemblage, whereas *S. spatiozus* and *T. pozaryskae* occur only in the Hirnantian strata of the Reinu quarry. Such differences are, however, largely of local significance, as the same taxa are known to have longer ranges in other sections. The Ärina and Varbola assemblages also share many species, but the differences seem to be more significant than near the base of the Hirnantian. First, some new species appear, and the proportion of paulinitids gradually increases in the Varbola Fm.

Polychaetids have not been found in the Silurian of the Reinu quarry. At present, it is difficult to assess whether the observed changes at the Ordovician–Silurian boundary can be fully attributed to the extinction and recovery or reflect, at least partly, a change in local environments. However, the Reinu collection shows that 20 out of the 40 taxa recorded in the latest Ordovician ranged into the Silurian. Thus, more than 50% of the jawed polychaete species likely survived the end-Ordovician mass extinction.

In the Baltic region, Hirnantian scolecodonts have previously been reported from the Valga (southern Estonia) and Stirnas (western Latvia) boreholes (Hints 2001; Hints et al. 2010), where they occur in the Kuldiga and Saldus formations. The scolecodonts are particularly abundant and diverse in the middle part of the Kuldiga Fm (lower part of the Edole Mb), sharing a number of species with the Reinu assemblage, including the dominant taxa such as *Pistoprion transitans*. However, the composition of polychaetaspid differs at the species level, and other characteristic elements also differ between the Ärina and Kuldiga faunas. For instance, *Mochtyella* cf. *cristata*, *Conjungaspis minutus*, Tetraprionidae gen. et sp. nov. are typical of the Kuldiga fauna, whereas *P. gladiata* is characteristic of the Ärina Fm. The interpretations of age relationships of these stratigraphic units (Meidla et al. 2023) suggest that the mid-Kuldiga interval is younger than most of the Ärina Fm in northern Estonia. We hypothesise that the revealed differences between the Ärina and Kuldiga assemblages are due to the succession of Hirnantian polychaete faunas in time rather than environmentally caused intra-basinal biogeographical differentiation.

Apart from Baltoscandia, taxonomically diverse latest Katian to Hirnantian jawed polychaete faunas are known from Anticosti Island, Canada, the Prague Basin, and the Arabian Peninsula. The Reinu assemblage shows the closest similarity and biogeographical links with the fauna from the Vauréal and Ellis Bay formations of Anticosti Island, Laurentia (Hints et al. 2016). The common species include, e.g., *P. transitans*, *V. kozlowskii* and *P. gladiata* among the dominant taxa. A number of species in the Reinu assemblage are also shared with the latest Katian and early Hirnantian assemblages from the Králův Dvůr and Kosov formations in the Levín section, Prague Basin (Tonarová et al. 2023). However, there are notable differences too. For instance, *Pistoprion* has not been recorded in the Prague Basin before the Llandovery. The latest Ordovician polychaete fauna from central Saudi Arabia, Gondwana (Hints et al. 2015), is the least similar to the Baltic faunas. Overall, such a biogeographical pattern corroborates the conclusions recently outlined by Tonarová et al. (2023).

## Conclusions

The main outcomes of the study are the following:

1. A diverse Hirnantian jawed polychaete fauna was documented for the first time from the shallow-water carbonates of the Ärina Formation.
2. The highest abundance of scolecodonts in the Baltic Ordovician was recorded, reaching 5400 maxillae per kilogram of rock.
3. Polychaete turnovers near the base of the Hirnantian appear to be relatively minor, and many species also range into the Silurian. This corroborates earlier opinions about

the resilience of polychaete faunas to the end-Ordovician mass extinction.

4. Palaeobiogeographically, the Reinu polychaete fauna shows the closest similarity with coeval assemblages from Anticosti Island and, to a lesser degree, the Prague Basin, and northern Gondwana.

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# A remarkable new halichondrid demosponge, *Ptilospongia hemisphaeroidalis*, from the latest Ordovician Beigong Biota, South China

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### ABSTRACT

A new halichondrid demosponge bubarid *Ptilospongia hemisphaeroidalis* gen. et sp. nov. is described from the latest Ordovician Beigong Biota in Jingxian County, Anhui Province, South China. The new taxon is well-preserved with a two-layer choanosomal skeleton structure (basal layer and erect monactines layer) and three different types of megascleres (styles, strongyles, strongyloxeas), providing an excellent insight into a bubarid affinity and indicating a previously unknown group. It probably represents the earliest known fossil record of bubarids, providing a more reliable calibration point currently available for taxonomic and molecular phylogenetic studies.

### Introduction

The Late Ordovician mass extinction is the earliest among the Big Five in Phanerozoic (Sepkoski 1996). It severely damaged the ecological structure and had a devastating influence on the marine ecosystem, resulting in a catastrophic decline in biodiversity, with at least 85% of species going extinct during this crisis (Sheehan 2001). Significantly, recent studies indicate that diverse and abundant sponges flourished rapidly during and after the second pulse of the Late Ordovician mass extinction, and dominated the benthic community of the marine ecosystem (Li et al. 2015, 2019, 2023; Botting et al. 2017, 2018a, 2018b). One of the well-known representatives is the Beigong Biota, an unusual deep-water sponge assemblage spanning the interval of the end-Ordovician mass extinction from the black siliceous mudstone of the Kaochiapien Formation (Upper Ordovician–Llandovery) at Beigong of Jingxian County, southern Anhui Province, South China (Li et al. 2015). This sponge assemblage is of latest Ordovician (late Hirnantian) to earliest Silurian (early Rhuddanian) age, extending across the Ordovician–Silurian boundary. As a whole, the Beigong Biota contains abundant and diverse fauna of siliceous sponges. More importantly, most of them are perfectly preserved with a nearly complete sponge skeleton. In addition, not only the Burgess Shale-type taxa, but also the taxa that resemble modern sponges were discovered in this biota. Notably, there is a considerable number of taxa in the biota, representing numerous missing links in the multiple Phanerozoic sponge lineages (Li et al. 2019, 2023). Thus, further studies on this unusual biota could potentially reveal a more complete picture of the evolution of Phanerozoic sponges.

In this paper, we describe a new demosponge found in the Beigong Biota, showing probably encrusting habit and a two-layer structure of choanosomal skeleton, which are unique to the family Bubaridae Topsent, 1894. The smooth diactines without any ornaments in the basal skeleton and a megasclere assemblage of three different types (styles, strongyles, strongyloxeas) indicate a previously unknown taxon in Bubaridae, allowing us to describe a new genus and a new species in this family.

## Material

The present new material is collected from a continuous sequence across the Ordovician–Silurian boundary at the Beigong section of Jingxian County, southern Anhui Province, South China (Fig. 1). The type species is from horizon SF14 of the lowermost Kaochiapien Formation, associated with graptolites such as *Neodiplograptus shanchongensis*, *Normalograptus angustus*, *N. sp. aff. indivisus*, *N. lacinosus*, *N.? lungmaensis*, *N. normalis*, *N. cf. ugurensis*, etc., which are typical taxa in the *Metabolograptus persculptus* Biozone, indicating the latest Ordovician (late Hirnantian) age (Li et al. 2015). The specimen is deposited at the Nanjing Institute of Geology and Palaeontology, Nanjing, China, and indicated by their accession numbers.

## Taxonomy

Phylum PORIFERA Grant, 1836  
 Class DEMOSPONGIAE Sollas, 1885  
 Order HALICHONDRIDA Gray, 1867  
 Family BUBARIDAE Topsent, 1894  
 Genus *PTILOSPONGIA* gen. nov.

*Type species. Ptilospongia hemisphaeroidalis* gen. et sp. nov.

*Etymology.* From Greek *ptilo*, plume; referring to the tracts of soft-looking and feathery spicules of this sponge.

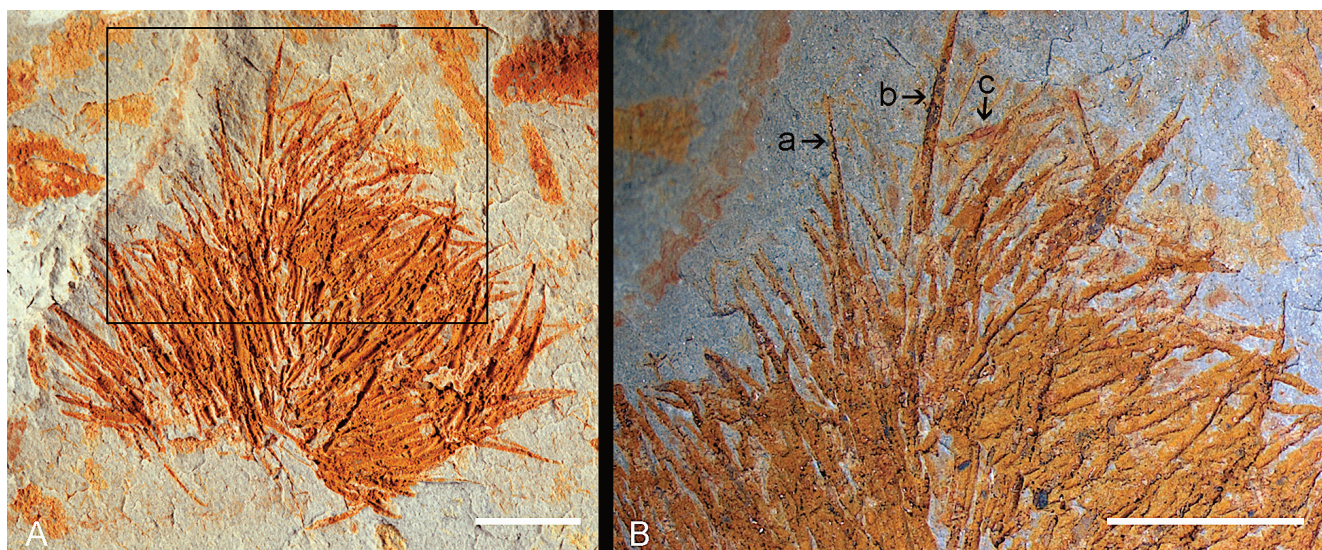
*Diagnosis.* Encrusting, hemispherical sponge with hispid surface. Ectosomal skeleton is absent. Choanosomal skeleton is mainly composed of bundles of long styles projecting perpendicularly to substrata with heads embedded in a basal layer of strongyles. Megascleres are long and smooth styles, strongyles and strongyloxeas.

*Remarks.* The new taxon found in the Beigong Biota probably shows encrusting habit and a two-layer structure. The basal layer is characterized by normal-appearing diactines and the perpendicular layer is formed of bundles of monactines with the bases embedded in the basal skeleton. This remarkable structure is in accordance with the diagnostic characters of the family Bubaridae Topsent, 1894.

At present, all the genera included in Bubaridae are modern ones, no fossil species have ever been found (Van Soest 2001; Alvarez and Van Soest 2002; Finks et al. 2004; Morrow and Cárdenas 2015). Significantly, modern sponges are classified mainly based on larval type, reproduction, megascleres and microscleres. It is clear that the first two characteristics are not applicable to fossil sponges. Therefore, the type of megascleres and microscleres as well as their arrangements in the sponge body become the key criteria of classification. Unfortunately, microscleres are rarely discovered, particularly in siliciclastics of the lower Palaeozoic, because of their tiny size and the fact that the main component (opaline silica) dissolved easily in seawater (Land 1976; Zhang



**Fig. 1.** Map showing the location of the Beigong section in Jingxian County, Anhui Province. The black irregular area with the red star is the location of Anhui Province. The red star indicates the position of the studied section.



**Fig. 2.** *Ptilospongia hemisphaeroidalis* gen. et sp. nov., holotype SF14-35. **A** – overall view of the complete and lateral compressed specimen; **B** – magnified view of the box area in A, the arrows show different types of megascleres: a – strongyloxea, b – style, c – strongyle. Scale bars = 5 mm.

and Pratt 2000). In the absence of microscleres, we can only differentiate varieties of fossil sponges according to the type and arrangement of megascleres.

Although microscleres cannot be identified in the new genus, the megascleres (styles, strongyles, strongyloxeas) and the two-layer choanosomal skeleton structure (basal layer and erect monactines layer) strongly suggest a bubarid affinity. Therefore, it seems reasonable to assign this new taxon to Bubaridae. However, there are no previously described taxa of Bubaridae showing close similarity in spicule morphology of basal skeleton with the new taxon described here, which probably represents a previously unknown group.

*Ptilospongia hemisphaeroidalis* gen. et sp. nov.

Figure 2

*Types.* SF14-35, one complete and well-preserved compressed specimen with iron hydroxide spicule replacements.

*Diagnosis.* As for genus.

*Etymology.* From Greek *hemi-*, half; *sphaeroidalis*, spherical, referring to the hemispherical shape of the sponge body. Gender feminine.

*Age/Occurrence.* *Metabolograptus persculptus* Biozone, Kaochiapien Formation, Jingxian County, Anhui Province, China.

*Description.* Small, hemispherical sponge with hispid surface giving a pompon-like appearance, up to 11.5 mm tall and 15.2 mm wide in the compressed specimen. The apex is located at the longitudinal axis of the sponge body, which is formed by megascleres in an upwardly plumose arrangement, prominently protruding from the surface. The maximum diameter is approximately in the lower third of the body height, narrowing upwards and downwards, with a diameter of about 5.2 mm near the bottom. Although the base is unrecognizable in the present specimen, the width of the sponge body decreasing toward the bottom probably indicates a rounded or

encrusting base to facilitate the fixation of the sponge (Fig. 2A).

There is no evidence of a distinct ectosomal skeleton, and it is therefore presumed to be absent.

Choanosomal skeleton differentiates into two layers, the basal layer is formed of relatively slender normal-appearing strongyles, and perpendicular to this layer long and stout styles with heads embedded in the basal skeleton, few strongyles and strongyloxeas are also present, scattering sporadically in the space between the stout styles (Fig. 2B). The most distinctive megascleres are stout styles, about 2.02–3.93 mm long, with a uniform thickness of around 0.13–0.25 mm from the base to three quarters of the spicule length, and then tapering smoothly to a sharp tip. Generally, the styles are smooth and straight, only slightly curved near the quarter of the tip. Compared to the styles, the strongyles are much slenderer, about 1.92–2.22 mm and 0.1–0.12 mm in diameter. Strongyloxeas are even slenderer but longer, up to 2.82 mm long and 0.08–0.09 mm in diameter. Strongyles and strongyloxeas are both straight, without curved tips. Microscleres are unrecognizable or absent.

*Remarks.* The new species bears superficial similarities to modern representatives of Bubaridae. However, there are some significant and prominent differences between the new species and modern sponges, mainly in terms of the spicule morphology and type of both basal and perpendicular layers.

Among the species of the four valid genera in the family Bubaridae (Alvarez and Van Soest 2002), *Bubaris vermiculata* (Bowerbank 1866) shows close similarities with the new species described herein as to the type of megascleres – both of which have three types of megascleres (styles, strongyles and strongyloxeas), with mainly styles projecting perpendicularly to substrata. However, unlike *B. vermiculata*, which is characterized by sinuous or vermicular diactines, the new species have much simpler basal diactines of smooth and normal-appearing strongyles.

The new species also shows certain similarities with another bubarid, *Cerbaris* Topsent, 1898. Nevertheless, com-

pared with the species belonging to *Cerbaris*, the new species bears simple basal diactines without any even or uneven acanthose ornaments which are quite common in the former. Moreover, the spicules in both the basal skeleton and the perpendicular layer of *Cerbaris* exhibit a more diverse pattern, including spicule types and size categories.

Except for the characters common to all species of Bubaridae, there are more significant differences between the species of the genus *Hymerhabdia* Topsent, 1892 and the new species. The basal skeleton of the former is composed of interlacing rhabdostyles and/or bent angulate oxeas, rather than of smooth strongyles that the latter has. Furthermore, although both of them have styles in the perpendicular layer, the associated subtylostyles and tylostyles in the *Hymerhabdia* as well as strongyles and strongyloxeas in the new species make them clearly distinguishable from each other.

Compared with species assigned to another bubarid, *Monocrepidium* Topsent, 1898, the new species has nearly the same smooth styles in the perpendicular layer as those in the former, although there is a subtle difference between the two in that the styles in the former are generally bent near the base, but are always curved near the tip of the latter. Moreover, the basal skeleton of the former is usually characterized by stout and ornamented diactines such as vermiculate, tuberculate or annulate strongyles or strongyloxeas that are occasionally arranged in a spiral. In contrast, the basal diactines of the new species exhibit a thinner and simple form of smooth strongyles without any ornaments.

Thus, it seems advisable to assign this new species to Bubaridae, and the remarkable differences make a more than generic separation between the new species and other taxa in Bubaridae.

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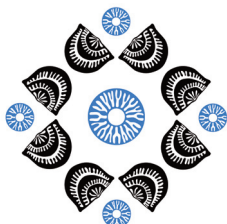
graptolite, biostratigraphy, Tremadocian, Ordovician, Northeast China

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# Tremadocian (Ordovician) reclined graptolites from Baishan, North China

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## ABSTRACT

The Erdaopuzi section in the Baishan area of Jilin Province, northeast China, contains abundant late Tremadoc graptolites. However, there are some taxonomic controversies regarding the characters of the hand specimens that are difficult to identify. In this paper, we present our restudy of isolated graptolites from acid residue and discuss the taxonomic problems of the subgenus *Clonograptus* (*Neoclonograptus*) Zhao and Zhang. Four genera and six species were identified, including *Adelograptus tenellus* (Linnarsson), *Ancoragraptus gracilis* (Zhao and Zhang), *Dictyonema* sp., *Psigraptus jacksoni* Rickards and Stait, *Psigraptus lenzi* Jackson, *Psigraptus arcticus* Jackson. According to the significant evolution of morphological characters, two graptolite zones (from bottom to top) can be identified in ascending order in the study area, i.e. *Adelograptus* Zone and the *Psigraptus* Zone.

## Introduction

The Baishan area (formerly the Hunjiang area) of Jilin Province, North China, is a classical research area of the Cambrian–Ordovician system, tectonically belonging to the Sino-Korean Craton. The Xiaoyangqiao section of Dayangcha in this area (Fig. 1A, B) is an ASSP section of the Cambrian–Ordovician boundary horizon (Wang et al. 2019). In the nearby Erdaopuzi section, abundant late Tremadoc graptolites have been collected from the Yehli Formation, making it an ideal section for studying late Tremadoc shallow-water graptolites.

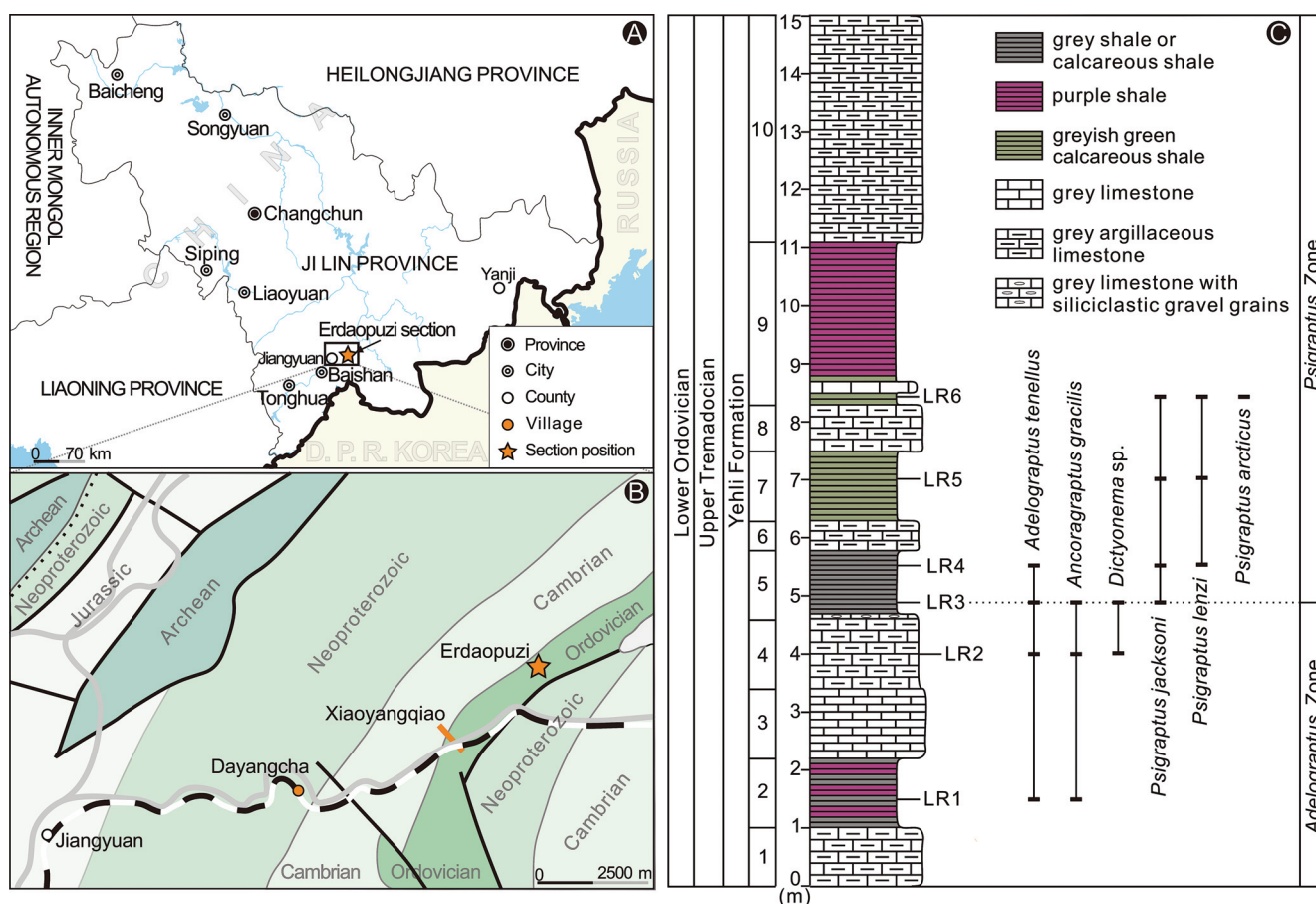
The Erdaopuzi section was originally studied by Zhao and Zhang (1985). According to the morphological difference of the reclined graptolites, they had successively established four new genera and one new subgenus, which include *Muenzhigraptus*, *Diphygraptus*, *Hunjianggraptus*, *Holpsigraptus* and *Neoclonograptus* (Zhao and Zhang 1985, 1986; Zhao et al. 1988). Most scholars believe that the above five (sub-)genera and *Yukongraptus* Lin, 1981 are all synonymous with *Psigraptus* (Wang and Erdtmann 1986; Rickards et al. 1991; Maletz 1992; Wang et al. 1996; Zhang and Erdtmann 2004), while others have also classified a group of morphologically similar graptolites as the subgenus *Clonograptus* (*Neoclonograptus*) Zhao and Zhang, 1985 into the genus *Ancoragraptus* (Cho et al. 2009).

Due to the morphological features of graptolites that are difficult to recognize on hand specimens, the taxonomy of reclined graptolites remains controversial. We recollected graptolite specimens from the Erdaopuzi section and obtained a number of isolated fossils by acid hydrolysis. All the isolated graptolites clearly show morphological features, thus providing some new evidence for taxonomy. The electronic documentation of the study on fossils and strata is deposited in the China Geological Survey Stratigraphy and Palaeontology Database <http://8.140.107.20:8080/navigator/index.aspx>.

## Materials and biostratigraphy

The Erdaopuzi section only includes the upper part of the Yehli Formation of the Lower Ordovician with a thickness of 31.9 m. Graptolites occur in the lower part of the section with a thickness of about 10.9 m, they are mainly preserved in shale or





**Fig. 1.** **A** – location map of the study area; **B** – geological map of the study area, with the location of the Erdaopuzi section northeast of the village of Dayangcha, Baishan, Jilin Province, Northeast China; **C** – biostratigraphy and lithostratigraphy of the Erdaopuzi section, colours used in the legend correspond to the colours of the fresh rock surfaces; **LR1–LR6** – number of the sampled graptolite-rich horizons.

calcareous shale, partly preserved in argillaceous limestone (Fig. 1C). A number of graptolite specimens were collected from six layers (LR1–LR6), and all the isolated graptolites were recovered from shale or calcareous shale (including LR1, LR3, LR5 and LR6).

The base of the section is characterized by argillaceous limestone with a thickness of about 1 m. It is overlain by grey and purple interbedded shale with a thickness of 1.2 m, and the former yields the graptolites *Adelograptus tenellus* (Linnarsson) and *Ancoragraptus gracilis* (Zhao and Zhang).

The overlying strata of LR1 are a medium thin layer of gravel limestone with a thickness of 1.2 m. It is overlain by grey argillaceous limestone (LR2) about 1 m thick, which contains the graptolites *Dictyonema* sp., *Adelograptus tenellus* (Linnarsson) and *Ancoragraptus gracilis* (Zhao and Zhang).

The strata overlying LR2 comprise grey calcareous shale, which are characterized by a layer of limestone with siliciclastic gravel grains at the base. The lower part of calcareous shale (LR3) contains the graptolites *Dictyonema* sp., *Adelograptus tennellus* (Linnarsson), *Ancoragraptus gracilis* (Zhao and Zhang) and *Psigraptus jacksoni* Rickards and Stait. The upper part of the calcareous shale (LR4) contains the graptolites *Psigraptus jacksoni* Rickards and Stait and *Psigraptus lenzi* Jackson.

The calcareous shale is overlain by argillaceous limestone with a thickness of about 0.5 m, succeeded by greyish

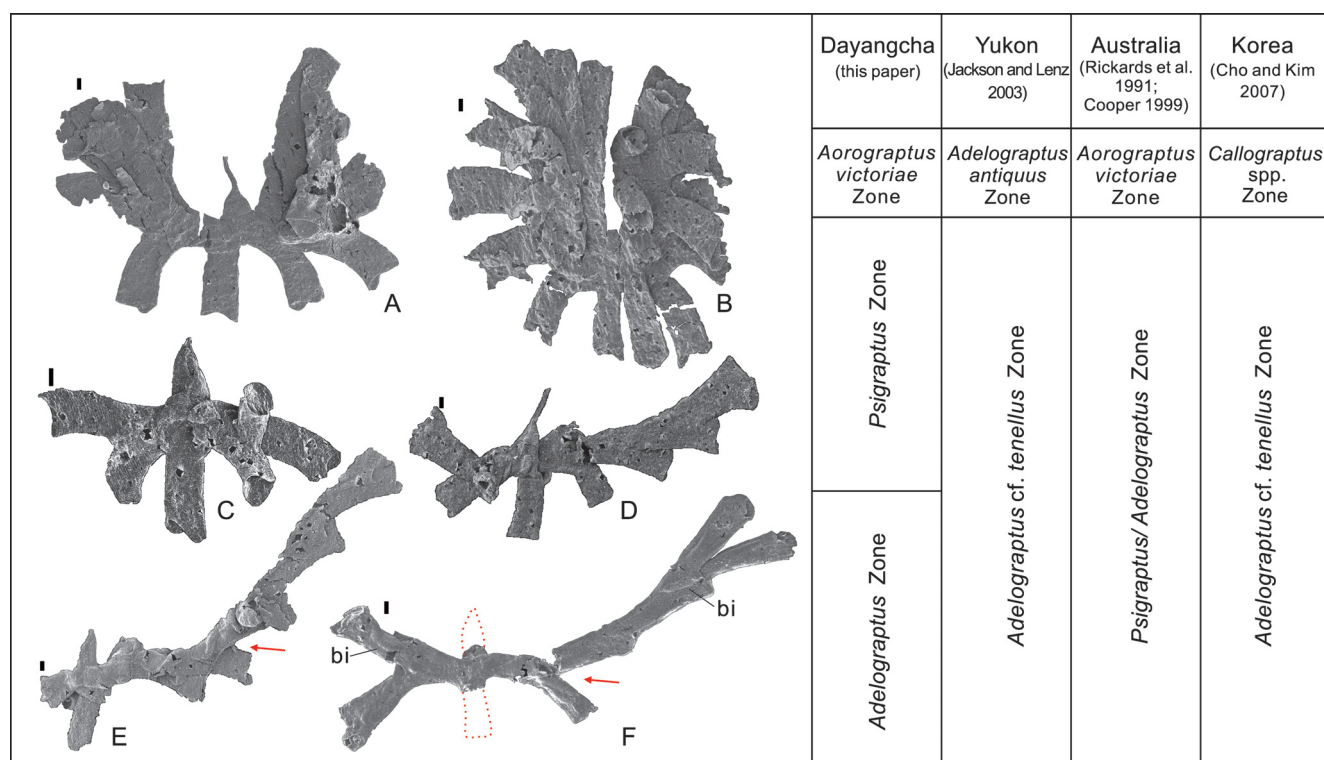
green calcareous shale with a thickness of 1.2 m (LR5), containing the graptolites *Psigraptus jacksoni* Rickards and Stait and *Psigraptus lenzi* Jackson.

The overlying strata of LR5 are grey argillaceous limestone with a thickness of 0.8 m. The strata are dominated by purple shale overlying the grey limestone with a thickness of 2.8 m. The bottom of this interval is greyish green calcareous shale intercalated with a thin layer of limestone, this part of the strata has a thickness of about 30 cm and contains graptolites (LR6) *Psigraptus jacksoni* Rickards and Stait, *Psigraptus lenzi* Jackson and *Psigraptus arcticus* Jackson.

The subsequent strata consist of limestone and shale, the latter commonly with purple shale and grey shale interlayers. The strata are about 21 m thick and contain no graptolites. Figure 1C shows only the basal part of this strata.

## Results and discussion

The study area and Yeongwol of Korea are both located in the Sino-Korean Craton, therefore the graptolite fauna is very similar in both areas (Kim et al. 2006; Cho and Kim 2007; Cho et al. 2009), except for the typical *Psigraptus lenzi* and *Psigraptus arcticus*, which are quite common in Baishan but not yet found in Korea. The study interval includes a variety of characteristic reclined graptolite species, which are important biostratigraphic markers (Fig. 2).



**Fig. 2.** Photos of isolated Tremadoc graptolites from the Erdaopuzi section of the Baishan area, and correlation of the late Tremadoc graptolite zones in Baishan with those in other parts of the world. **A** – *Psigraptus lenzi* Jackson, specimen LR5-1-5; **B** – *Psigraptus arcticus* Jackson, specimen LR6-1-5; **C–D** – *Psigraptus jacksoni* Rickards and Stait, specimens LR3-44 and LR3-3-2; **E–F** – *Ancoragraptus gracilis* (Zhao and Zhang), specimens LR1-1 and LR1-15. Scale bar: 100  $\mu$ m. The red arrows point at the first branch position on the stipe, the red dotted line indicates the inferred morphology of sicula. Abbreviation: bi – bitheca.

The base of the Upper Tremadocian is identified by the first appearance of *Adelograptus tenellus* (Linnarsson), associated with *Ancoragraptus gracilis* (Zhao and Zhang). *Ancoragraptus gracilis* was originally defined by Zhao and Zhang (1985) as *Clonograptus* (*Neoclonograptus*) *gracilis*, but subsequently considered the synonym of *Psigraptus jacksoni* Rickards and Stait (Wang and Erdtmann 1986; Rickards et al. 1991; Maletz 1992; Wang et al. 1996; Jackson and Lenz 2003; Zhang and Erdtmann 2004). Based on the reclined rhabdosome with free metasicula and non-free metathecae, Cho et al. (2009) assigned the subgenus *Neoclonograptus* to the genus *Ancoragraptus* Jackson and Lenz. In the studied section, ‘*Neoclonograptus*’ is very different from *Psigraptus jacksoni* (Fig. 2), in the former the theca on the stipe usually buds from the metatheca (Fig. 2E), whereas in the latter it buds from the protheca, resulting there in a higher thecal overlap (Fig. 2D). Notably, ‘*Neoclonograptus*’ has a distinct bitheca on the stipes (Fig. 2F) and an obviously isolated metasicula, suggesting an *Ancoragraptus* affinity.

From the first occurrence of the reclined *Psigraptus* in layer LR3, the stipes of *Psigraptus* begin to recline upwards (Fig. 2D), up to layer LR6 they are nearly parallel (Fig. 2B). From layer LR1 to layer LR6, the direction of extension of graptolite stipes gradually evolved from declined or horizontal to reclined and nearly parallel, and the isolation degree of thecal aperture gradually enhanced. The trigger remains unknown until more work is conducted, but it is speculated that the morphological evolution could have been caused by

sea-level fluctuations. The lowest fossiliferous layer LR1–LR2 yields the declined to slightly reclined graptolites *Adelograptus* and *Ancoragraptus*, also the apparently reclined *Psigraptus* occurs from layer LR3 onwards. In the studied section, the characters such as free metathecae, budding from protheca and distinct reclined stipes first appear in layer LR3. It is suggested that the *Adelograptus tennellus* Zone can be subdivided into the *Adelograptus* Zone and the *Psigraptus* Zone in the study area.

## Conclusions

The reclined graptolites reported here come from the upper Tremadoc in the Erdaopuzi section. The isolated graptolites show that the subgenus *Clonograptus* (*Neoclonograptus*) Zhao and Zhang, 1985 with free metasicula and smaller overlap of the thecae is significantly different from *Psigraptus* and shows close similarity to *Ancoragraptus* Jackson et Lenz, 2003. The significant morphological changes of graptolites are probably related to the local sea-level changes. Based on the remarkable morphological evolution, two graptolite zones, the *Adelograptus* Zone and the *Psigraptus* Zone, have been identified in the studied section, in ascending order. These two graptolite zones could be correlated with the *Adelograptus* cf. *tenellus* Zone in South Korea (Cho and Kim 2007), the *Psigraptus/Adelograptus* Zone in Australia (Rickards et al. 1991; Cooper 1999) and the *Adelograptus* cf. *tenellus* Zone in the Yukon region (Jackson and Lenz 2003) (Fig. 2).

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# On future directions of Ordovician chitinozoan research

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## ABSTRACT

Chitinozoans have been known to science for nearly a century. Due to their biostratigraphic utility, chitinozoans were intensively studied from the 1960s to the 1980s, and they have an important place in Ordovician stratigraphy nowadays, alongside graptolites and conodonts. However, identifying chitinozoans is often complicated due to poorly illustrated and documented type specimens. During the last decades, descriptions of new species have decreased significantly, whereas open nomenclature has been adopted widely. The affinity of chitinozoans has been discussed in several recent papers, but further exceptional specimens and the application of up-to-date study techniques are needed to understand their biological functioning. The Ordovician chitinozoan biozonal schemes were mostly established in the 1990s. With much more data subsequently reported, many biozones currently need revision, and possibly new useful zones could be established. Herein we discuss how to tackle the problems in chitinozoan research by building an open-access database and restudying the poorly documented type materials using advanced techniques. This would foster progress and facilitate studies in systematics, evolution, biostratigraphy, palaeogeography and the biological affinity of chitinozoans.

## Introduction

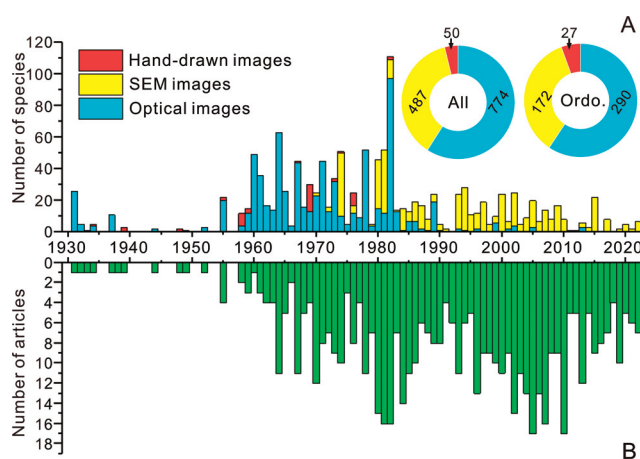
Ninety-two years have passed since the first report of chitinozoans by Eisenack (1931). In the history of chitinozoan research, three episodes can be recognised: (1) mainly systematic studies from the 1930s to the 1950s, (2) a rapid development period from the 1960s to the 1980s, mainly due to the demand from the oil industry, and (3) an era of applied biostratigraphy since then. The questions on biological affinity, biodiversity, and biogeography have been discussed in different periods, however, with a limited number of publications compared to biostratigraphic studies. Servais et al. (2013) reviewed the first eighty years of chitinozoan studies, and a more detailed history with supporting references could be found there.

The Ordovician was a crucial period for chitinozoans. The oldest taxa are widely reported from the middle Tremadocian without regard to the debating report from the Cambrian (Shen et al. 2013). The group flourished in the late Darriwilian to the Sandbian and had a significant diversity decrease during the end-Ordovician extinction (Achab and Paris 2007). Ordovician chitinozoan biozonations in Baltica, North America and North Gondwana were established around the 1990s (Achab 1989; Paris 1990; Nõlvak and Grahn 1993) and proved useful in regional and global correlations, especially where graptolites and conodonts were rare or missing. The key materials supporting different arguments for the chitinozoan biological affinity are mostly from the Ordovician, including the clusters supporting the metazoan egg hypothesis (Paris and Nõlvak 1999) and the reproductive specimens suggesting protist biology (Liang et al. 2020).

Modern palaeontology has set higher goals for high-resolution biostratigraphy and comprehensive pursuits based on big data to decode major biological events and the motivation behind them. However, the contribution from chitinozoans has remained somewhat limited. In terms of past work experience on chitinozoans, we review some problems in contemporary chitinozoan research and put forward ideas on what could be done to further advance chitinozoan research.

## Current trends and problems in chitinozoan research

**Taxonomy.** In total, 563 publications (excluding abstracts) related to chitinozoans have been analysed, and 1131 species from 57 genera have been erected (Fig. 1) according to Paris et al. (1999). About two-thirds of all species were erected from the 1960s to



**Fig. 1.** Erected chitinozoan species (A) and publications (B) over the past 92 years. The data are based on the CHITINOVOSP database of Florentin Paris from 2014, publications listed in the ChitDB (Hints et al. 2018) online database, and supplementary data we have assembled.

the 1980s. The number of new species described in the 1990s and the 2000s decreased significantly, while the number of publications slightly increased. In the 2010s, only 51 species were formally established. However, identifications using open nomenclature have become more common. The main reasons for the decrease in new taxonomy might be: (1) the biostratigraphic significance motivated most of the chitinozoan study, and once the main biostratigraphic indicators were described, other species mattered less since conducting systematics is very time-consuming; (2) chitinozoan taxonomic data were preserved in a scattered way, therefore not being readily available, hampering comparison and identification; (3) perhaps most importantly, due to the lack of standard criteria and with limited imaging techniques adopted in early chitinozoan research, poor images and insufficient descriptions of type specimens left confusion in the taxonomy of some early established chitinozoans. Also, many species have been erected based on a very small collection or even a single specimen (e.g., Taugourdeau and de Jekhowsky 1960; Combaz and Peniguel 1972; Obut 1973). Only about a third of holotypes have a scanning electron microscopy (SEM) image available, while the rest were photographed under an optical microscope or were hand-drawn (Fig. 1A). These imaging methods usually fail to provide detailed morphological information. This, in turn, has a negative impact on the systematics of chitinozoans.

Revision of such poorly documented type specimens is not easy. The holotypes are kept in many different institutions worldwide and some holotypes have been lost or broken due to various reasons and circumstances. Recently, a case study of a revision of the widely distributed and well-known *Lagenochitina esthonica* has been carried out (Liang et al. 2022), providing an example of how to solve such issues. The most important part of the work is that the materials are from the same area and stratigraphic level as the lost holotype. At the same time, a sufficient number of specimens and high-quality SEM images are statistically analysed to present the variation in shape and size, which further distinguishes the two species within the group. The stratigraphic ranges sum-

marised based on all the reported occurrence data provide a solid support for such revisions.

**Biostratigraphy and biogeography.** Ordovician chitinozoan biostratigraphic schemes in the main palaeocontinents were established around the 1990s, and only relatively minor updates have been made since then. However, abundant new occurrence data has been accumulated since the 1990s, and some biozones need revision to better meet the high-resolution biostratigraphic standards. For example, the *Euconochitina symmetrica* Biozone was put forward to be coincident with the base of the Floian in North America and North Gondwana (Webby et al. 2004; Cooper and Sadler 2012). However, Tremadocian occurrences were reported from South China (Zhang and Chen 2009; Wang et al. 2013; Liang et al. 2017), Avalonia (Amberg et al. 2017), and also North Gondwana (Nowak et al. 2016). A recent revision of graptolites and chitinozoans from the type horizon of *E. symmetrica* suggests that *E. symmetrica* characterises the upper Tremadocian *Sagenograptus murrayi* Graptolite Zone and could reach the Floian (Achab and Maletz 2021). *E. symmetrica* is not the only case. Zonal species such as *Lagenochitina esthonica*, *Conochitina raymondii*, *Eremochitina baculata* and *Eremochitina brevis*, to name but a few, all have new occurrence data below or above the initially proposed range of the zone. Therefore, an updated composite global range chart considering all the occurrence data of these biozonal species has to be prepared to better serve stratigraphic correlations.

Chitinozoans are generally considered to represent geographically widespread plankton, with limited implications for palaeogeography. However, in the Ordovician, it seems that at least three major chitinozoan palaeobiogeographic provinces could be recognised with specific biozonations, i.e., Baltica, North America and North Gondwana palaeobiogeographical provinces, almost corresponding to part of the three palaeocontinents. The concept of chitinozoan provinces has been discussed in several studies (e.g., Paris 1990, 1993, 1996), but the formal definition of provinces still requires a compilation of global occurrence data and statistical analysis. How much do the chitinozoan assemblages vary between different palaeocontinents and between different environments within palaeocontinents? How do chitinozoan assemblages change over time? These aspects need to be much better understood using direct evidence and occurrence data. Then, chitinozoans could play a more important and reliable role in biostratigraphy.

**Biological affinity.** The biological affinity of chitinozoans has bothered palaeontologists since the 1930s. A thorough summary of the history of exploration of what chitinozoans are has been presented by Servais et al. (2013). Most commonly, chitinozoans have been considered to be eggs or cysts of unknown marine metazoans for the past three decades, after a series of publications (Taugourdeau 1981; Jaglin and Paris 1992; Paris and Nölvak 1999). However, two recent studies have challenged the ‘metazoan egg hypothesis’ based on the huge size variation of chitinozoan species and exceptionally preserved specimens possibly showing the reproduction moments (Liang et al. 2019, 2020). These new data have advocated most probably a protistan rather than a metazoan origin of chitinozoans. However, Vodička et al. (2022) have pre-

sented new evidence on monospecific chitinozoan clusters, interpreted as egg masses. Regardless of which hypothesis gains more support, the biological affinity of chitinozoans has re-attracted much attention after 20 years, which is undoubtedly a good trend to further improve our knowledge of this aspect. **Big data.** Digitalisation and visualisation of palaeontological data have become key areas in palaeontology, providing a completely new view of global palaeobiodiversity patterns, palaeobiological events, palaeoecology and palaeogeography (e.g., Alroy 2001; Kiessling 2005; Wagner et al. 2006; Alroy et al. 2008; Fan et al, 2020). At present, very limited chitinozoan data are available in the largest palaeontological database, the Paleobiology Database (PBDB, <https://paleobiodb.org>), and the Geobiodiversity Database (GBDB, <http://geobiodiversity.com>). Several specialised chitinozoan databases have also been developed, two of which are very helpful in chitinozoan studies. One of these is CHITINOVOSP, a chitinozoan type species database which stores information on the taxonomy, references, holotype images and the general stratigraphic range and palaeogeographic distribution. The other is ChitDB (<https://chitinozoa.net>; Hints et al. 2018), an online database that stores information on Ordovician–Silurian chitinozoans of the Baltic region. However, these two databases have their shortages: CHITINOVOSP is a static proprietary desktop application and is not easily available and accessible to researchers. The ChitDB is currently focused on Baltica, mostly only on the East Baltic region. Both databases have no or limited support to allow community-based assembly and editing of chitinozoan data. In addition, Achab et al. (2000) put forward the chitinozoan image and data acquisition system CHITINOS, which is intended for capturing chitinozoan data during palynological work or for assembly of data taken from the literature. However, the system is no longer in use. Verniers et al. (2002) also introduced the database CHITREF with published references and a list of all chitinozoan species. However, no further information has been updated since then.

## Discussion and conclusions

To effectively facilitate chitinozoan studies, we suggest designing and constructing an open-access chitinozoan database for all documented chitinozoan species. The database could be built on the GBDB platform for two reasons: GBDB is one of the official databases of the International Commission on Stratigraphy and International Palaeontological Association; there is stable support and full-time technicians in charge of the database. The data structure will resemble the ChitDB and present combined information such as taxonomy, morphological features, high-resolution images, sample localities, specimen data, ages, and related references. All internet users can freely access and download the data, and registered users can participate in data entry, editing, and analysing. In short, the database would include all occurrence data globally and, once complete, will provide data services for studying chitinozoan macroevolution, biostratigraphy, palaeobiogeography and palaeoecology.

With all the information being freely accessible to everyone, it will substantially improve the study of chitinozoans.

It will save considerable time and energy in searching data and thus systematic identification becomes much easier. Moreover, further revisions on the poorly documented chitinozoans will be easier to carry out through global collaboration. Nowadays, chitinozoan experts are few, and the type collections are stored in different countries and institutions. With a platform presenting the wait-to-solve issues, palaeontologists who have access to those questionable holotypes or topotypic material could collaborate with interested chitinozoan specialists. Once the improved data on type specimens are accessible, the systematics will be greatly facilitated.

In updating the taxonomic issues and solving the palaeobiological queries, advanced imaging techniques, such as near-infrared microscopy, focused ion beam scanning electron microscopy, field emission scanning electron microscopy and X-ray computed micro-tomography could be applied and are essential for documenting interior structures and ultrastructures. In palaeobiological studies, detailed morphological examination of exceptionally preserved specimens and key structures, such as the prosome and operculum, will be of critical importance.

Furthermore, a revised taxonomy based on updated morphological and biological information, and global occurrence data will largely facilitate chitinozoan study in palaeobiogeography and palaeoecology, which, in turn, will lead to refined biostratigraphy.

As a small microfossil group with a relatively short geological history, we have to find a way for chitinozoan research not only because they could provide some valuable suggestions for biostratigraphy, but also because they existed in history with many unknown mysteries. The creation of a global community-driven chitinozoan database and revisions of poorly documented chitinozoan species with more high-resolution morphological features decoded by advanced techniques will be an inevitable stage. It will bring significant advances for chitinozoan studies. Once these tasks have been achieved, it might bring a new era for chitinozoan research and will be an important case study to show how far basic research can go with the support of big data and advanced techniques.

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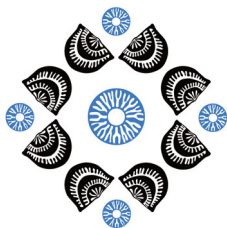
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# New contributions to the Ordovician biostratigraphy of the Western Precordillera, Argentina

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### ABSTRACT

Upper Ordovician graptolites and conodonts are recorded from the Yerba Loca Formation in two sections, in the El Toro and Las Viudas creeks, from the El Tigre Range in the Western Precordillera of San Juan Province, Argentina. A collection of graptolites from the late Sandbian *Climacograptus bicornis* Zone and conodonts on bedding plane surfaces corresponding to the *Amorphognathus tvaerensis* Zone are presented. Graptolites apparently corresponding to the early Sandbian *Nemagraptus gracilis* Zone have also been recorded. The fossils determined allow for regional and global correlations, revealing sections suitable for future integrated studies on deep marine environments that are poorly known in the Argentine Precordillera.

### Introduction

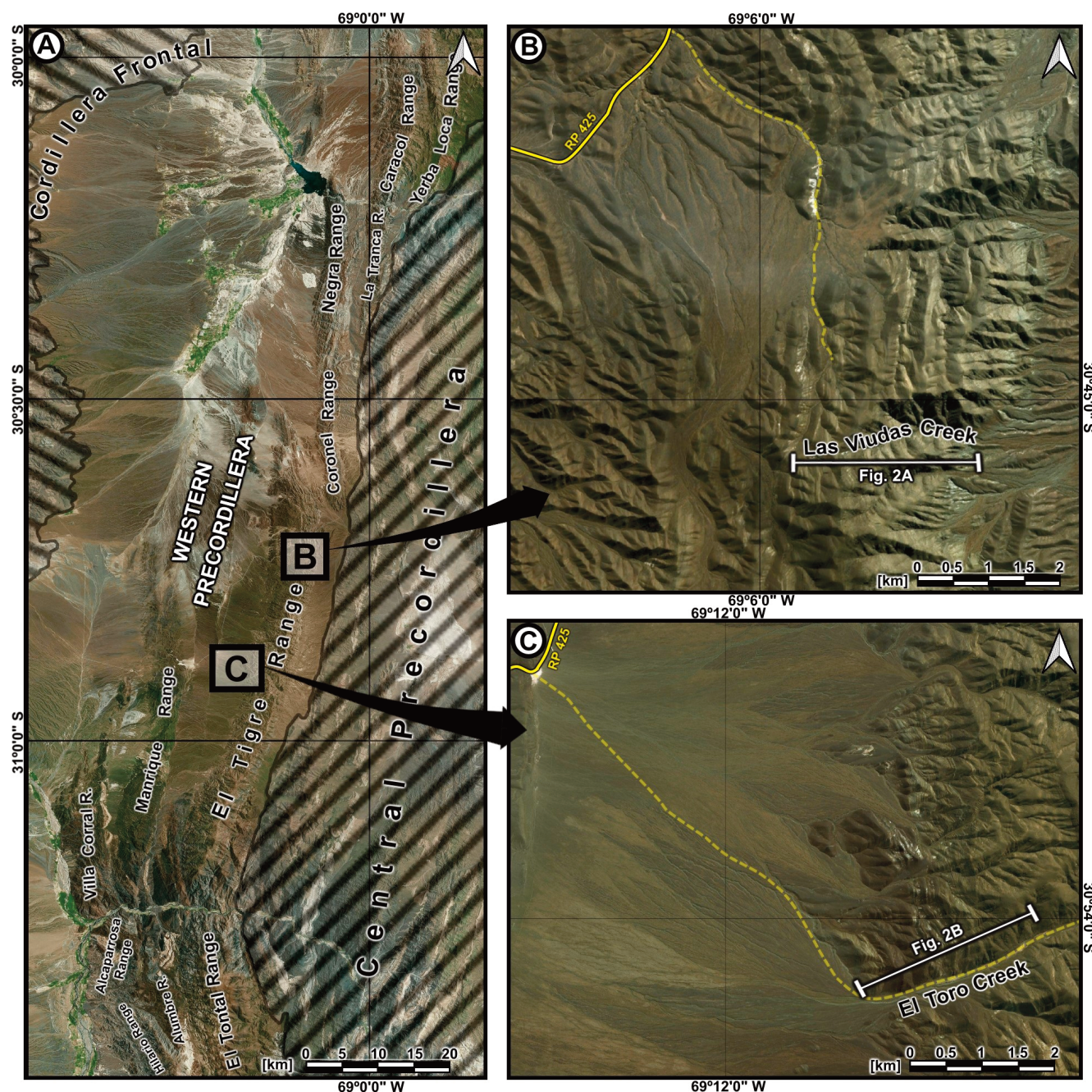
The Western Precordillera, located in the west of Argentina, has vast outcrops of siliciclastic, carbonate, and igneous rocks of Ordovician age, distributed throughout its ranges. Furthermore, the tectono-magmatic cycles that occurred in the western part of Gondwana have caused pervasive low-grade metamorphism, and the associated tectonic features make biostratigraphic studies complicated.

Several Ordovician formations have been described in the Western Precordillera with two lithological features: olistostromic mélanges, such as the Los Sombreros Formation, and turbiditic or hemipelagic deposits, such as the Alcaparrosa, Cabeceras, Cortaderas, Portezuelo del Tontal, and Yerba Loca formations.

The Yerba Loca Formation, studied herein, is composed of conglomerates, sandstones, black and gray shales, carbonates, and Ordovician intrusive-extrusive basic igneous rocks. Its main studied sections are located in the Yerba Loca, Negra, La Tranca, and El Tigre ranges (Fig. 1). The fossil content is bare, mostly composed of graptolites, conodonts, brachiopods, arthropods, and traces. Graptolites referable to the early Darriwilian *Levisograptus austrodentatus* or probably *L. dentatus* zones, and conodonts from the *Yangtzeplacognathus crassus* and *Eoplacognathus pseudoplanus* zones of middle Darriwilian age were found in the Yerba Loca Range (Albanesi et al. 2022). In the Negra Range, the early Sandbian *Nemagraptus gracilis* Zone was recorded (Blasco and Ramos 1976), and in the El Tigre Range, the late Sandbian *Climacograptus bicornis* Zone and early Katian graptolites were identified (Ortega et al. 1991; Caballé et al. 1993; Brussa 1995). Recently, Lopez et al. (2022) extended the range of the *C. bicornis* Zone to the El Toro Creek, El Tigre Range, mentioning an assemblage composed of the eponymous species, *Hallograptus* sp., *Dicellograptus* sp., and *Dicranograptus* sp. Accordingly, the biostratigraphic records constrain the age of the Yerba Loca Formation between the early Darriwilian and the late Sandbian–early Katian.

This study introduces one new Ordovician fossiliferous section for the Western Precordillera and expands the knowledge of a recently discovered section, i.e. Las Viudas and El Toro creeks, respectively, both located in the El Tigre Range in the Western Precordillera. Graptolites of the *Climacograptus bicornis* Zone





**Fig. 1.** **A** – location map showing the principal ranges of the Western Precordillera of San Juan; **B** – detailed map of the Las Viudas Creek section, northern area of the El Tigre Range; **C** – closer view of the El Toro Creek section, central part of the El Tigre Range.

and conodonts on bedding planes corresponding to the *Amorphognathus tvaerensis* Zone indicate a late Sandbian age. Furthermore, graptolites provisionally referred to as the *Nemagraptus gracilis* Zone (Lower Sandbian) are reported. These new sections show great potential to increase the paleontological and biostratigraphic knowledge of a critical time and place to untangle the complex geological history of the western margin of Gondwana.

### Materials and methods

The graptolite samples were collected from the Las Viudas and El Toro creeks, from sandstones, gray and black shales, and present a poor to moderate preservation. Conodont elements and possible brachiopod specimens were recorded from bedding planes. All material is housed in the

Repositorio-INGEO Emiliano P. Aparicio, FCFN, Universidad Nacional de San Juan, under the acronym INGEO-PI-1988–2001.

### Results and discussion

**El Tigre Range sections.** The first section, referred to as the Las Viudas Creek, is located on the eastern slope of the range,  $30^{\circ}45'21''\text{S}$  and  $69^{\circ}05'25''\text{W}$ , 4 km south of RP 425 (Fig. 1B). This outcrop is characterized by a west-dipping 969 m thick stratigraphic succession, with faulted base and top, composed mainly of thick beds of sandstones, gray shales, siltstones, and occasional conglomerates and calcarenite beds. Several basic Ordovician igneous bodies, sills and pillows were found across the section, which thermally affected the surrounding strata and fossil preservation. Only a few

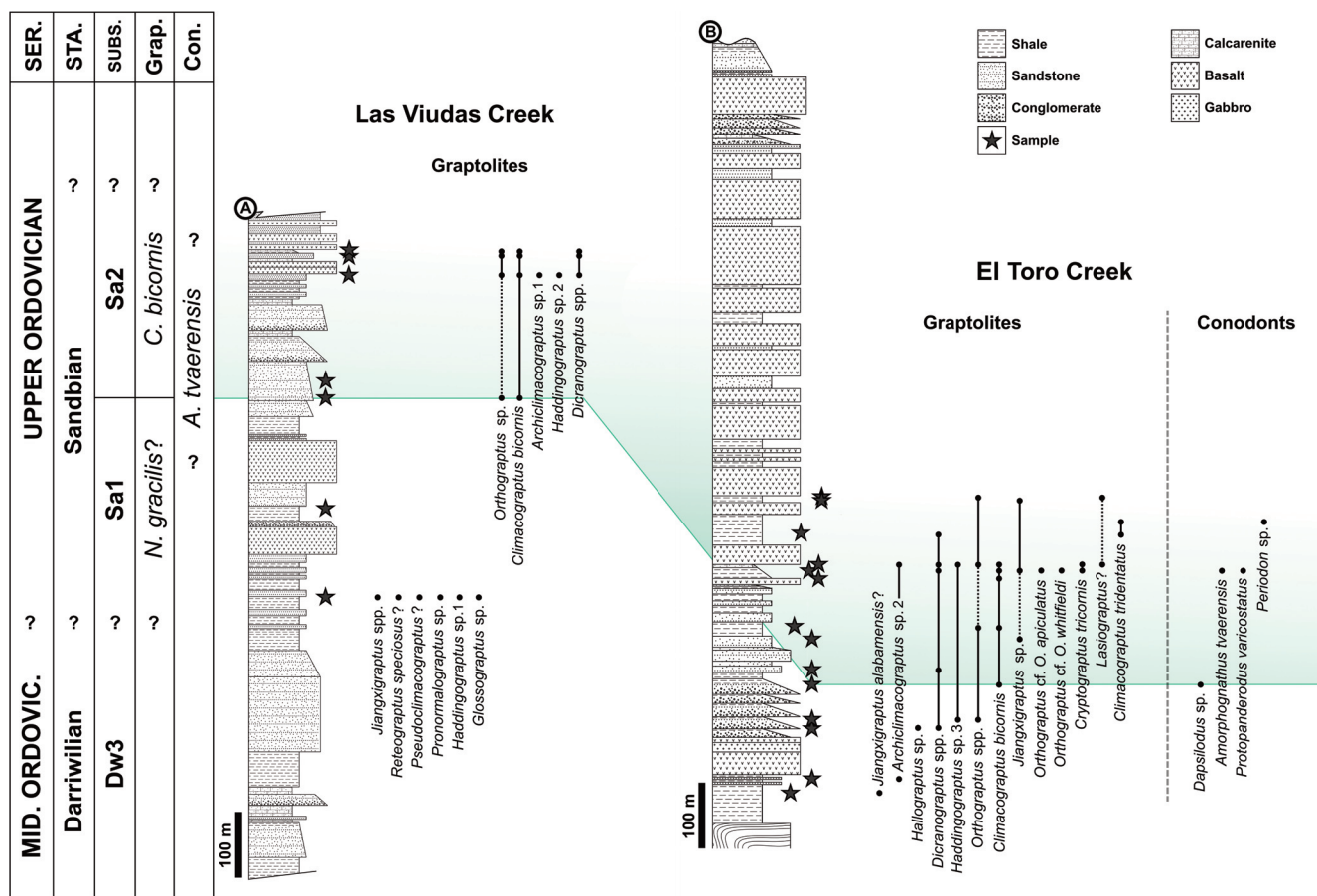


Fig. 2. Stratigraphic data of the Yerba Loca Formation in sections: A – Las Viudas Creek, northern column; B – El Toro Creek, southern column. Sample positions are indicated by the star symbol. Abbreviations: SER. – Series, STA. – Stage, SUBS. – Substage, Grap. – Graptolites, Con. – Conodonts, MID. ORDOVIC. – Middle Ordovician.

fossiliferous strata were found, including five graptolite-bearing levels (Fig. 2A).

418 m above the base of the section, the graptolite assemblage is preliminary composed of *Jiangxigraptus* spp., *Glossograptus* sp., *Haddingograptus* sp. 1, *Pronormalograptus* sp., *Pseudoclimacograptus?* sp. and *Reteograptus speciosus?*, suggesting an early Sandbian age, though a late Darriwilian age remains possible. At 729 m, the late Sandbian *Climacograptus bicornis* Zone starts with the record of the eponymous species, *Archiclimacograptus* sp. 1, *Dicranograptus* spp., *Haddingograptus* sp. 2 and *Orthograptus* sp. (Fig. 2A).

The El Toro Creek section is located in the western margin of the El Tigre Range, 30°54'15"S and 69°10'26"W, 6.5 km south-east of RP 425 (Fig. 1C). A west-dipping succession, 1266 m thick, with a folded base and covered top is described. More abundant graptolitic black shales were found interbedded between sandstones and igneous levels. The sampling provided 17 graptolite-containing layers from the base to the middle of the section (Fig. 2B).

Graptolites preliminary referred to as *Archiclimacograptus* sp. 2, *Dicranograptus* spp., *Haddingograptus* sp. 3, *Hallograptus* sp., *Jiangxigraptus alabamensis?* and *Orthograptus* spp. are recorded from the base up to the level at 212 m. This graptolite assemblage could be preliminarily referred to as the Lower Sandbian. The first occurrence of *Climacograptus bicornis* indicates the homonymous biozone

at 212 m from the base, containing *Archiclimacograptus* sp. 2, *Cryptograptus tricornis*, *Dicranograptus* spp., *Haddingograptus* sp. 3, *Jiangxigraptus* sp., *Lasiograptus?*, *Orthograptus* cf. *O. apiculatus*, *O. cf. O. whitfieldi* and *Orthograptus* spp. Tubaria of *Climacograptus tridentatus* are frequent in the upper part of this assemblage, above the range of *C. bicornis*. Additionally, conodont elements of the index species *Amorphognathus tvaerensis* preserved as casts on bedding plane surfaces are reported (Fig. 2B).

**Age considerations and correlations.** Preliminary studies of the two sections allow to propose a more accurate correlation with other Ordovician outcrops in the Western Precordillera. Considering the great thicknesses of both sections, the Darriwilian Stage could be represented in the barren lower part of the respective successions.

The *Nemagraptus gracilis* Zone is not recorded in the studied sections, although it was documented in the Negra Range section (Blasco and Ramos 1976) and possibly in the La Antena section, El Tontal Range (Peralta et al. 2003; Fig. 1). The graptolite assemblages collected below the strata with *C. bicornis* in the Las Viudas and El Toro sections could be assigned to the *N. gracilis* Zone, despite the fact that the nominal species is not present.

The *Climacograptus bicornis* Zone is recorded in both sections, together with the index conodont *Amorphognathus tvaerensis*, allowing the correlation of these outcrops with those in the northern area of the El Tigre Range; with the Los

Azules, Las Vacas and Sierra de La Invernada formations (Central Precordillera; Ortega and Brussa 1990; Ortega et al. 2007a; Ortega et al. 2008), the Empozada Formation (South Precordillera; Ortega et al. 2007b), the Pavón Formation (San Rafael Block; Cuerda and Cingolani 1998), and the Las Lagunitas Formation (Cordillera Frontal; Tikyj et al. 2009). Globally, a number of sections from Scandinavia, Great Britain, North America, Australasia, and China can be confidently correlated.

## Conclusions

New biostratigraphic studies are presented after surveys carried out in the El Toro and Las Viudas creeks, from the El Tigre Range, Western Precordillera of San Juan Province, Argentina. Graptolites of the *Climacograptus bicornis* Zone and conodonts on bedding plane surfaces corresponding to the *Amorphognathus tvaerensis* Zone were collected, indicating a late Sandbian age for the bearer strata. Graptolites possibly referable to the early Sandbian *Nemagraptus gracilis* Zone have also been recorded. These two sections reveal important paleontological and biostratigraphic potential for the study of the Upper Ordovician in poorly known deep marine environments from the Western Precordillera of Argentina.

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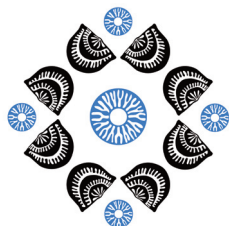
Neitla section, Porkuni–Juuru boundary,  
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# Boundary between the Porkuni and Juuru regional stages in the Neitla section, Estonia

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### ABSTRACT

Conodonts and chitinozoans were studied from the Neitla section, which exposes the boundary between the Porkuni and Juuru regional stages. This level, although not proved biostratigraphically, has been traditionally considered to correspond to the Ordovician–Silurian boundary. However, stable carbon isotope data indicate that the system boundary lies higher in the succession, in the lower part of the Juuru Regional Stage. Rare conodonts and chitinozoans discovered in the section do not provide any criteria for locating the boundary. Although conodonts are represented by taxa characteristic of the Silurian, all of them are known to have already appeared elsewhere in the Upper Ordovician.

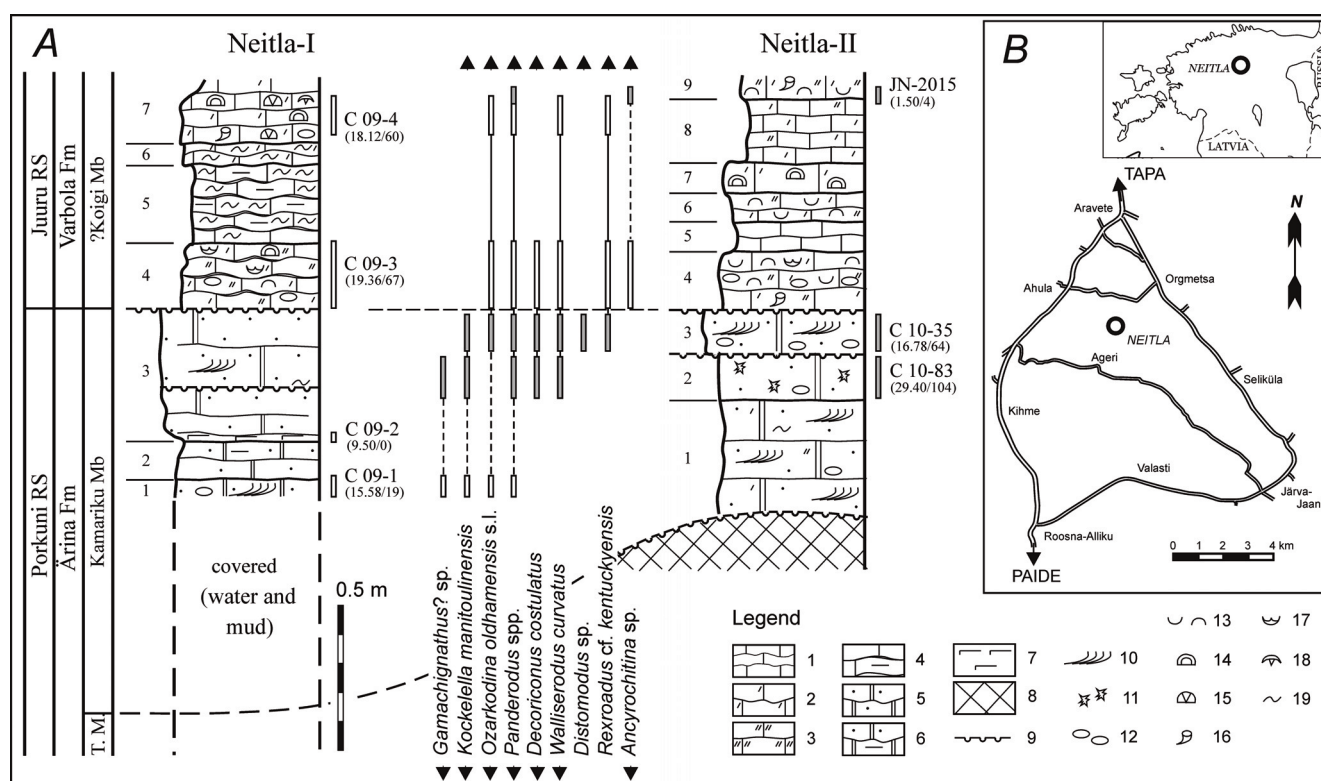
### Introduction

The boundary interval between the Porkuni and Juuru regional stages (RSs) is poorly exposed in Estonia. For about two decades, only one small outcrop section, Neitla, was known. Recently, boundary strata were also exposed in the active Reinu quarry in west-central Estonia, but this has not been studied in detail yet. Biostratigraphical location of the RSs boundary in a section is often complicated and, traditionally, it is identified based on lithological criteria. In the outcrop area, a lithologically distinct contact between the Ärina and Varbola formations (Fms) has been treated historically as the stage boundary. The Ärina Fm is represented by a succession of shallow-water sediments (Hints L. and Meidla 1997). The dolostone with interbeds rich in fragments of crinoid ossicles at the base of the formation (Rõa Member (Mb)) is overlain by stromatoporoid-tabulate reefs (Tõrevere Mb) and their surrounding facies, skeletal limestone and kerogenous dolostone, traditionally treated as the Vohilaid and Siuge Mbs, respectively. The uppermost Ärina Fm consists of quartz-sand-rich dolostone of the Kamariku Mb. The Ärina Fm is overlain by an intercalation of marlstones and calcareous wackestones of the lower Varbola Fm. In some sections, a thin interval of micro- to cryptocrystalline limestone (calcareous mudstone) of the Koigi Mb occurs at the base of the Varbola Fm.

Conodonts are rare in both the Porkuni and Juuru RSs and nearly absent in the boundary beds of these units in northern Estonia. Until recently, the boundary has been studied in the core sections only. Due to the limited size of samples and the generally rare occurrence of conodonts in this interval, most of the samples processed so far were barren. In 2006, a small exposure of bedrock exposing the contact between the Kamariku and probable Koigi Mbs was discovered in the Neitla gravel-pit (Einasto 2007; Fig. 1). The discovery of this section provided the first opportunity to collect and process conodont samples of larger size in the hope of obtaining better information about these microfossils in the regional stage boundary interval and to search for new regional biostratigraphic criteria for this boundary. The results of these investigations are summarised in this paper.

### Materials and methods

Two sections (Neitla-I and Neitla-II, see Fig. 1A) on the bottom of the gravel pit, with a distance of about 10 m between them, were described and sampled in 2009, 2010 and 2015. Both expose the uppermost Ärina Fm (Kamariku Mb) and the lowermost Varbola Fm (Koigi? Mb) underlain by reef limestone of the Tõrevere Mb.



**Fig. 1.** Studied sections (A) and the location of the Neitla gravel pit (B). **A** (from left to right) – regional stratigraphy; lithological log of the profile Neitla-I with bed numbers on the left; samples with their numbers, below the sample numbers in brackets are the weight of the sample (in kg) and the number of conodont specimens discovered in it; distribution of taxa; log of the profile Neitla-II with bed numbers on the left and the location of samples, their numbers, weights and numbers of conodont specimens. Arrowheads above and below the ranges of the taxa indicate their longer ranges in the Estonian succession. Legend: 1 – cryptocrystalline limestone (lmst), 2 – detrital lmst, 3 – bioclastic lmst, 4 – argillaceous lmst, 5 – dolostone rich in quartz sand, 6 – argillaceous dolostone rich in quartz sand, 7 – marlstone, 8 – reef lmst, 9 – discontinuity surface, 10 – cross-bedding, 11 – vugs, 12 – pebbles, 13 – various shell fragments, 14 – stromatoporate, 15 – tabulate coral, 16 – rugose coral, 17 – brachiopod, 18 – trilobite, 19 – bioturbation. Abbreviations: T. M. – Tõrevere Member, RS – Regional Stage, Fm – Formation, Mb – Member. **B** – location of the studied section (indicated by a circle).

The contact between the reef and the overlying Kamariku Mb is marked by a strongly undulating erosional surface. Due to this, the thickness of the Kamariku Mb varies considerably.

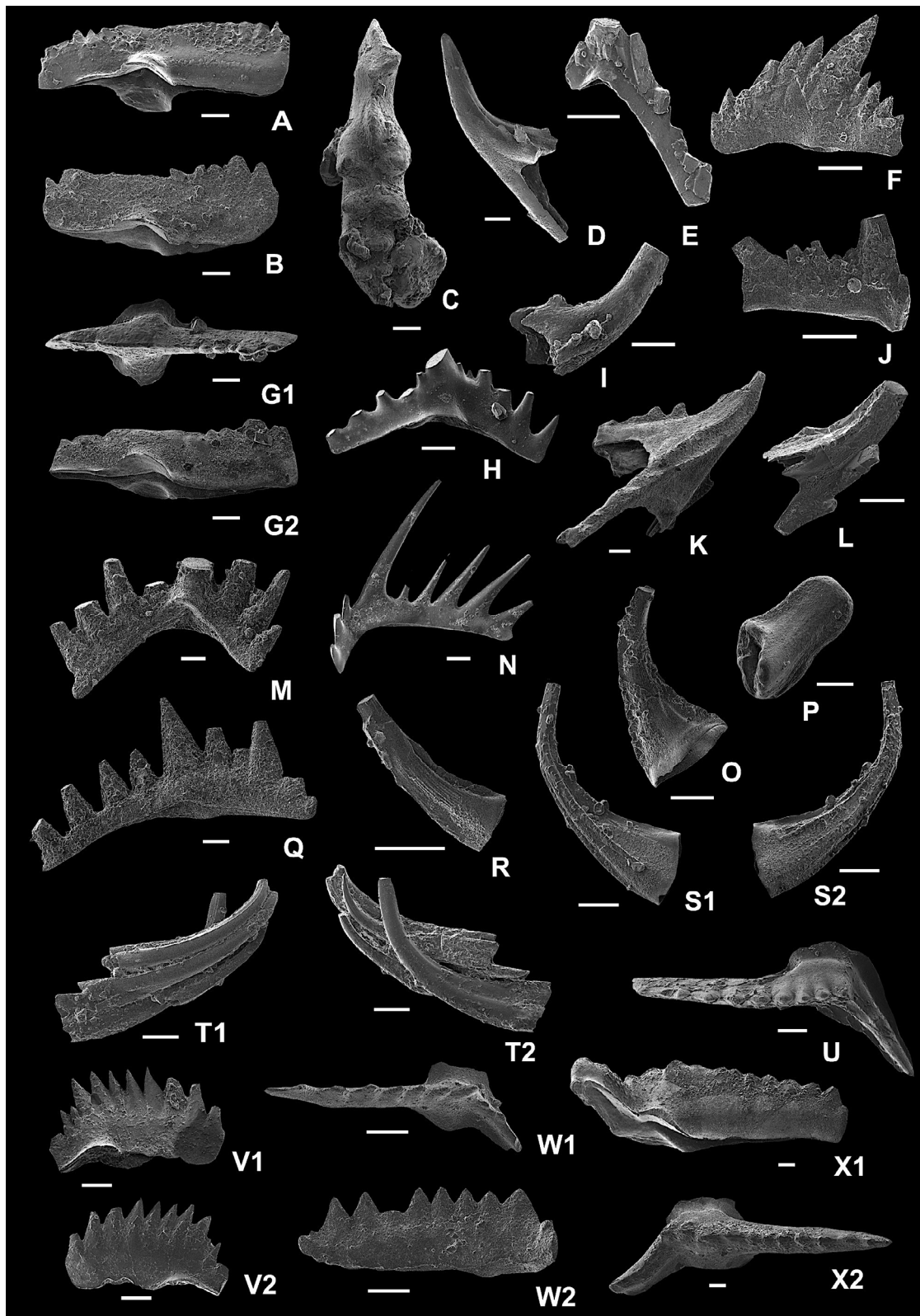
The samples weighing between 9.50 and 29.40 kg were processed using standard methods (Jeppsson and Anehus 1995; Jeppsson et al. 1999). Additionally, a loose piece of limestone (wackestone-packstone rich in small silicified rugose corals, 1.50 kg) from the uppermost part of the Neitla-II section was dissolved. All samples, except for C 09-2, yielded conodonts. Preservation of the specimens is variable; many elements are broken, and the surface of most specimens is covered with a secondary coating of apatite, complicating the identification of simple-cone elements. The colour of the specimens is pale yellow (CAI = 1). A few poorly preserved chitinozoans were found in only two samples from the Varbola Fm. All illustrated specimens are housed at the Department of Geology, Tallinn University of Technology (collections GIT254, 889, 890).

## Results and discussion

Conodonts are rare in the studied samples, only few specimens per kilogram of rock (Fig. 1A). All productive samples (excluding C09-1) are strongly dominated by *Panderodus* (up to 75% of specimens). Poor preservation does not allow their reliable identification, but based on rare, better preserved

specimens, at least two taxa are represented, likely *P. serratus* (Rexroad) and a species of the *P. equicostatus* (Rhodes) group (Fig. 1A). The most common conodont in sample C09-1 is *Kockelella manitoulinensis* (Pollock, Rexroad and Nicoll) (Fig. 2W), which in the Neitla section is restricted to the Kamariku Mb. So far, *K. manitoulinensis* was mainly known from the Raikküla RS (upper Rhuddanian and Aeronian; Männik 1994) in Estonia. Below this level, only few probable elements (including a single Pa) of this species were found in the Porkuni RS, in the back-reef facies ('Siuge Mb') of the Ärina Fm in the Porkuni quarry (Hints, L. and Männik 2014; identified as *Kockelella?* sp. (aff. *K. manitoulinensis*); Fig. 2V). In the Neitla section, *K. manitoulinensis* ranges into the upper part of the Kamariku Mb (samples C 10-83 and C 10-35; Figs 1A, 2X) but is missing in the overlying Varbola Fm. Morphologically, the Pa elements of *K. manitoulinensis* in the Neitla section are identical to those from the Raikküla RS (Fig. 2U; Männik 1994, pl. 4, figs 2, 4, 7). The specimen from the Porkuni quarry is shorter and taller, but has a posterior process turned outwards and bears considerably lower denticles than those on the anterior process of the element. Both features are characteristic of the Pa element of *K. manitoulinensis*.

In the upper Kamariku Mb, *K. manitoulinensis* occurs together with *Walliserodus curvatus* (Branson and Branson) (Fig. 2O, S), *Decoriconus costulatus* (Rexroad) (Fig. 2R),



**Fig. 2.** Selected conodonts from the Neitla, Porkuni and Pusku sections. Scale bar represents 100  $\mu\text{m}$ . All samples come from the Neitla section unless stated otherwise. **A, B, E–G, J** – *Ozarkodina oldhamensis* s.l. (Pollock, Rexroad and Nicoll): A, B, G – Pa elements, GIT889-1, 2, 3; E – M element, GIT889-4; F – Pb element, GIT889-5; J – Sc element, GIT889-6. A, E – from sample C10-35; B, G – from sample C09-4; F, J – from sample C09-1. **C, D, I** – *Distomodus* sp.: C – Pa element (fragment), GIT889-7; D – Sb element, GIT889-8; I – Sa? element, GIT889-9. All from sample C10-35. **H, M, N, Q** – *Rexroadus* cf. *kentuckyensis* (Branson and Branson): H – Pb element, GIT889-10; M – Sb element, GIT889-11; N – Sc element, GIT889-12; Q – Pa element, GIT889-13. All from sample C09-4. **K, L, P?** – *Gamachignathus* sp.: K – Pc? element, GIT889-14; L – Sb element, GIT889-15; P? – M element, GIT889-16. K and L – from sample C10-83, P? – from sample C09-1. **R** – *Decoriconus costulatus* (Rexroad), paltodontiform element, GIT889-17, sample C09-3. **O, S** – *Walliserodus curvatus* (Branson and Branson): O – curvatiform element, GIT889-18, sample C09-3; S – multicostatiform element, GIT889-19, sample C10-83. **T** – *Panderodus* sp., cluster of elements, GIT889-20, sample C09-4. **U, W, X** – *Kockelella manitoulinensis* (Pollock, Rexroad and Nicoll): Pa elements, W – GIT889-21, sample C09-1; X – GIT889-22, sample C10-35; U – GIT254-52, Pusku quarry, sample M-226. **V** – *Kockelella* cf. *manitoulinensis* (Pollock, Rexroad and Nicoll), Pa element, GIT890-1, Porkuni quarry, sample M-334.

*Rexroadus* cf. *kentuckyensis* (Branson and Branson) (Fig. 2H, M, N, Q), *Distomodius* sp. (Fig. 2C, D, I) and *Ozarkodina oldhamensis* s.l. (Rexroad) (Fig. 2A, B, E–G, J). All these taxa are present also in the Varbola Fm in the Neitla-I section and are known from the strata of Rhuddanian and Aeronian age from other sections in Estonia and elsewhere. Also, in the Porkuni quarry the probable specimens of *K. manitoulinensis* occur together with *Decoriconus* sp., *P. equicostatus* s.l. and *Walliserodus* sp. (Hints, L. and Männik 2014). The uppermost sample, JN-2015 from Neitla-II yielded only four unidentifiable specimens of *Panderodus* sp.

Chitinozoans were found in two samples from the Varbola Fm: 2 specimens from Neitla-I (sample C 09-3) and 30 specimens from Neitla-II (sample JN-2015). The specimens are very poorly preserved, but all seem to belong to the same taxon, *Ancyrochitina* spp., which appears in Estonia in the lower Katian (Oandu RS) and is widely distributed in the Silurian.

Although the conodont assemblage in the Neitla section is mainly represented by taxa characteristic of the Rhuddanian, all of them are known to have already appeared in the (upper) Hirnantian elsewhere (e.g., Armstrong 1996). Considering the distribution of conodonts in the Estonian succession, most of the taxa found in the Neitla section so far were previously known to have appeared in the lower(most) Juuru RS. Only *D. costulatus* is also common in the Upper Ordovician and rare specimens of *Oz. oldhamensis* s.l. were recorded from the Porkuni RS. The only ‘typical’ Ordovician conodont, i.e., so far not identified from the strata of the Silurian age, found in the Neitla section is *Gamachignathus?* sp. (Fig. 2K, L, P).

Traditionally, the boundary between the Porkuni and Juuru RSs has been considered to correspond to the Ordovician–Silurian boundary. This conclusion was based on the occurrence of Hirnantian trilobites and brachiopods in the Porkuni RS in western Latvia and Lithuania, and on the records of *Stricklandia lens prima* Williams from the lower part of the Juuru RS in (northern) Estonia (Kaljo et al. 1988). In all known sections, a gap and a sharp change in lithology mark this stage boundary, but because of the lack of diagnostic taxa, its correlation with the Ordovician–Silurian boundary is highly problematic. Moreover, the results of  $\delta^{13}\text{C}$  studies suggest that the lowermost Juuru RS might be of late Hirnantian age (Meidla et al. 2023). The  $\delta^{13}\text{C}$  data from the Porkuni quarry indicate that the Ärina Fm exposed in that section corresponds to the rising limb of the Hirnantian Carbon Isotope Excursion (HICE) and correlates with the lower Hirnantian, whereas the strata exposed in Neitla (the Kamariku Mb and the lowermost Varbola Fm) correspond to its falling limb and correlate with the upper Hirnantian (Hints, L. and Männik 2014; Gul et al. 2021). The conodont assemblage from the Neitla section does not contradict or support this conclusion.

## Conclusions

Conodonts and chitinozoans are rare in the Neitla section. The low-diversity conodont assemblage discovered in this section

is not age-diagnostic. Although it is represented by taxa that were formerly considered to be characteristic of the Silurian in the Baltic region, all of them are known to have already appeared elsewhere in the Upper Ordovician. The assemblages in the Ärina and Varbola Fms are almost identical and do not provide any criteria for the identification of the boundary between the Porkuni and Juuru RSs. The only possibility to locate the level in a succession might be the disappearance of *Gamachignathus*, but further studies are needed to prove this. The study also confirmed that *K. manitoulinensis* appears in the Estonian succession already in the Porkunis RS, as previously assumed, based on the occurrence of a few probable specimens of this species in the Porkuni quarry.

## Acknowledgements

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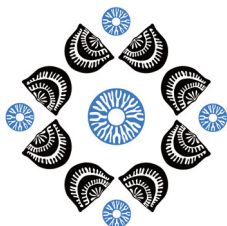
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# Searching for the Ordovician–Silurian boundary in Estonia, Latvia and Lithuania

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### ABSTRACT

The present study focuses on determining the position of the lower boundary of the Silurian System in the eastern Baltic region. To achieve this, we conducted a comprehensive analysis of stable isotopic curves, combined with previously published data on the graptolite record. Our isotopic correlations are primarily based on the  $\delta^{13}\text{C}_{\text{org}}$  curve of the Dob's Linn section, the GSSP of the Silurian System, and the  $\delta^{13}\text{C}_{\text{carb}}$  curve of the Monitor Range section in Nevada. Our results provide robust evidence for correlating the basal Varbola Formation, the lower part of the Öhne Formation and the Stačiūnai Formation, and suggest their latest Ordovician age. The integration of stable isotopic data and graptolite records allows for a more accurate characterisation of the Ordovician–Silurian boundary in this region.

### Introduction

Until the 2000s, the lower boundary of the Silurian System in the Baltic region was correlated with a major gap and turnover in shelly faunas. A major hiatus is observable in nearly all outcrop and subsurface sections of the eastern Baltic area. The formation of the hiatus was ascribed to the glacioeustatic sea-level fall already in the 1970–80s (e.g., Jaanusson 1979; Kaljo et al. 1988). The most remarkable change in fossil assemblages in the Ordovician–Silurian transition interval is confined to this particular level (see Nestor et al. 1991 for a summary). The post-extinction interval is characterised by the gradual appearance of new species in all fossil groups. The first new taxa were usually regarded as the ‘Silurian fauna’ in most papers. Even in the offshore sections, the hiatus marks a complete turnover, and the overlying strata are characterised by an impoverished fossil assemblage that was formerly regarded as of Silurian age, such as in the Jurmala core section in western Latvia (see Meidla et al. 2020). The occurrence of a hiatus in the deep-shelf Jurmala section proves that the drop in sea level was prominent, compared to other less remarkable sea-level fluctuations recorded in the Ordovician succession of the region (Kiipli and Kiipli 2020).

During the last decade, research advances, particularly new data from stable isotopic geochemistry, have questioned the traditional concept of the lower boundary of the Silurian System, and this is also causing problems for Ordovician stratigraphy.

The general understanding that the latest Hirnantian, after the second Hirnantian extinction wave, is characterised by a survival fauna has long been reflected in research papers (e.g., Brenchley et al. 1994; Marshall et al. 1997; Hammarlund et al. 2012, etc.). However, it did not affect the correlations in the Ordovician–Silurian boundary interval in Estonia, Latvia and Lithuania. The position of the system boundary in the regional succession was first challenged on the basis of the stable carbon isotopic record, after the discovery of a long falling limb of the Hirnantian Carbon Isotopic Excursion (HICE), reaching the strata traditionally attributed to the Silurian in several sections (Meidla et al. 2011; Bauert et al. 2014; Ainsaar et al. 2015). A later study (Meidla et al. 2020) on the comparison of the regional succession with the North American Monitor Range section suggests that in the middle-lower ramp sections the system boundary occurs more than 10 m higher than previously believed. However, because of the lack of diagnostic graptolites and conodonts, a proper biostratigraphic marker for this boundary could not be identified in the particular succession (Meidla et al. 2016). This view added new aspects to earlier interpretations of the stable carbon isotopic profiles of the region (e.g., Brenchley et al. 2003, fig. 13), but did not propose a new marker for the boundary.



This paper aims to discuss the possibilities of locating this important stratigraphic boundary in the regional succession, supplementary boundary criteria and correlation of the rock units in the Ordovician–Silurian boundary interval in Estonia, Latvia and northernmost Lithuania.

## Materials and methods

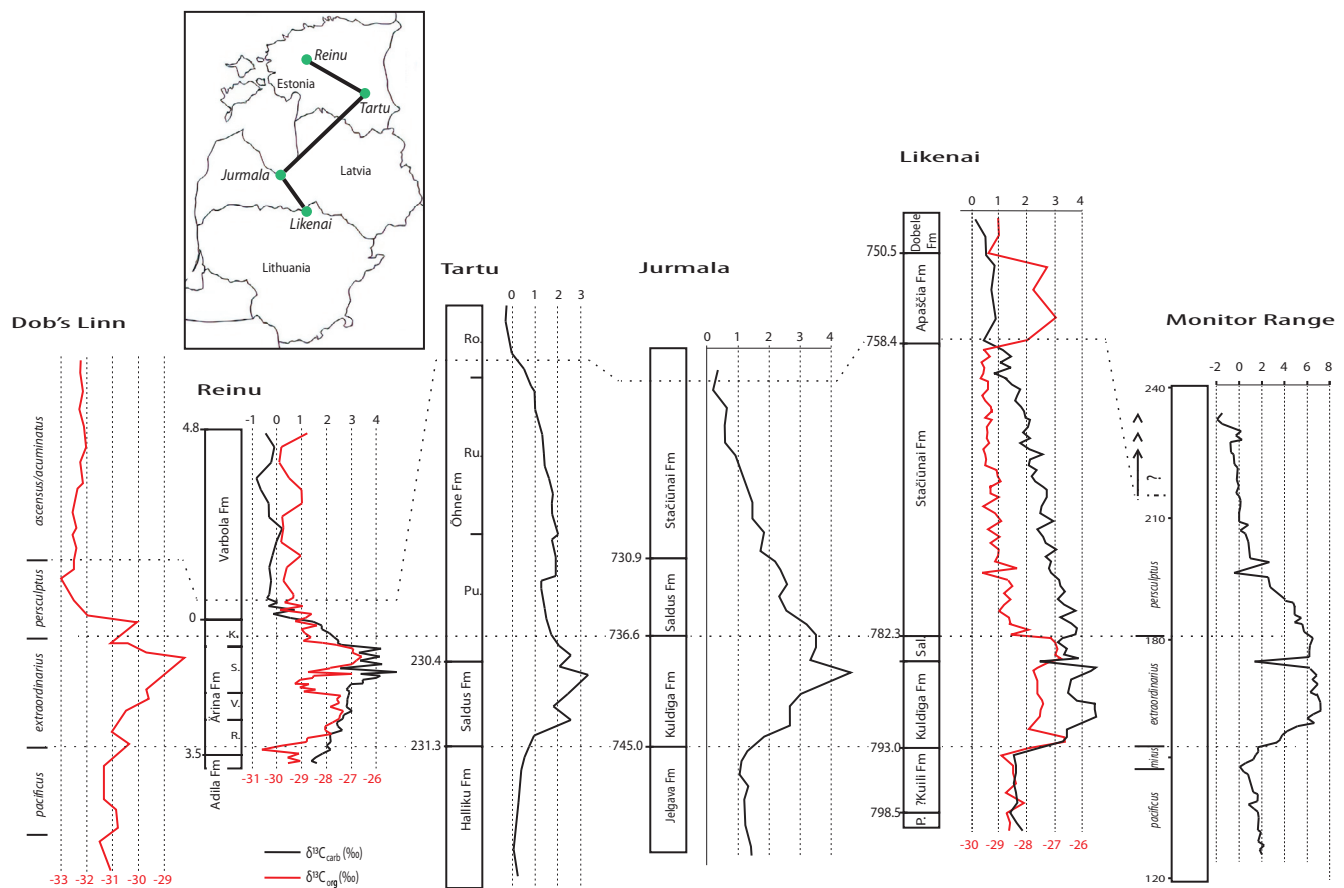
This paper summarises the most recent palaeontological and stable isotopic evidence from the Ordovician–Silurian transition interval of the study area, published and in press. The new paired carbonate and organic matter carbon isotopic curve of the Reinu section is complemented with data from the Tartu (Bauert et al. 2014), Jurmala (Meidla et al. 2011) and Likēnai (Hints et al. in press) core sections. The biostratigraphically dated global key sections referred to in this paper are the Dob’s Linn (GSSP of the Silurian System; Jones et al. 2011) and the Monitor Range sections (after Finney et al. 1999 and LaPorte et al. 2009).

## Results and discussion

Recent  $\delta^{13}\text{C}$  studies in the Ordovician–Silurian transition interval have revealed a number of sections where, in biostratigraphic sense, the ‘basal Silurian strata’ correspond to the falling limb of the HICE. This is true for the lower part of the Stačiūnai Formation in the Jurmala core (Meidla et al.

2011), the lower part of the Õhne Formation in the Tartu core section (Bauert et al. 2014) and the lowermost part of the Varbola Formation in Estonia – the Koigi Member and some overlying strata in the Karinu, Viki and Kamariku core sections (Hints et al. 2014; Ainsaar et al. 2015). The same applies to the newly studied section in the Reinu quarry, northern Estonia (see Fig. 1). Some of the sections also reveal a slow appearance of post-extinction ‘Silurian’ species of various shelly fossil groups and chitinozoans. Several of these species were traditionally used for locating the system boundary in the non-graptoliferous Ordovician–Silurian boundary successions all over the eastern Baltic area. This is true for several chitinozoan species (*Spinachitina fragilis* – see Pöldvere et al. 1998, *Ancyrochitina laevaensis* – see Hints et al. 2014; Nölvak et al. 2023), conodonts (*Ozarkodina* ex gr. *oldhamensis* – see Kaljo et al. 2008) and ostracods (*Longiscula smithii*, *Rectella procera*, *Microcheilinella mobile*, *M. rozhdestvenskaja*, *Bipunctoprimitia bipunctata* – see Meidla et al. 2011). The macrofossil record in the sections with distinctive stable carbon isotopic signatures is very limited, but the ranges of all taxa previously recorded in the lower Varbola, Õhne and Stačiūnai formations need to be validated.

The organic carbon isotopic ( $\delta^{13}\text{C}_{\text{org}}$ ) curves add a new aspect to the ongoing discussion. The shape of this curve in the Tartu and particularly in the Likēnai (e.g. Hints et al. in press) sections is remarkably different from the corresponding  $\delta^{13}\text{C}_{\text{carb}}$  curves. The  $\delta^{13}\text{C}_{\text{org}}$  values are high only in a short



**Fig. 1.** Stable carbon isotopic correlation of the sections along the Reinu-Tartu-Jurmala-Likēnai profile and with the biostratigraphically dated global reference sections at Dob’s Linn, UK (after Jones et al. 2011) and the Monitor Range, US (after Finney et al. 1999 and Laporte et al. 2009). Abbreviations: Fm – formation, K. – Kamariku Member (Mb), P. – Parovēja Fm, Pu. – Puikule Mb, R. – Rõa Mb, Ro. – Rozeni Mb, Ru. – Rūja Mb, S. – Siuge Mb, Sal. – Saldus Fm, V. – Vohilaid Mb.

System	Stage	Regional stage	Formations				
			C&W Lithuania S&W Latvia	S Estonia N Latvia	N & C Estonia		
Silurian	Aer.	RAIK-KÜLA	Dobele	Saarde	Nurme-kund	Raik-küla	Hilliste
	Rhud.	JUURU	Apasčia Remte	Öhne	Tamsalu Varbola		
Ordovician	Hirnantian	POR-KUNI	Stačiūnai	Saldus	Saldus		
			Kuldiga	Kuldiga			
	K.	PIRGU	Kuiļi	Kuiļi	Arina		

**Fig. 2.** Correlation of the Ordovician–Silurian boundary strata in Estonia and Latvia with the graptolite zones and the global standard. The compilation is based on Gailite et al. 1987, Nestor 2012, Männik 2014, Meidla et al. 2020 and the authors' new data. Abbreviations: C – Central, N – North, W – West, S – South, K. – Katian, Rhud. – Rhuddanian, Aer. – Aeronian, *Coronogr.* – *Coronograptus*.

interval that is biostratigraphically confined to the Porkuni Regional Stage (RS). The  $\delta^{13}\text{C}_{\text{carb}}$  curves of stratigraphically more complete sections reveal a long decline in the values in the Juuru RS. In the Jurmala and Likēnai core sections (Fig. 1), the falling limb of the HICE extends throughout the entire Stačiūnai Formation. This discrepancy may look controversial, but comparison with the stratotype section in Dob's Linn, Scotland, and the Laframboise Point section in Anticosti, Canada, suggests that the interval of high  $\delta^{13}\text{C}_{\text{org}}$  values may correspond to the *Metabolograptus extraordinarius* Graptolite Zone (Jones et al. 2011), whilst the HICE does most probably range up into the *M. persculptus* Zone in the eastern Baltic area (Meidla et al. 2020).

However, the question about the position of the system boundary is still open. The correlation with the global standard remains complicated because of the poor graptolite record of the Ordovician–Silurian transition in a large area reaching from northwestern Estonia (Nestor and Einasto 1997) across Latvia (Gailite et al. 1987) and Lithuania (Paškevičius 1997) to marginal northeastern Poland (Podhalańska 1977). The only known section with graptolites in the boundary interval (Ulst 1992) has not been studied for other fossil groups and stable isotopes. In other sections all over the region, the graptolite record seems to begin in the *Coronograptus cyphus* Graptolite Zone, i.e., in the upper Rhuddanian.

In the hope of covering this 'information gap' in the biostratigraphic succession, we tried to use the upper limits of the stable carbon isotopic excursions (both  $\delta^{13}\text{C}_{\text{org}}$  and  $\delta^{13}\text{C}_{\text{carb}}$ ) as correlation markers. Figure 1 displays the stable carbon isotopic correlation of the sections along the Reintartu–Jurmala–Likēnai profile and with the biostratigraphically dated global reference sections. Based on the Dob's Linn section, the *Metabolograptus extraordinarius* Zone is taken as nearly equivalent to the prominent Hirnantian  $\delta^{13}\text{C}_{\text{org}}$  excursion. The *M. persculptus* Zone is correlated with the falling limb of the HICE, as in the Monitor Range section. These results suggest an improved correlation with the Ordovician–Silurian boundary strata in Estonia and Latvia.

The correlation of the Ordovician–Silurian boundary strata in Fig. 2 is a compilation based on Gailite et al. 1987,

Nestor 2012, Männik 2014, Meidla et al. 2020 and the correlation in Fig. 1. The basal part of the Varbola Fm corresponding to the limit of the falling limb of the HICE has been attributed to the Ordovician in several papers already. The same is true for the lower part of the Öhne Fm (Meidla 2020 and references therein) and for the Stačiūnai Fm (see Fig. 1). The topmost part of the Öhne Fm in the Ikla core reveals graptolites indicative of the *Coronograptus cyphus* Zone (Kaljo and Vingisaar 1969). According to Gailite et al. (1987), the same is true for the topmost Remte Fm, but not for the Apasčia Fm, which still remains poorly dated. The Dobele Fm is characterised by graptolites from the *Demirastrites pectinatus*–*D. triangulatus* Zone up to the *Stimulograptus sedgwickii* Zone, whilst a tentative gap between the Apasčia and Dobele formations is drawn as equivalent to the *C. cyphus* Zone, which may be missing in the Apasčia–Dobele transition interval, judging from the published data (mainly Gailite et al. 1987).

## Conclusions

Regional Ordovician and Silurian correlation charts of the eastern Baltic area have mainly been based on biostratigraphic evidence, but the data on the Ordovician–Silurian transition interval are poor and controversial. Integration of the stable isotopic evidence with the limited data on the distribution of graptolites allows the correlation of the Varbola, Öhne and Stačiūnai formations to be justified. As the lower boundary of the Silurian System still does not have a proper biostratigraphic marker in the regional succession, the ranges of all zonal microfossil taxa previously recorded in the lower Varbola, Öhne and Stačiūnai formations need to be validated for its definition.

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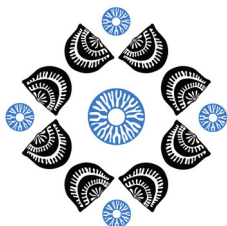
Fezouata Biota, Fossil-Lagerstätten,  
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# A new species of the problematic organism *Webbyites* from the Early Ordovician Fezouata Biota of Morocco

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### ABSTRACT

The problematic colonial organism *Webbyites* has previously been considered to be a hydroid (phylum Cnidaria). In this paper, we describe a new species, *Webbyites felix* sp. nov., from the Early Ordovician Fezouata Konservat-Lagerstätte of Morocco. One specimen preserves some soft-tissue zooid remains. The presence of a stolon system in the new species and the type species indicates that *Webbyites* is a benthic graptolite. *Webbyites* lacks bithecae; thus, it is not a dendroid graptolite.

### Introduction

The Lower Ordovician Fezouata Formation of Morocco has yielded a diverse variety of exceptionally preserved fossils from a large number of sites around the city of Zagora (Van Roy et al. 2010, 2015). Groups exhibiting exceptional preservation include trilobites, non-biomineralised arthropods, annelids, echinoderms, graptolites, hyolithids, palaeoscolecoid worms, and sponges (Van Roy et al. 2015).

Gutiérrez-Marco et al. (2022, fig. 13a) illustrated a specimen from the Fezouata Formation, which they regarded as a possible hydroid, compared with the *Plumalina*-like form listed by Van Roy et al. (2015). The specimen lacks location data, but was purchased from a local seller in Erfoud (Morocco), and was offered for sale together with other Fezouata fossils that were mostly obtained from the well-known fossil locality at the foot of the Jbel Bou Zeroual, which is regarded as middle Floian in age on the basis of the occurrence of *Baltograptus jacksoni* Biozone graptolites (Lefebvre et al. 2016, locality Z-F0). However, this circumstance is incidental and the provenance of the fossil remains unknown.

The offer on the Internet of better-preserved material of the same species, among them an exceptional specimen (now the holotype) led J. C. Gutiérrez-Marco to travel to the Anti-Atlas to search for new material and obtain data on their geographic origin and stratigraphic age. This was possible with the help of Lahcen Ben Moula (Taichoute, SW Alnif), who recently discovered new material of *Webbyites* in the Oued Ouaoufrount section (Z-F6 according to previous authors: see Lefebvre et al. 2016; Lebrun 2017). This section contains eight fossiliferous beds (a–h) that have yielded upper Tremadocian graptolites, identified as part of the study of Gutiérrez-Marco and Martin (2016). The newly collected specimens were associated with some trilobites of long stratigraphic range within the Fezouata Shale, such as *Euloma filacovi* (Bergeron), *Asaphellus* aff. *jujuanus* Harrington, *Ampyx priscus* Thoral, and *Kierarges morrisoni* Corbacho, which have a range extending back to the upper Tremadocian (personal observation by J. C. Gutiérrez-Marco; Martin et al. 2016).

### Materials and methods

Macro photographs were obtained using a Canon EOS 5DS R fitted with a Hoya Pro1 Digital Circular Polarizing Filter. Illumination was provided by two LED lamps (Kaiser RB 5020 DS 2), each covered with a sheet of polarising filter.

Microphotographs were taken using a GXCAM HICHROME AF MET 2-megapixel digital camera (GX Microscopes, Wickhambrook, Suffolk, UK) attached to a Leica S8APO (Leica, Wetzlar, Germany), with illumination from a Leica LED3000 RL ring light with attached polarising filters. The imaging software used was GX Capture-T (GX Microscopes), and stacked images were produced using Helicon Focus. Both macro- and microphotographs were taken using cross-polarised light, which is useful for increasing contrast in fossil material (e.g. Muir et al. 2021).

The studied specimens have been deposited in the palaeontological collections of the Faculté des Sciences et Techniques of the Cadi Ayyad University of Marrakesh, Morocco (registration prefix AA).

### Systematic palaeontology

Phylum Hemichordata Bateson, 1885

Class Pterobranchia Lankester, 1877

Order and Family unknown

Genus *Webbyites* Kraft, Kraft and Prokop, 2001

*Type species.* *Thamnograptus* (?) *rokycanensis* Bouček, 1956

*Other species.* *Webbyites felix* sp. nov., *Webbyites?* sp. of Gutiérrez-Marco et al. 2022

*Remarks.* Dzik et al. (2016) included *Webbyites* in the family Crinisdendridae, together with the problematic organism *Crinisdendrum*; however, the branches in the two genera are markedly different in structure: those of *Webbyites* consist of lines of distinct thecae, whereas those of *Crinisdendrum* appear to be hollow tubes with a distinctive ‘plaited’ structure. We have no particular reason to think that these two taxa were closely related, thus do not consider it useful to use this family.

*Webbyites felix* sp. nov.

Figures 1, 2

?2015 *Plumalina*-like form, Van Roy et al., table 1

2022 *Plumalina*-like probable cnidarian, Gutiérrez-Marco et al., fig. 13a

*Etymology.* Latin *felix*, happy, and in honour of Félix Collantes, an amateur palaeontologist who donated the holotype for study.

*Holotype.* Specimen number AA.TER.OI.32a–b (part and counterpart).

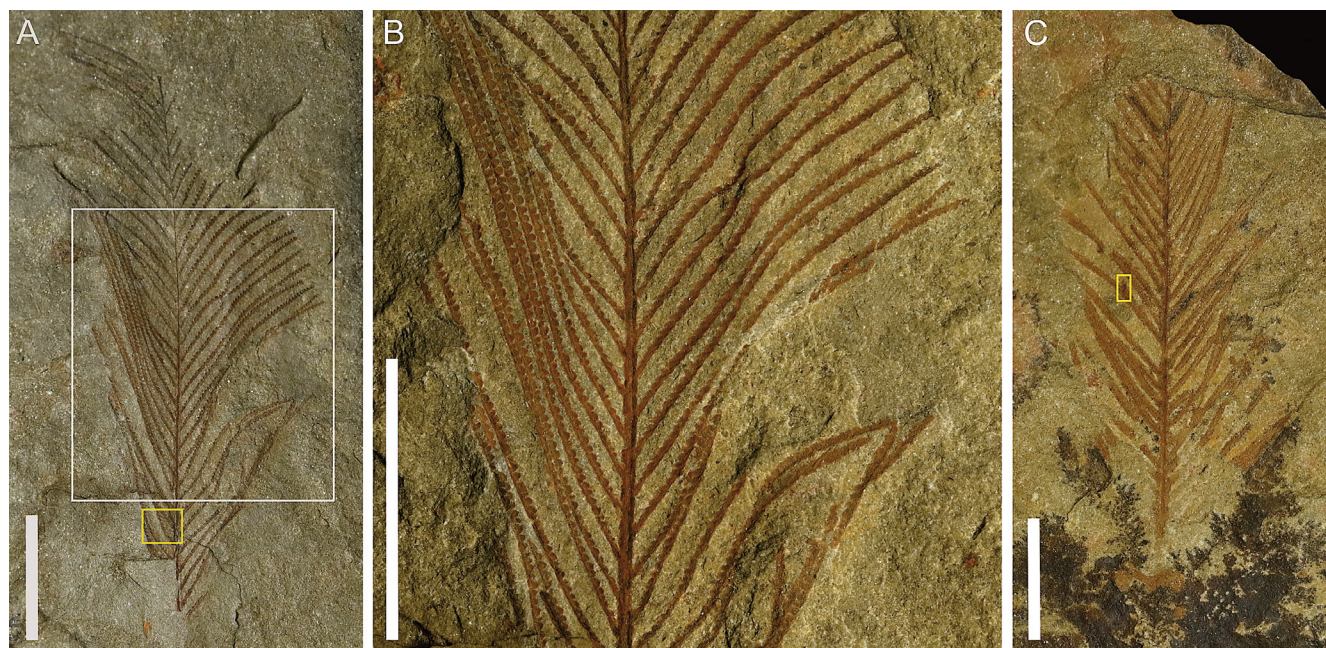
*Paratypes.* AA.JBZ.OI.201a–b, AA.TER.OI.33, AA.TER.OI.34.

*Type locality.* Oued Ouaufrout, ca 24 km NW of Zagora. Shales of probable late Tremadocian age.

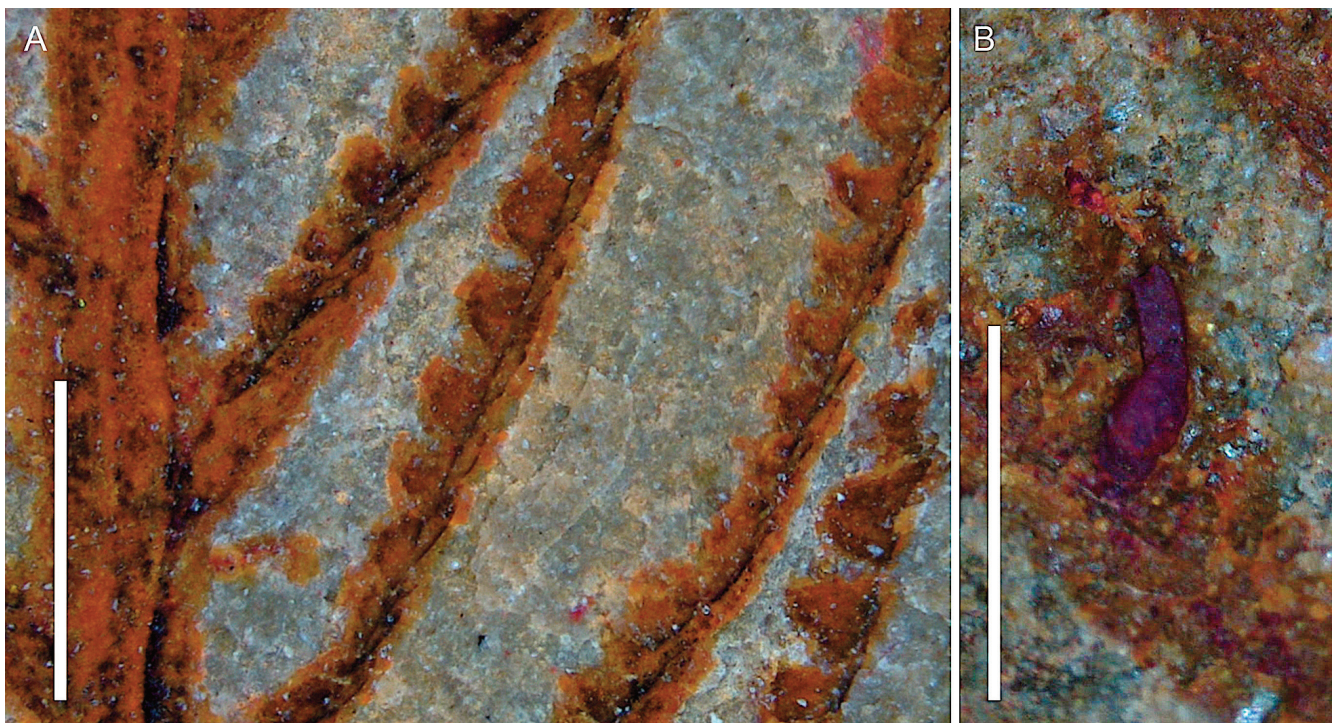
*Diagnosis.* *Webbyites* with non-spinose thecae.

*Description.* The colony consists of a central axis with closely spaced branches, which branch alternately (rather than oppositely) from the axis (Fig. 1). The branches are spaced at intervals of 1.1–1.2 mm along each side of the axis. The branches are straight or slightly curved, and do not themselves branch.

The specimens have preserved lengths of 35–45 mm and preserved widths of 20–25 mm. The proximal and distal ends are not preserved in any of the specimens; thus, no details of a holdfast, which we assume to have been present, are available. The axis becomes notably narrower towards the distal end of the colony, from 0.3–0.45 mm to 0.1 mm. The branch length appears to be consistent throughout the colony; there appears to be no trend for branches to become shorter or longer with colony growth. Each branch narrows slightly towards its distal end. Traces of the stolon system are preserved in many branches and in the stem (Fig. 2A).



**Fig. 1.** *Webbyites felix* sp. nov.: **A** – holotype, specimen AA.TER.OI.32a, overall view; **B** – close-up of the middle part of the holotype (indicated by the white box in part A); **C** – specimen AA.JBZ.OI.201b. The yellow box in part A indicates the location of Fig. 2A, the yellow box in part C indicates the location of Fig. 2B. Scale bars = 10 mm.



**Fig. 2.** *Webbyites felix* sp. nov.: **A** – close-up of the counterpart of the holotype (specimen number AA.TER.OI.32b) showing the stolon system (black) in axis and branches; **B** – soft-tissue remains, specimen AA.JBZ.OI.201b. Scale bars = 1 mm.

The branches are straight or slightly curved. Some branches overlap each other on the bedding surface, implying that the skeletal material of the colony was flexible during the organism's lifetime. The thecae are simple cups, without spines, and with the apertures facing towards the axis. Each branch contains one row of thecae; the axis does not contain thecae. The thecae are consistent in size throughout the colony. There are approximately three thecae per millimetre. One specimen preserves soft-tissue remains of a zooid within a theca (Fig. 2B). The zooid is preserved as a reddish blob (assumed to be composed of a weathered iron mineral) 0.61 mm long and 0.17 mm wide. The zooid appears to be attached to the stolon.

*Remarks.* *Webbyites felix* sp. nov. is probably the 'Plumalina-like form' that was listed (but not illustrated) by Van Roy et al. (2015). Specimen AA-JBZ-OI.201 was previously illustrated as 'Plumalina-like probable cnidarian, possibly similar to the "Plumalina-like form" of Van Roy et al. (2015)' by Gutiérrez-Marco et al. (2022, fig. 13a).

*Webbyites felix* sp. nov. differs from the type species *W. rokycanensis* in bearing simple, rather than spinose, thecae. The new species is similar to the previously described probable hydroids *Plumalina* Hall, 1858 and *Pennalina* Cope, 2005. *Webbyites* and *Plumalina* differ in that branching is alternate in the former and opposite in the latter (Muscente and Allmon 2013). *Webbyites felix* sp. nov. can be distinguished from *Pennalina crossi* Cope, 2005 by the branches of *P. crossi* being curved rather than straight. In *Pennalina* sp. A of Cope (2005), the branch width becomes distally smaller, rather than remaining constant.

Several organisms that are currently interpreted as algae are similar in form to *Webbyites*. *Buthograptus* Hall, 1861

has a cylindrical central axis and unbranched pinnules, and is interpreted as an alga (LoDuca 2019). The pinnules of *Buthograptus*, however, appear to be cylindrical, are slightly curved, and do not bear any structure that might be interpreted as thecae (LoDuca 2019), thus clearly different from those of *Webbyites*. *Whiteavesia* Fry, 1983 from the Upper Ordovician Cat Head Member of the Red River Formation of Manitoba, Canada, which was described as an alga, differs from *Webbyites* in the spiral arrangement of the branches. In addition, the appendages of *Whiteavesia* are markedly less thick than the main stem (Fry 1983). The presence of a stolon system and the preservation of a zooid in *Webbyites felix* sp. nov. proves that this species is not an alga.

## Discussion

The presence of a stolon system (Fig. 2A) indicates that *W. felix* sp. nov. is not a hydroid, because hydroids do not possess stolons (Muscente et al. 2016). A stolon system is also present in *W. rokycanensis*, the type species (Kraft et al. 2001). A stolon system is strongly indicative of a graptolite affinity, prompting comparisons with acanthograptids and dendroids such as *Ptilograptus*; however, *W. felix* sp. nov. does not possess the diagnostic dendroid character of bithecae (Maletz 2020), thus cannot be assigned to the Dendroidea. As indicated by Kraft et al. (2001), the close thecal spacing of *Webbyites* is otherwise unknown in graptolites. We conclude that *Webbyites* is a benthic graptolite of uncertain affinity.

This occurrence of *Webbyites* is from Lower Ordovician strata of Morocco. Previous records of *Webbyites* are from Lower and Middle Ordovician rocks of the Czech Republic (Kraft et al. 2001) and Upper Ordovician strata of Morocco (Gutiérrez-Marco et al. 2022). The distribution of the genus

is consistent with the well-known pattern of faunal similarity between Bohemia and North Africa during the Ordovician (e.g. Gutiérrez-Marco et al. 2022).

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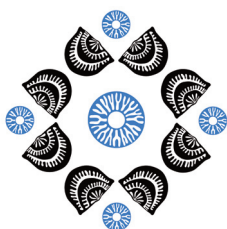
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# Nitrogen and organic carbon isotope record in Tremadocian highly metalliferous black shales from Baltica

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#### ABSTRACT

Tremadocian highly metalliferous black shales and associated grey shales from the Aseri PH012B drill core (NE Estonia) in the innermost part of the Baltic Palaeobasin were targeted to record their nitrogen and organic carbon isotope variance combined with the total organic carbon and total nitrogen record. The obtained molar C/N ratios of black shales from 26 to 52 indicate a considerable loss of N compared to primary biomass. The recorded  $\delta^{15}\text{N}$  values from  $-2.5$  to  $0.2\%$  likely evolved due to isotopic fractionation related to  $\text{N}_2$  fixation by primary producers, superimposed by later anoxic ammonium oxidation processes within the uppermost sediments. The high net primary productivity, which controlled the accumulation of organic-rich shallow-water complexes, was fuelled by the internal cycling of P in the sea basin and combined with intensive N exchange between marine and atmospheric pools.

#### Introduction

An interval from the middle Cambrian to the Early Ordovician, represented by vast black shale complexes in the Baltic Palaeobasin, is recognized as a period of major environmental and biodiversity changes. The accumulation of organic-rich sediment throughout the outer and inner shelf of the palaeobasin has been attributed to elevated nutrient input, enhanced bioproduction, and prevailing anoxia in the lower water column, the latter likely disrupted by short-lived oxygenation events (Dahl et al. 2019). However, many fundamental questions remain regarding their genesis. Herein, we present coupled nitrogen ( $\delta^{15}\text{N}_{\text{tot}}$ ) and carbon ( $\delta^{13}\text{C}_{\text{org}}$ ) isotope records from the highly V-, U-, and Mo-enriched Tremadocian black shales and related metal-poor black and grey shales (*Cordylodus angulatus*–*Paltodus deltifer pristinus* biozones) from the inner shelf of the palaeobasin to decipher possible interrelated changes in the nutrient cycle, primary productivity, and redox conditions during their accumulation.

The dynamics of the deep-time biogeochemical cycle of N can be derived from the isotopic composition of the deposits. The cycle is closely tied to the redox state of the ocean and the atmosphere, and the N isotope values that are preserved in organic matter (OM) can reflect the redox state of the water column, as well as metabolic processes and pathways (Algeo et al. 2014). Nitrogen plays a crucial role in the biogeochemical cycling of C and other nutrients in the oceans (Stüeken et al. 2016). It can exist in different forms, including the diatomic molecule ( $\text{N}_2$ ), nitrate ( $\text{NO}_3^-$ ), nitrite ( $\text{NO}_2^-$ ), ammonium ( $\text{NH}_4^+$ ), and dissolved organic nitrogen (DON). Autotrophs in the marine system can fix atmospheric  $\text{N}_2$  ( $\delta^{15}\text{N} = 0\%$ ) into OM with minimal isotopic fractionation ( $\epsilon_{\text{org-N}_2}$  is  $\sim -3$  to  $+1\%$ ) (Zerkle et al. 2008; Valley and Cole 2001). The decomposing OM first undergoes ammonification, which also involves little isotopic alteration. Further, under oxic conditions, nitrification converts  $\text{NH}_4^+$  to dissolved  $\text{NO}_3^-$ . The process potentially has a large net isotope fraction effect in settings where incomplete nitrification is favoured (Deutsch et al. 2007). However, it has minor importance in well-oxygenated seawater, where all generated  $\text{NH}_4^+$  is effectively oxidized to  $\text{NO}_3^-$ . Under suboxic conditions, part of the N can escape from the nitrate pool through denitrification, with a potentially large isotopic effect (Valley and Cole 2019). Such an effect is, however, suppressed if quantitative denitrification takes place (Sigman and Fripiat 2001). In the anoxic seawater and sediment column,



N-loss could be further promoted by mineralization of OM through processes such as anoxic ammonium oxidation (anammox) with nitrates or alternative electron acceptors. The N mineralization pathways in anoxic sediments are still poorly understood. Importantly, depletion of bioavailable N-compounds in the water column supports the growth of diazotrophs if other nutrients are available. Interpretations of ancient sedimentary records exhibiting near-zero  $\delta^{15}\text{N}_{\text{tot}}$  values, untypical of modern settings, have conventionally assumed that  $\text{N}_2$ -fixation should have dominated as the main source of N, thus pointing to the nitrate-poor oxygen-depleted photic zone. For the Tremadocian black shales from the inner part of Baltica a single previously reported  $\delta^{15}\text{N}$  value of  $\sim -2\text{‰}$  is in the aforementioned range (Kiipli and Kiipli 2013).

Our research aimed at better understanding the distribution of  $\delta^{15}\text{N}_{\text{tot}}$ ,  $\delta^{13}\text{C}_{\text{org}}$ , total organic carbon (TOC) and total nitrogen (TN) in those palaeoenvironments. We hypothesized that significant changes in the local nitrogen cycle would coincide with changes in the preservation of OM and the enrichment of redox-sensitive elements (RSE) in the black shales.

### Geological setting

The analysed samples come from the Aseri PH012B (59.426053, 26.755267) drill core. During the Tremadocian period, the study area was the innermost shallowest part of the Baltic Palaeobasin. The thin complex of black shales of the Türisalu Formation ( $\sim 1.1$  m) deposited during the transgressive phase above the coastal and shallow-marine bio- and siliciclastic complexes of the Kallavere Formation. The latter is rich in phosphatic brachiopod detritus, but also shows cyclic alteration of black shale interbeds and siltstones in its uppermost part. The Türisalu Formation is overlain by grey shales of the Varangu Formation. The mineral matrix of the organic-rich black shales consists of K-feldspars, quartz, illite/mica, and illite/smectite, while pyrite content varies from 4 to 6%. Also, the presence of thin cyclic biosilica and sulphidic silty interlayers as well as glendonite-like carbonate concretions is characteristic of the study area. The OM of the Türisalu Formation is thermally immature (Schovsbo et al. 2012), purely marine in origin, largely amorphous, and compliant with Type-II kerogen with an average atomic H/C ratio of 1.24 and O/C ratio of 0.16 (Veski and Palu 2003). Lille (2003) suggested that its primary biomass could have been produced by cyanobacteria and possibly by green sulphur bacteria. Very high enrichment of RSE, with maximum content of V  $\sim 2300$  ppm, U  $\sim 500$  ppm, and Mo  $\sim 2700$  ppm, has been documented in the basal and middle part of the Türisalu Formation in the Aseri PH012B section using the same sample set (Ndiaye et al. in press).

### Materials and methods

To determine TOC and TN content, 186 samples of the Türisalu Formation and adjacent strata were analysed using combustion in a FLASH 2000 organic elemental analyser.

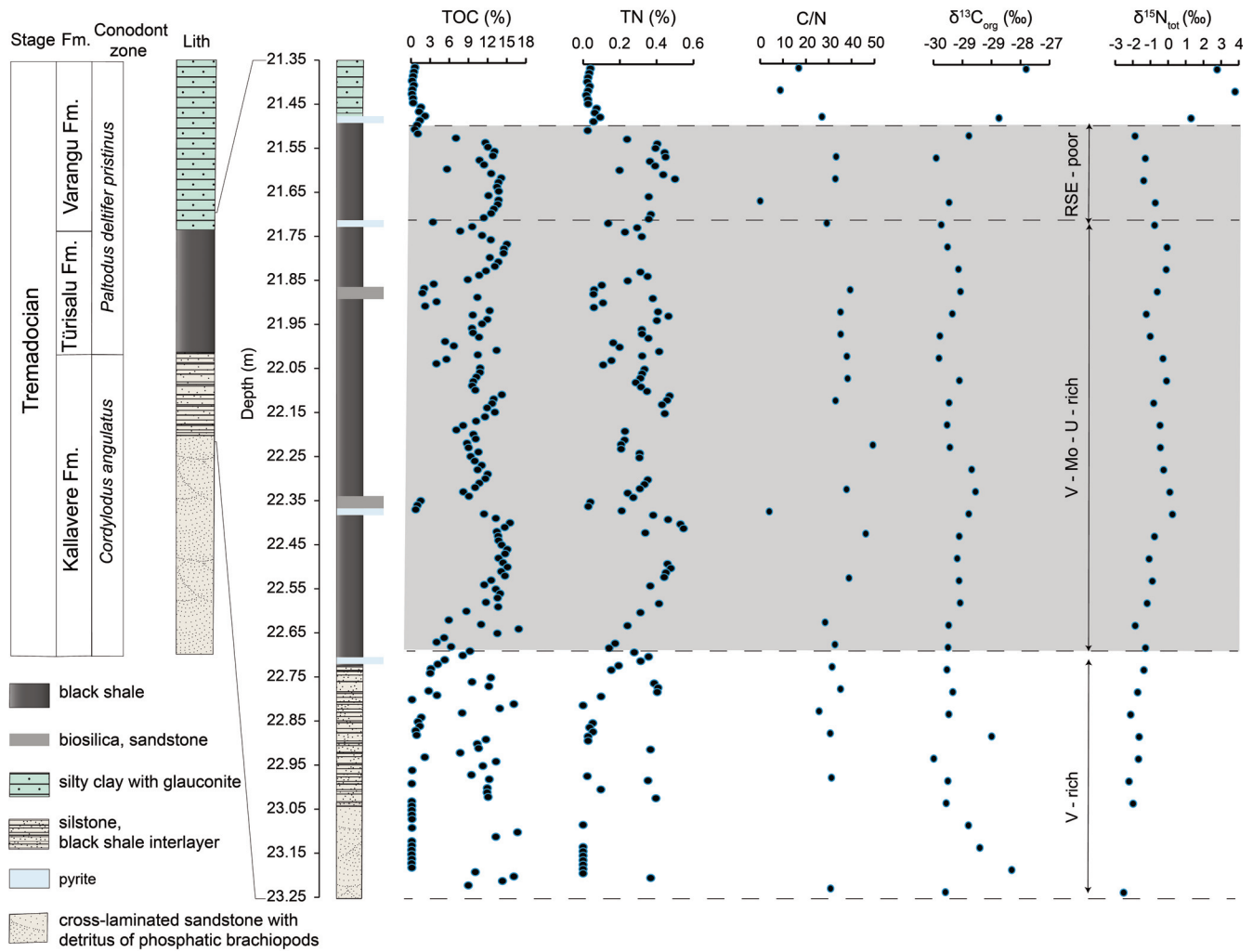
Each sample was approximately 1 cm thick, and 4–15 mg of powdered sediment was used depending on loss-on-ignition values. The samples were pretreated with 10% HCl, dried, and then wrapped into granules before being packed into Sn containers for combustion. Cystine was used as the standard, and organic carbon-rich sediment was used as the reference material.

Selected samples ( $n = 26$ ) were analysed for  $\delta^{13}\text{C}_{\text{org}}$  and  $\delta^{15}\text{N}_{\text{tot}}$ . Approximately 1 g of sample powder was treated with 10% HCl, rinsed, and dried. The C isotopic ratios were measured using a FlashEA 1112 and a Delta V Advantage isotope ratio mass spectrometer. The results were expressed as relative deviations from V-PDB. Standards from the IAEA and IVA Analysentechnik were used for precision and calibration.

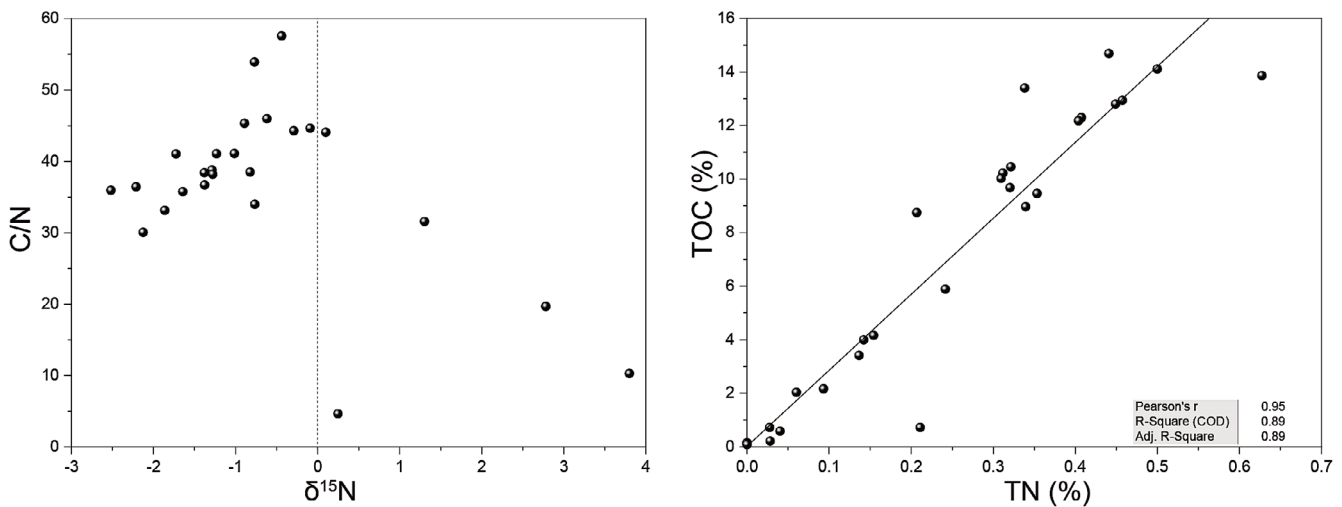
For  $\delta^{15}\text{N}_{\text{tot}}$  analysis, 7 to 20 mg of sample powder was weighed into Sn capsules. The N isotopic ratios of the samples were measured using a FlashEA 1112, coupled via a ConFlo IV to a Delta V Advantage isotope ratio mass spectrometer. The  $\delta^{15}\text{N}_{\text{tot}}$  values are expressed as the relative deviations from the measured  $^{15}\text{N}/^{14}\text{N}$  ratio and with respect to atmospheric  $\text{N}_2$ . Sample precision and data calibration were performed using IAEA standards IAEA-N-1 (+0.43‰) and IAEA-N-2 (+20.41‰) and IVA Analysentechnik Urea Isotopic Working Standard (−0.32‰).

### Results and discussion

The TOC content was consistently high in the black shale samples from Kallavere and Türisalu formations, ranging between 8 and 15% ( $n = 108$ ) and low  $<1\%$  ( $n = 16$ ) in the Varangu Formation (Fig. 1). TN values varied accordingly from 0 to 0.66% and  $<0.07\%$ , presenting strong positive covariance with TOC distribution ( $R^2 = 0.89$ ,  $n = 26$ ; Fig. 2). This suggests that most of the N resides in OM (note, however, that same samples also present consistent covariance between TOC, TN, and clay fraction indices). The average C/N atomic ratios from black shale of the Türisalu Formation, black shale interbeds from the Kallavere Formation, and grey shales from the Varangu Formation were  $\sim 37$  ( $n = 108$ ),  $\sim 29$  ( $n = 60$ ), and  $\sim 15$  ( $n = 16$ ), respectively. The  $\delta^{13}\text{C}_{\text{org}}$  values of the black shales generally showed low variability ranging between  $-29.8$  and  $-29.0\text{‰}$  ( $n = 35$ ), matching the values reported from Tremadocian complexes from the deeper part of the basin (Terfelt et al. 2014). Heavier  $\delta^{13}\text{C}_{\text{org}}$  values (as high as  $-27.3\text{‰}$ ) were detected in the organic-poor samples of the Varangu Formation and in a few intervals of coarse-grained black shales, with  $\delta^{13}\text{C}_{\text{org}}$  increasing in phase with TOC, TN, and decreasing in C/N. The black shale samples characteristically showed  $\delta^{15}\text{N}_{\text{tot}} \sim 0\text{‰}$ , with an average value for the Türisalu Formation  $-0.7\text{‰}$  ( $n = 24$ ) and for the Kallavere Formation  $-1.8\text{‰}$  ( $n = 8$ ). The  $\delta^{15}\text{N}_{\text{tot}}$  signal range from the uppermost metal-poor part of the Türisalu Formation was similar to that observed for the Kallavere Formation. The total  $\delta^{15}\text{N}_{\text{tot}}$  variance from  $-2.5$  to  $0.2\text{‰}$  is in the same range with typical organic-rich black shales, including those from the Baltic Palaeobasin (Kiipli and Kiipli 2013; Hammer and Svensen 2017). A distinctly different



**Fig. 1.** Distribution of TOC, TN, molar C/N ratios,  $\delta^{13}C_{org}$  and  $\delta^{15}N_{tot}$  in the Aseri PH012B drill core. Abbreviations: Fm. – Formation, Lith – Lithology. Biozone boundaries after Heinsalu et al. (2003).



**Fig. 2.** Scatterplots of C/N ratios versus  $\delta^{15}N$  and TOC versus TN for samples from the Aseri PH012B drill core. Abbreviation: Adj. – Adjusted.

$\delta^{15}N_{tot}$  range, between 1 and 4‰, was found in three samples from the Varangu Formation. No clear covariance was detected between TOC and  $\delta^{13}C_{org}$  and between TOC and  $\delta^{15}N_{tot}$ . The distribution of  $\delta^{15}N_{tot}$  versus C/N demonstrates that the loss of N from the black shale organic matter (assuming that primary biomass had a Redfield-like stoichiometry C:N  $\approx$  16:106) is accompanied by a shift of

$\delta^{15}N_{tot}$  signal towards atmosphere-like unfractionated values.

We suggest, based on the observed variance, that  $N_2$  fixation functioned as the dominant source of N for phytoplankton, helping to maintain a very high net primary production. The low negative  $\delta^{15}N_{tot}$  values of the primary biomass (ranging from  $\sim$ -2.5 to -1‰) can be explained by

efficient biomass transfer to the sea bottom due to a shallow oxygen-depleted water column in which quantitative denitrification processes dominated. The following release of N near the sediment-water interface via OM mineralization by conventional or sulphate-reducing anammox, combined with decreased net sediment rates, controlled the modification of the sediment N isotope composition and led to a small positive shift ( $\sim 1\%$ ) in  $\delta^{15}\text{N}_{\text{tot}}$  (Hammer and Svensen 2017). Alternatively, the lower  $\delta^{15}\text{N}_{\text{tot}}$  values in the Kallavere Formation and the RSE-poor part of the Türisalu Formation could be explained simply by a switch to alternative nitrogenase-using species due to Mo-limitation (Zhang et al. 2014) or a switch to another  $^{15}\text{N}$ -depleted source of N. Nevertheless, the co-occurring decrease in the C/N ratios and  $\delta^{15}\text{N}_{\text{tot}}$  suggests that the loss of N was most likely the reason behind the observed isotopic variance. The beginning of the accumulation of grey mud in the Varangu Formation marked the principal rearrangement in the nutrient cycle and redox architecture in the considered shallow shelf areas, establishing new equilibria in which  $\text{NO}_3^-$  assimilation became the major source of N for primary producers in a better oxygenated water column.

## Conclusions

The relatively low  $\delta^{15}\text{N}$  values of  $-2.5$  to  $0.2\%$ , combined with high C/N, suggest that bioproduction during the deposition of organic-rich muds was likely nitrogen-limited.  $\text{N}_2$ -fixation, as well as  $\text{N}_2$ -outgassing through denitrification and anoxic mineralization of OM in sediments, played a significant role in the biochemical cycling of nitrogen. The mineralization of OM in anoxic sediments slightly shifted the  $\delta^{15}\text{N}_{\text{tot}}$  of the remaining OM towards heavier isotopic compositions. The principal transition in the local cycle of N in the considered inner shelf settings of Baltica occurred with the start of sediment accumulation in the Varangu Formation with a likely switch from diazotrophic-dependent to nitrate-based primary production, as evidenced by a shift towards positive  $\delta^{15}\text{N}_{\text{tot}}$  values.

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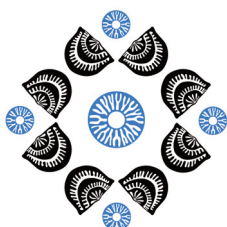
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# Latest Ordovician age of the *Spinachitina fragilis* Chitinozoan Biozone in Baltoscandia

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## ABSTRACT

The global *Spinachitina fragilis* Chitinozoan Biozone has been considered the lowermost Silurian zone in most publications. *S. fragilis* was first described from the Ohesaare drill core, Estonia, and utilised as a Baltic regional zonal taxon together with *Ancyrochitina laevaensis*. Despite its wide geographical occurrence, *S. fragilis* has remained poorly documented in its type region. This has created confusion in taxonomy and distribution of the species. Herein, we have restudied material from the type locality and supplementary sections in the East Baltic region. *S. fragilis* generally has a very short stratigraphic range, which, according to new data on carbon isotope chemostratigraphy, coincides with the falling limb of the Hirnantian carbon isotope excursion. This suggests the latest Hirnantian rather than the early Rhuddanian age of the *Spinachitina fragilis* Chitinozoan Biozone in Baltoscandia. Based on this view, we revise the latest Ordovician chitinozoan biozonal scheme for the region. Globally, the *S. fragilis* Biozone may span across the Ordovician–Silurian boundary.

## Introduction

The identification of the base of the Silurian System is challenging in sections lacking graptolites, such as those in carbonate-dominated settings of the Baltic Palaeobasin. This is because of stratigraphic gaps and the scarcity of reliable index fossils among conodonts, ostracods, and other organisms, which were severely affected by the end-Ordovician extinction. Although chitinozoans also exhibit significantly reduced diversity in the Ordovician–Silurian boundary interval (Hints et al. 2018), they have traditionally provided some valuable reference levels. Verniers et al. (1995) established the global *Spinachitina fragilis* Chitinozoan Biozone, which has been considered the lowermost chitinozoan biozone in the Silurian, coeval with the *A. ascensus* Graptolite Biozone (Melchin et al. 2020). Many studies in previous decades have utilised this zone to identify the basal part of the Silurian in different regions (e.g., Dufka et al. 1995; Paris et al. 1995; Butcher 2009; Vandenbroucke et al. 2009; Le Hérisse et al. 2013; Ghavidel-Syooki 2022). In Baltoscandia, where *S. fragilis* was first described by Nestor (1980), the lowermost regional chitinozoan biozone in the Silurian has been the *S. fragilis*–*A. laevaensis* Biozone in recent compilations (Nestor 2012). However, *S. fragilis* has remained poorly illustrated and understood in the type region and elsewhere. This has created confusion and contrasting ideas regarding the taxonomy as well as the age of the *S. fragilis* Biozone and its potential to efficiently identify the base of Silurian.

The aim of this report is to review the distribution of chitinozoans in the Ohesaare drill core from western Estonia, which serves as the type section for the global *S. fragilis* Chitinozoan Biozone. We examine the topotypic specimens of *S. fragilis* and analyse the distribution of coeval chitinozoans in other East Baltic sections in order to provide insights into the taxonomic puzzle and the latest Ordovician chitinozoan biostratigraphy. The studied collection has been obtained using conventional microfossil extraction techniques (Nõlvak et al. 2022) and is deposited at the Department of Geology, Tallinn University of Technology (institutional abbreviation GIT).

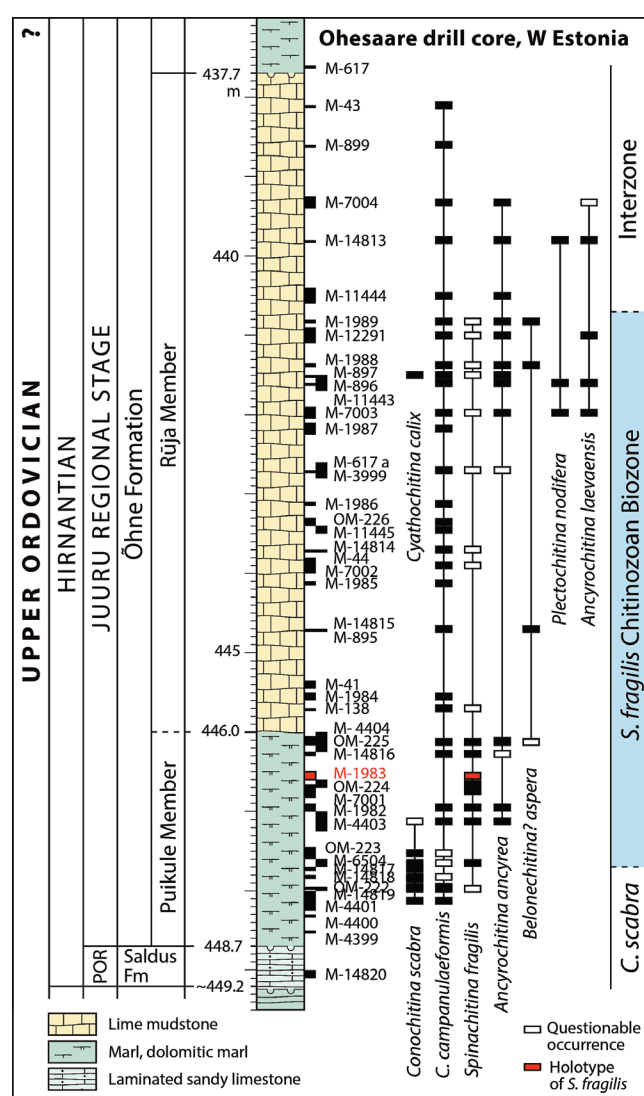
## Results

The Ordovician–Silurian boundary interval in the Ohesaare drill core is represented by the Saldus Formation (Fm), Porkuni Regional Stage, and the overlying Öhne Fm,

Juuru Regional Stage. Conventionally, the Ordovician–Silurian boundary has been correlated with the base of the Õhne Fm and the Juuru Stage (e.g., Nestor 1994). In the lower part of the Õhne Fm, two distinct members are distinguished: the Puikule Member (Mb) of dolomitic marls and the Rūja Mb of lime mudstones, overlain by marls and marly limestones of the Rozeni Mb (Fig. 1).

The chitinozoan assemblage was studied in 47 samples from core depths of ca 437.6–449.0 m. The Saldus Fm proved to be barren of chitinozoans, but the lower Õhne Fm contained eight species, including zonal indices. The lowermost part of the Puikule Mb is characterised by the abundant occurrence of *Conochitina scabra*, marking the respective biozone. In total, more than a thousand specimens were recovered.

The first specimens of *S. fragilis* are found at a depth of 447.7 m, but the typical forms and an almost continuous



**Fig. 1.** Distribution of the latest Ordovician chitinozoans in the Ohesaare drill core, western Estonia. The exact position of the Ordovician–Silurian boundary remains unclear; in earlier publications, it has been drawn at the discontinuity surface at a core depth of 448.7 m, coinciding with the base of the Õhne Formation. The base of the *Spinachitina fragilis* Biozone is drawn here at a depth of 447.7 m (sample M-6504), but its top is taken at the last occurrence of *S. fragilis* in sample M-1989, following Nestor (1994, fig. 20:1). Abbreviations: POR – Porkuni Regional Stage, Roz – Rozeni Member.

range start ca 0.3 m higher and extend up to the top of the Puikule Mb at ca 446 m. That interval includes sample M-1983, from which the holotype of *S. fragilis* was derived (Fig. 1; Nestor 1980). Within the overlying Rūja Mb, the specimens of *S. fragilis* have a slightly different look, being somewhat translucent due to the thin vesicle wall. Closely similar specimens have also been observed in other Baltic sections; however, they are usually very rare. Nestor (2012, fig. 4B) has identified all these specimens as *S. fragilis*, and the name of the species also denotes ‘fragile nature’, referring to the thin wall and usually deformed shape. Altogether, the Ohesaare collection includes a few hundred specimens assigned to *S. fragilis*. Some examples from this collection are illustrated in Fig. 2.

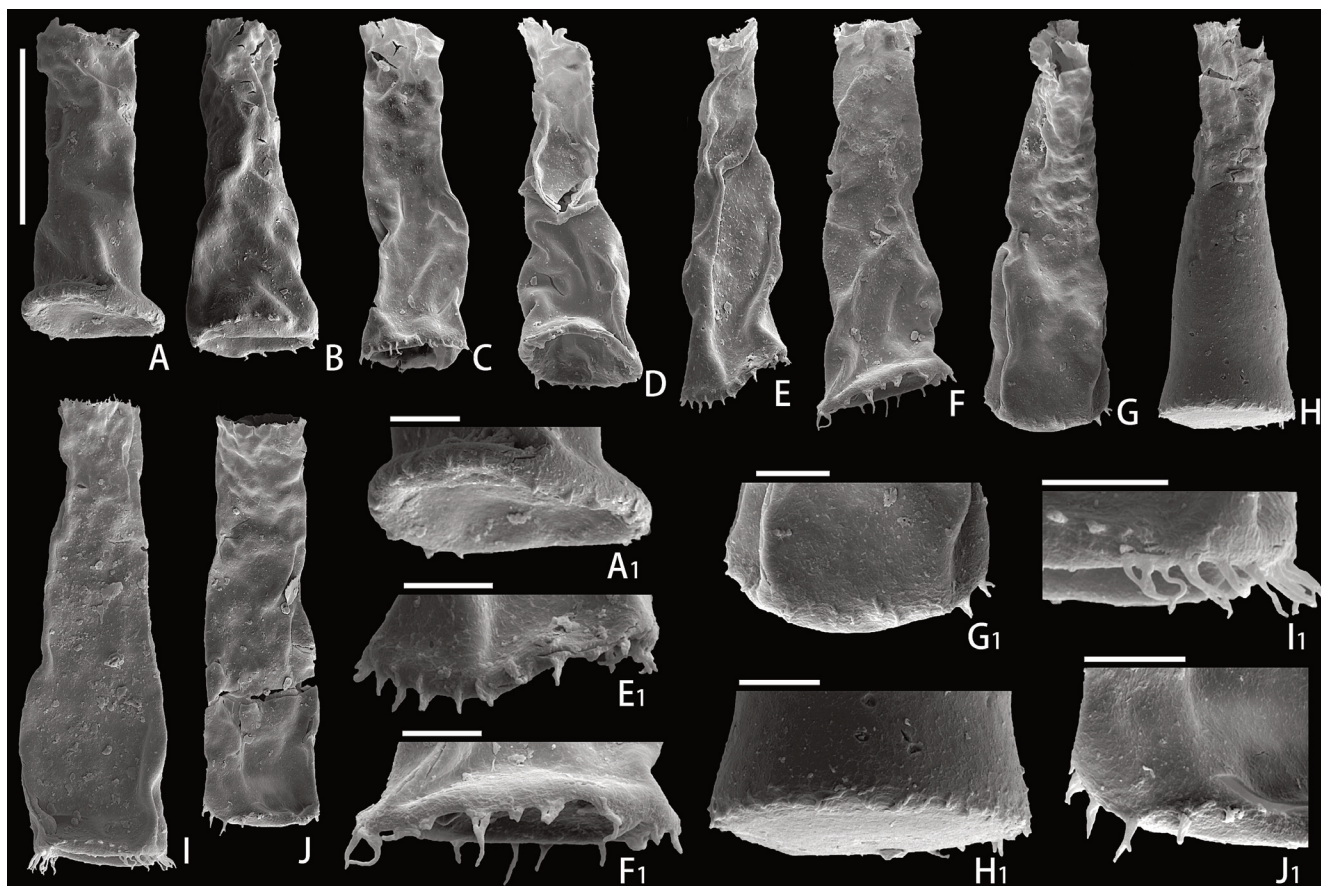
The third biostratigraphically important species, *Ancyrochitina laevaensis*, was identified from the upper part of the Rūja Mb, at a depth of ca 439 to 442 m. However, it is very rare, with less than ten specimens recovered from the Ohesaare core. Additionally, *Cyathochitina campanulaeformis* and *Ancyrochitina ancyrea* are common through the Puikule and Rūja members in the Ohesaare core. In other sections, these taxa are known from older as well as younger strata and represent the survivors from the end-Ordovician extinction. Other species have been identified in a few samples only, and thus the overall diversity of the studied assemblage is low, with up to 5 species in a sample (Fig. 1).

Carbon stable isotope data from the Ohesaare drill core are currently limited, but the few bulk samples analysed from the Puikule and Rūja members show  $\delta^{13}\text{C}_{\text{carb}}$  values between 2.3 and 3.5‰ below the depth of 440 m. This is on par with the falling limb of the Hirnantian carbon isotope curve (HICE) in other sections (cf. Meidla et al. 2023b).

## Discussion

The distribution of *S. fragilis* in the East Baltic region is stratigraphically consistent. It occurs above or sometimes together with *C. scabra* and has a very short stratigraphic range. Usually it is found in one or a few samples closely above the base of the Õhne or Stačiūnai formations. Examples come from the Seliste, Ristikūla, Laeva-13, Taagepera, Tartu-554, Likenai and Ketrzyn IG-1 drill cores in Estonia, Lithuania and Poland. In the proximal part of the Baltic basin, for instance, in the Viki reference core, *S. fragilis* has not been recovered, probably due to a more extended stratigraphic gap. The unusually long stratigraphic range of *S. cf. fragilis* in the Heimtali core reported by Nestor et al. (2003) requires further analysis. *S. fragilis* and the corresponding biozone have been identified by several authors around the world; for review, see Butcher (2009), Thusu et al. (2013) and Ghavidel-Syooki (2022).

Paris et al. (2000) erected a closely similar species, *Spinachitina oulebsiri*, from the latest Ordovician of Algeria. That species was later discussed and considered synonymous with *S. fragilis* by Butcher (2009). Vandenbroucke et al. (2009), however, applied the name *S. oulebsiri* and erected another similar form – *S. verniersi* – from the Soom Shale of South Africa. The latter species is characterised by less



**Fig. 2.** SEM images of *Spinachitina fragilis*. All specimens are from the Ohesaare drill core, sample M-4403 from a core depth of 447.0–447.25 m, Õhne Formation, Puikule Member. The scale bar corresponds to 100 µm, except in detail photos where it corresponds to 20 µm. The specimens have been assigned consecutive collection numbers from GIT 891-1 to 891-10.

prominent spines, and it co-occurs with *S. oulebsiri* in several sections. Considering the range of variability of the re-examined Baltic material (Fig. 2) and the occurrence of various transitional forms, it is possible that both *S. oulebsiri* and *S. verniersi* are junior synonyms of *S. fragilis*. This would indirectly support the late Hirnantian age of the *S. fragilis* Biozone in the East Baltic region, which is otherwise indicated by carbon isotope stratigraphy (Meidla et al. 2020, 2023a, 2023b). The possibility of the Hirnantian age of the *S. fragilis* Biozone was argued by Melchin and Holmden (2006), also based on the chemostratigraphic evidence.

Additionally, Vandenbroucke et al. (2008, 408, fig. 5) reported a single specimen designated as *S. ?fragilis* near the top of the *M. persculptus* Biozone, from the historical type area of the Hirnantian in Wales. However, in the subsurface of Jordan, *S. fragilis* is dated by graptolites and appears to belong to the *ascensus/acuminatus* Graptolite Biozone (Butcher 2009). Thus, it seems that globally the *S. fragilis* Biozone spans the Ordovician–Silurian boundary.

In Estonia, the lowermost Silurian chitinozoan zone was the *A. laevaensis* Zone (Nestor 1994), later upgraded to the *S. fragilis*–*A. laevaensis* regional concurrent range biozone. A thorough discussion on *A. laevaensis* is beyond the scope of this report, but it is necessary to stress that the definition of the species is based on very limited material (Nestor 1980). It is scarce in the type locality and type region, and in case of poorly preserved material, it is difficult to distinguish it from some other taxa, including the co-occurring *A. ancyrea s.l.*

These issues have been discussed, e.g., by Ghavidel-Syooki and Vecoli (2007) and Butcher (2009). Moreover, *A. laevaensis* is also closely similar to *A. ellisbayensis* (cf. Verniers and Vandenbroucke 2006, figs 4A, C), which makes its usage in high-resolution biostratigraphy further problematic.

Based on the restudied material, we propose the following revision of the Baltic regional biostratigraphic scheme:

***Conochitina scabra* Biozone** is defined as a partial range zone from the first appearance (FAD) of the nominal species to the FAD of *S. fragilis*. When the latter species is not present, the top of the zone can be approximated with the last appearance (LAD) of *C. scabra*.

***Spinachitina fragilis* Biozone** is defined as a range zone based on the nominal species. We suggest abandoning the usage of *A. laevaensis* as a nominal index species due to its scarcity and taxonomically problematic nature; however, if present, it may be used as an additional criterion for distinguishing the regional *S. fragilis* Biozone.

The interval above the *S. fragilis* Biozone was designated as an interzone by Nestor (2012) to represent the strata between the LAD of *S. fragilis* and the FAD of *Belonechitina postrobusta*. This interval is not entirely barren of chitinozoans, but is characterised by low abundance and the lack of suitable index taxa. In the global biozonal scheme (Verniers et al. 1995), the top of the *S. fragilis* Biozone is defined by the FAD of *B. postrobusta*, the nominal taxon of the overlying biozone. However, here we prefer to retain the ‘interzone’ in the regional scheme in order to keep the LAD of

*S. fragilis* as a formal marker horizon. The Ordovician–Silurian boundary most likely falls into this interval in the East Baltic region. The innovations among most groups of acid-resistant microfauna, including the first chitinozoans with Silurian affinity, appear in this area in Rhuddanian–Aeronian boundary beds near the base of the *Spinachitina maennili* Biozone (Männik et al. 2015).

## Conclusions

The restudy of chitinozoans from the Ohesaare drill core and complementary sections from southern Estonia showed that *Spinachitina fragilis* is most likely of late Hirnantian age, corresponding at least partly to the *M. persculptus* Graptolite Biozone. This allowed revision of the chitinozoan biozonation in the Ordovician–Silurian boundary interval and has implications for global correlations. The *S. fragilis* Biozone appears to be a valuable correlation tool for the latest Ordovician strata in Baltoscandia. Further studies are necessary to identify the *B. postrobusta* Biozone and apply a high-resolution carbon isotope chemostratigraphy in the Ohesaare reference drill core to find criteria for delineating the base of the Silurian System in the East Baltic region.

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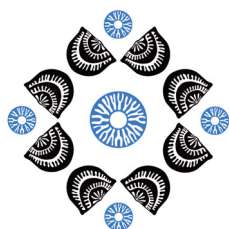
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# First report of the mitrate *Mitrocystella* (Echinodermata, Stylophora) in the Middle Ordovician of the Crozon Peninsula, Brittany (France)

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#### ABSTRACT

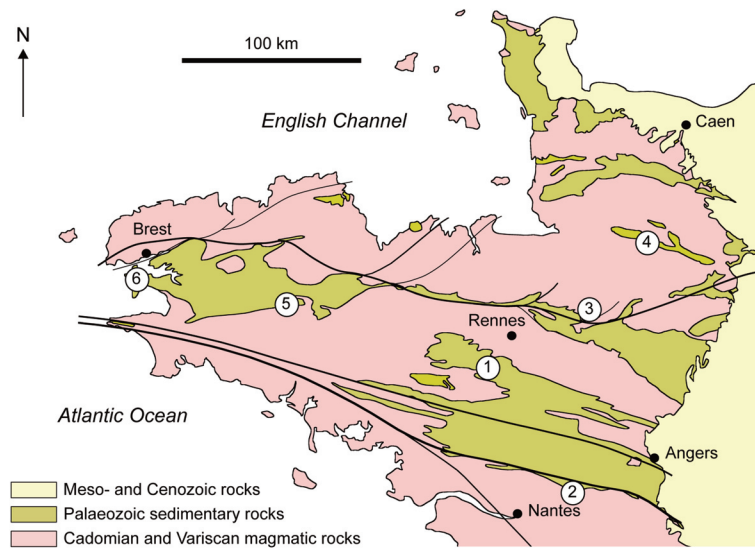
The mid-Ordovician mitrocystitid mitrate *Mitrocystella incipiens* was one of the most widespread stylophorans in the high latitude Mediterranean Province, with occurrences in the Armorican Massif (France), the Iberian Peninsula (Portugal and Spain) and the Prague Basin (Czech Republic), all restricted so far to the late Darriwilian (*Hustedograptus teretiusculus* Zone). The description of this taxon in the Corrèjou Member (Postolonnec Formation) of the Crozon Peninsula (western Brittany, France) not only extends its spatial distribution within the Armorican Massif, but also its stratigraphic range into the mid-Darriwilian (*Didymograptus artus* Zone). The remarkable preservation of the new material and associated sedimentological evidence both suggest rapid burial by storm deposits.

#### Introduction

Stylophorans (cornutes, mitrates) are a clade of extinct, vagile echinoderms, which initially diversified on soft substrates during the Miaolingian (Zamora et al. 2013). In the Furongian–Floian interval, they were, along with eocrinoids and glyptocystitid rhombiferans, one of the dominant members of the low-diversity echinoderm faunas occurring worldwide before the major diversification of crinoids on hard substrates (Lefebvre and Fatka 2003). After this late Cambrian–Early Ordovician peak in both diversity and palaeobiogeographic distribution, stylophorans remained minor elements of benthic communities until their last appearance in the fossil record, in the Pennsylvanian of Oklahoma (Kolata et al. 1991). During the Darriwilian, the Armorican Massif (western France; Fig. 1) represents, along with the Prague Basin (Czech Republic), one of the two major diversity hotspots for stylophorans (Lefebvre and Fatka 2003; Lefebvre et al. 2022). This situation possibly results from the combination of originally favourable environmental conditions (widespread siliciclastic soft substrates) and over 150 years of regional sampling and scientific descriptions. Specimen labels in the collections of Rennes University indicate that in April 1850 several individuals of the mitrate *Mitrocystella incipiens* were collected at Guichen (Ille-et-Vilaine; Fig. 1.1) by Marie Rouault in concretions of the Traveusot Formation (Darriwilian). Although possible occurrences of *Anatifopsis* sp. were mentioned by Tromelin and Lebesconte (1876) and Kerforne (1901) in regional faunal lists of Ordovician taxa, the first descriptions of Darriwilian stylophorans from the Armorican Massif were made by Chauvel (1937, 1941).

In the last decades, ten stylophoran taxa were described in the Middle Ordovician of six distinct areas of the Armorican Massif (see Lefebvre 2000; Lefebvre et al. 2022





**Fig. 1.** Simplified geological map of the Armorican Massif (western France) showing the six main areas yielding Darriwilian stylophorans: 1 – Martigné-Ferchaud Syncline (Traveusot Formation); 2 – Ancenis Syncline (Pierre Meslière Formation); 3 – Menez-Belair Syncline (Andouillé Formation); 4 – Mortain-Domfront Syncline (Le Pissot Formation); 5 – eastern part of the Châteaulin Basin (Postolonnec Formation); 6 – Crozon Peninsula (Postolonnec Formation).

and references therein). In the Martigné-Ferchaud Syncline (Fig. 1.1), fine siltstones of the lower part of the Traveusot Formation (*Didymograptus artus* Zone) provided rare specimens of poorly preserved cornutes (*Domfrontia?* sp.) and mitrocystitid mitrates (*Aspidocarpus* sp.). In the same area, silico-aluminous concretions and shales of the upper part of the Traveusot Formation (*Hustedograptus teretiusculus* Zone) yielded the most diverse stylophoran assemblage of the Armorican Massif. This assemblage is dominated by extremely abundant remains of *M. incipiens*, associated with relatively common kirkocystid mitrates (*Anatifopsis minuta* and *Balanocystites primus*), and rare representatives of anomalcystitids (*Diamphidiocystis regnaulti*), cornutes (*Domfrontia pissotensis*, *Milonicystis kerfornei* and *Thoralicarpus guillouii*), and lagynocystids (*Lagynocystis pyramidalis*). In the Ancenis Syncline (Fig. 1.2), the concretions of the Pierre Meslière Formation (*D. artus*–*Didymograptus murchisoni* zones) yielded rare individuals of the two mitrates *Lagynocystis pyramidalis* and *Mitrocystites mitra*. In the Menez-Belair Syncline (Fig. 1.3), several specimens of *M. incipiens* were found at La Croixille, in upper Darriwilian shales (*H. teretiusculus* Zone) of the Andouillé Formation. In the Mortain-Domfront Syncline (Fig. 1.4), abundant remains of the cornute *Domfrontia pissotensis* were described in the fine siltstones of the Le Pissot Formation (*H. teretiusculus* Zone). In the eastern part of the Châteaulin Syncline (Fig. 1.5), a single echinoderm-rich bed in shales of the upper part of the Postolonnec Formation (*H. teretiusculus* Zone) provided several flattened specimens of the mitrates *M. incipiens* and *D. regnaulti*. Finally, in the Crozon Peninsula (Fig. 1.6), the same levels yielded three specimens of *Aspidocarpus* sp.

The aims of this paper are to report the first occurrence of the mitrate *Mitrocystella* in the Crozon Peninsula and to discuss its preservation and palaeobiogeographic implications.

## Materials and methods

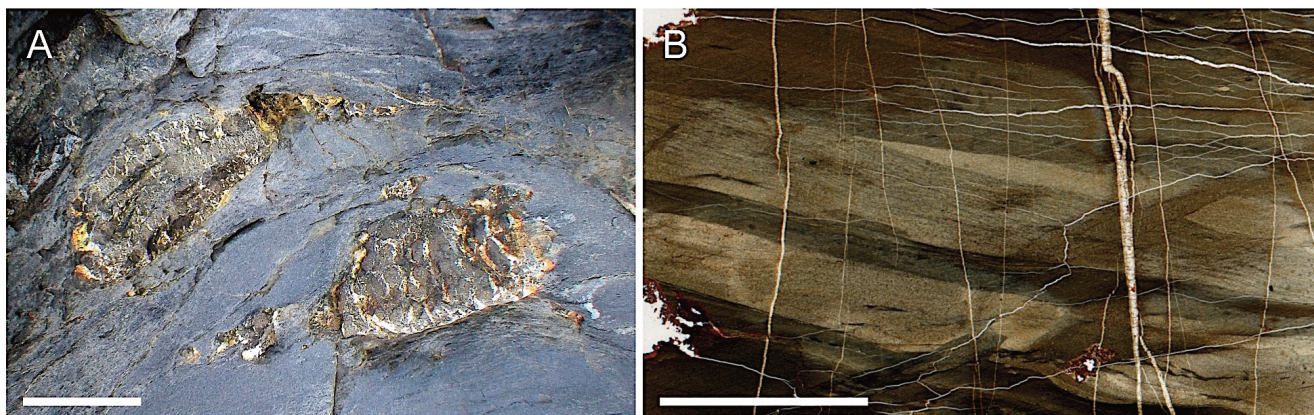
In March 2021, several mitrate-like pyritized fossils were identified in the lowermost part of the Corrèjou Member of the Postolonnec Formation (*D. artus* Zone, mid Darriwilian; Dabard et al. 2015) exposed on the Notinau beach in Camaret

(Crozon Peninsula, Finistère; Fig. 1.6), on the territory of the regional natural reserve of Crozon Peninsula (for a detailed description of local stratigraphy and palaeontology, please see e.g. Henry 1980; Guillocheau 1983; Loi and Dabard 2002; Dabard et al. 2007, 2015; Vidal et al. 2011). Once all official authorizations were obtained, a large rock sample containing the two side-by-side, best preserved specimens (Fig. 2A) was extracted from the cliff and registered in the palaeontological collections of the University of Western Brittany in Brest. Two thin sections (also registered at the Brest University) were made perpendicular to the bedding plane (Fig. 2B), so as to describe the associated lithology. As the two mitrates are preserved as ‘negative’ empty moulds in the rock, they were cast with latex to better visualize their original ‘positive’ morphology. The two individuals were drawn with a camera lucida apparatus mounted on a Zeiss SteREO Discovery.V8 stereomicroscope binocular. Photographs were taken with a Canon 5DSR camera equipped with a MP-E 65 mm macro lens.

## Results and discussion

Although they are strongly flattened, the two individuals can be unambiguously identified as stylophorans, based on the presence of two distinct parts: a relatively massive, polyplated theca and, articulated to it, a single feeding appendage (aulacophore) comprising a wide proximal region made of several telescopic rings, and a narrower distal part (Fig. 2A). Moreover, the preservation of their aulacophore in a recurved position indicates that these two stylophorans correspond to mitrates (cornutes were unable to flex their distal appendage; Lefebvre 2003). The absence of posterior spines (digital and/or glossal), along with the main features of their plate pattern on the two contrasted thecal sides, makes it possible to unambiguously assign these two mitrates to the mitrocystitid *M. incipiens* (see, e.g., Hunter et al. 2007 for similarly preserved specimens of *M. incipiens* in the shales of the same formation, in the eastern part of Châteaulin Basin; Fig. 1.5).

The material collected in Camaret (Notinau beach; Fig. 1.6) at the base of the Corrèjou Member thus represents the stratigraphically earliest occurrence of *M. incipiens* in the



**Fig. 2.** **A** – two original individuals of *Mitrocystella incipiens* in the lower (left specimen) and upper aspect (right specimen), LPB 10711, Corréjou Member, Postolonnec Formation (*Didymograptus artus* Zone, middle Darriwilian), Notinau beach (Camaret, Finistère); **B** – thin section (BR3184/Notinau1) cut perpendicular to the mitrate-bearing rock sample, with two distinct beds of very fine siltstones (distal tempestites) embedded within thinly laminated mudstones (background sedimentation). All scale bars: 10 mm.

Armorican Massif (*D. artus* Zone, middle Darriwilian). In all other localities (Martigné-Ferchaud and Menez-Belair synclines, eastern part of the Chateaulin Basin; Fig. 1.1,3,5), it was always found within the same, younger stratigraphic interval (*H. teretiusculus* Zone, upper Darriwilian). However, the palaeobiogeographic distribution of *M. incipiens* is not restricted to the Armorican Massif. During the Middle Ordovician, this mitrate was widely distributed in several other regions of the high-latitude Mediterranean Province. It was originally described in the Prague Basin, where it is relatively common in silico-aluminous concretions of the Dobrotivá Formation (*H. teretiusculus* Zone) (Barrande 1887; Chauvel 1941; Prokop and Petr 1999). Rare specimens of *M. incipiens* were also reported in the lower Guindo Shales (*H. teretiusculus* Zone) in the Hesperian Massif, Spain (Chauvel and Meléndez 1978; Gutiérrez-Marco and Meléndez 1987), and in the Valongo Formation (*H. teretiusculus* Zone) in northern Portugal (Gutiérrez-Marco and Meléndez 1987; Couto and Gutiérrez-Marco 2000). Finally, a single specimen of mitrocystitid from the Pontyfenni Formation (Dapingien) of Wales was tentatively described as *Mitrocystella?* sp. by Jefferies (1987). However, its incomplete preservation (posterior half of the theca is missing) precludes any firm taxonomic assignment. Consequently, this overview of all known occurrences of *M. incipiens* indicates that the specimens from the lowermost levels of the Corréjou Member in Camaret represent the earliest known record of this taxon. Everywhere else, its stratigraphic distribution is restricted to the late Darriwilian.

Thin sections (Fig. 2B) exhibit thinly laminated sediment, with mudstones interbedded with two distinct beds, each with a sharp base and consisting of siltstones to very fine sandstones with low-angle to planar, wavy laminations. These observations suggest the occurrence of two distinct ‘event beds’ (very fine sandstones), probably corresponding to relatively distal storm deposits, interbedded with thinly laminated mudstones suggesting relatively quiet environmental shelf conditions (background sedimentation). This interpretation is in good accordance with previous field observations and detailed sedimentological analyses of the lower part of the

Postolonnec Formation (base of the Corréjou Member) in Crozon Peninsula, all of which indicate environmental conditions corresponding to a storm-influenced shelf (Guillocheau 1983; Loi and Dabard 2002; Dabard et al. 2007, 2015).

Similarly to the situation regarding extant echinoderms (Brett et al. 1997), it is very likely that the stylophoran multi-plate endoskeleton disarticulated rapidly (i.e. within a few weeks) after the death of the organism (Lefebvre 2007). Consequently, the preservation of intact, fully articulated mitrates in Camaret (Fig. 2A) implies that they were buried either alive or shortly after death. This interpretation is further supported by the preservation of their aulacophores in a flexed position, which is generally interpreted as either a distressed posture and/or resulting from the post-mortem, ligament-induced contraction of the appendage (Lefebvre 2003). When they are preserved in life position, mitrates have their feeding appendage held almost straight over the sea floor (Parsley and Gutiérrez-Marco 2005; Lefebvre and Ausich 2021). Moreover, the opposite, upside-down orientations of the two side-by-side individuals (one is in the upper aspect and the other one in the lower aspect) clearly demonstrate that they are not preserved in life position. These taphonomic observations are in good accordance with sedimentological data (see above), suggesting storm-influenced environmental conditions. Consequently, the remarkable preservation of the two specimens of *M. incipiens* from Camaret probably results from their rapid burial, soon after death, by storm deposits.

## Conclusions

The description of the mitrate *Mitrocystella incipiens* in the lower part of the Postolonnec Formation (Corréjou Member) in the Crozon Peninsula not only increases its distribution across the Armorican Massif, but it also represents the earliest known record of this taxon in the whole Mediterranean Province. Both the taphonomic characteristics of the specimens and the associated sedimentological structures suggest that the Notinau mitrates were very likely buried soon after death by storm deposits.

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# Early Tremadocian graptolites from the Arivechi area, Sonora, northern Mexico

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### ABSTRACT

Graptolites from the early Tremadocian *Anisograptus matanensis* Biozone are identified from east-central Sonora, northwestern Mexico, within a carbonate-shelf succession deposited on the southwestern continental shelf margin of Laurentia. This is the second occurrence of typical anisograptid graptolites in Mexico, after its original record in the Oaxaca area, which belongs to a Gondwana-related paleogeographical realm. The graptolites from Sonora represent the second global occurrence of any member of the *Rhabdinopora flabelliformis* group in the Ordovician equatorial shelf region.

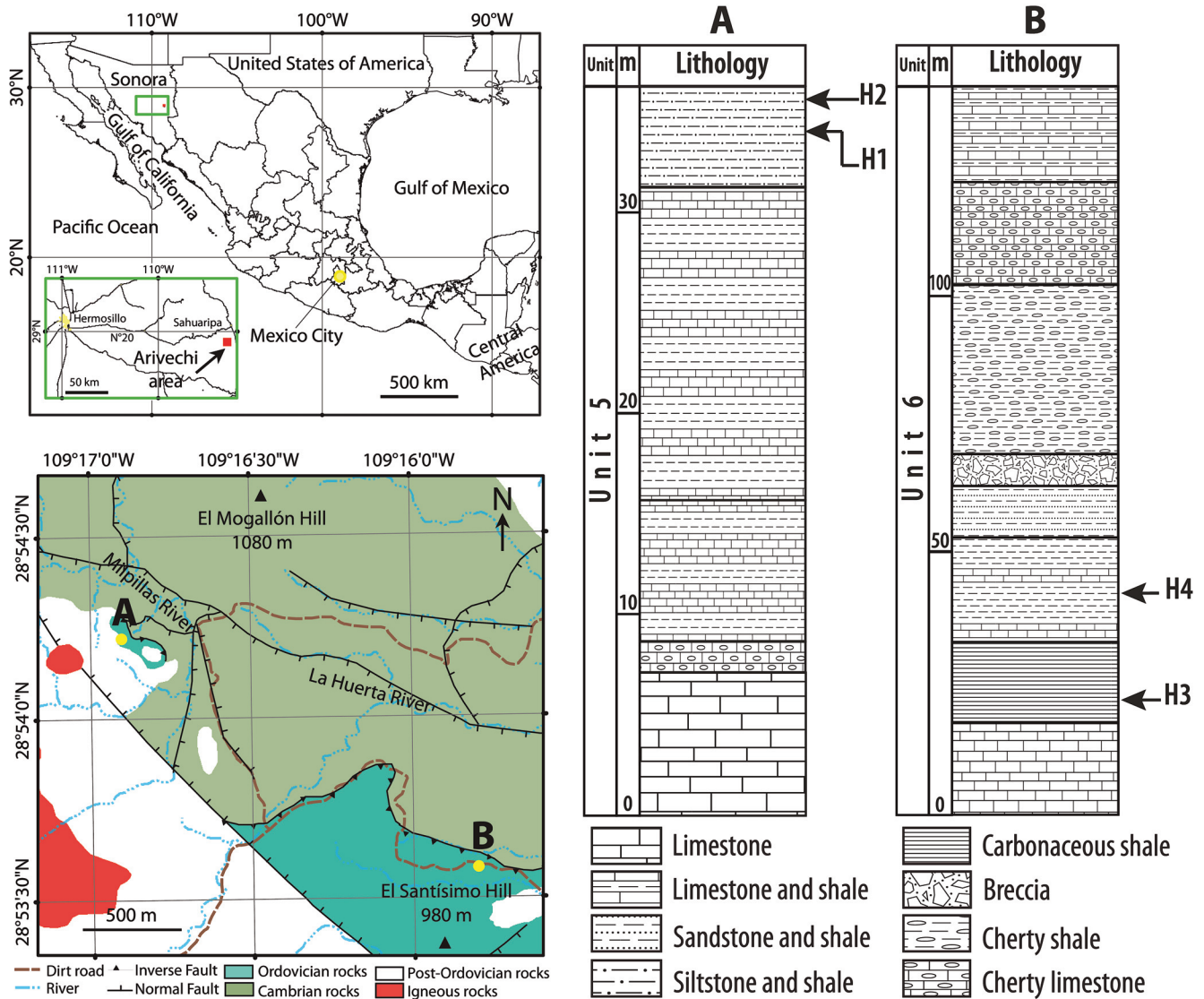
### Introduction

Early Ordovician graptolites from Mexico were first reported from the lower part of the Río Salinas (=upper) Member of the Tiñú Formation, in two sections of the Nochixtlán region, Oaxaca State, where some material was illustrated and partially described by Sour and Buitrón (1987) and Landing et al. (2007). The succession includes, from base to top, a lower (but not lowermost) Tremadocian (Tr1) graptolite assemblage, dominated by *Rhabdinopora* and with possible presence of *Anisograptus*, followed by middle Tremadocian (Tr2) benthic faunas and conodont assemblages of the *Paltodus deltifer* Biozone (Landing et al. 2007). In this paper we present the discovery of early Tremadocian graptolites in a region located further north, in east-central Sonora, within a very different paleogeographical context (see below). To date, the oldest known graptolites from this region were some specimens of *Adelograptus* spp. (early Tr2), mentioned by Poole et al. (1995a) but never described or illustrated, from two localities in the El Quemado Formation exposed in the northern part of the Barita de Sonora mine area.

### Geological setting

Tremadocian (Lower Ordovician) rocks in Sonora occur as scattered outcrops at several localities northwest and east of Hermosillo. These are Sierra López, Sierra Martínez, Rancho Las Norias, Cerro El Santísimo, Sierra Agua Verde, and Barita de Sonora, and the strata have been correlated by conodonts and trilobites (Almazán-Vázquez 1989; Poole et al. 1995a, 1995b; Stewart et al. 1999). They are further mentioned in syntheses on the Paleozoic of Mexico (a.o., Buitrón-Sánchez 1992; Page et al. 2012; Cuen-Romero et al. 2023).

The studied area is located in the Sierra Madre Occidental, ca 220 km east of Hermosillo and WSW of the town of Arivechi (Fig. 1). The Lower Paleozoic succession is composed of seven Cambrian and Ordovician lithostratigraphic units, in



**Fig. 1.** Location map of the Arivechi area (above left) and geological sketch map (below) with the position of the two Early Ordovician graptolitic sections south of the Milpillas River (A) and northeast of El Santísimo Hill (B). To the right, simplified stratigraphic columns of units 5 (locality A) and 6 (locality B), showing the position of the four new graptolite horizons (H1–H4).

part informally described as formations by Almazán-Vázquez (1989). Our (unnamed) units 5 and 6 would be somewhat equivalent to a minor part of the El Santísimo Formation (Ordovician) of that author, who reported Tremadocian trilobites from the *Symphysurina* Zone in a section different from those studied here, but partly correlatable with our Unit 6 (its “member B”). Unpublished reports on Ordovician conodonts in the Arivechi area (Reyes-Montoya 2017; Becuar-Daniels 2019) come from different strata, mainly from our (here undescribed) Unit 7.

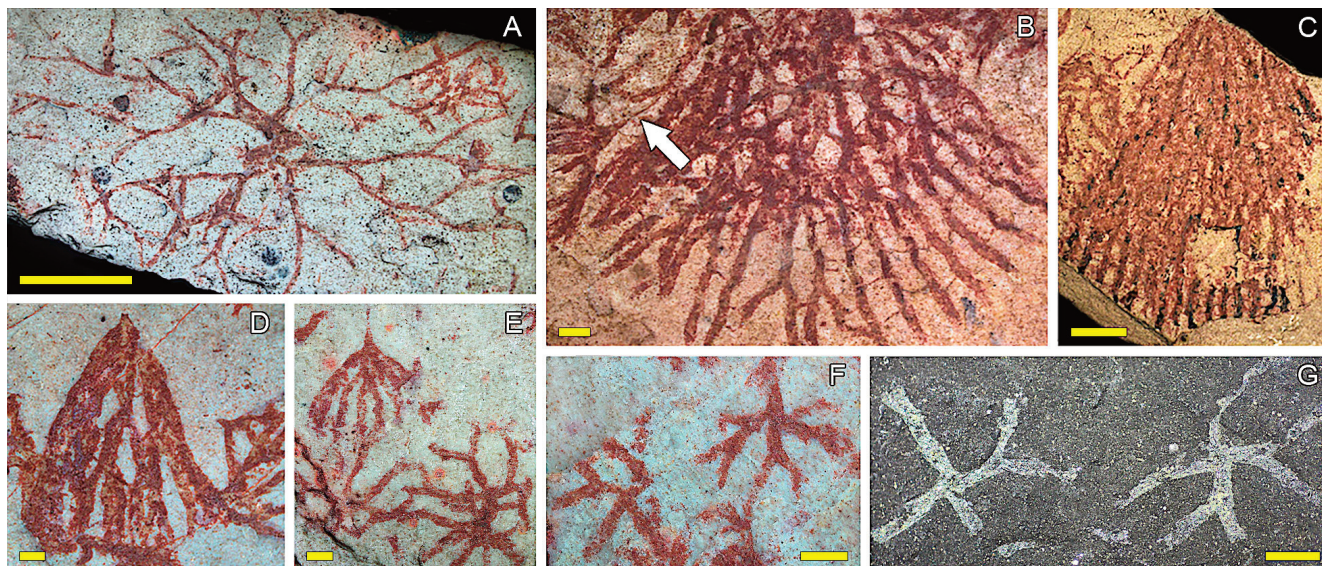
Unit 5 has been characterized on the southern slope of a hill located south of the Milpillas River (Fig. 1A on detailed map) and is a carbonate succession ca 36 m thick, dominated by thick-bedded limestone in the lower part, passing gradually to thin-bedded limestone with chert nodules, a thick alternation of medium-bedded limestone and shale, and ending with an alternation of red siltstone and shale (Fig. 1, column A). Two graptolite horizons have been located in these uppermost shales (Fig. 1, H1 and H2).

Unit 6 was characterized on the northern slope of El Santísimo Hill (Fig. 1B on detailed map) and consists

of 140 m of medium- and thin-bedded limestone, alternating shale with limestone or sandstone, and also carbonaceous shale towards the lower part, some beds of sedimentary breccia towards the middle part, and shale with intercalations of bedded chert towards the upper part. Two additional graptolite horizons are in the lower third of this unit (Fig. 1, H3 and H4), whose stratigraphic relationships with Unit 5 cannot be established due to the lack of continuity between their respective outcrops. However, due to structural criteria, it is provisionally assumed that Unit 6 postdates the succession represented by Unit 5.

### Paleontological results

The studied graptolite material is preserved largely as flattened tubaria, showing weathering impregnation with iron minerals in the two horizons located near the top of Unit 5 (Fig. 2A–F). Specimens from the two other horizons located in Unit 6 are also flattened but are apparently preserved as coalified organic material occurring in thin layers of black shale, as suggested by the silvery shine of their tubaria (Fig. 2G).



**Fig. 2.** Early Tremadocian graptolites from units 5 (A–F) and 6 (G): horizons H1 (B–D), H2 (A, E–F) and H3 (G). **A** – *Anisograptus matanensis* in dorsal view; **B–C** – *Rhabdinopora* cf. *canadensis* (arrow points to the nema of the left specimen); **D–F** – *Rhabdinopora* sp. (**D** – small distorted tubarium; **E–F** – small specimens in lateral and discoidal preservation, with apparent lack of dissepiments, the “pointed” sicula is visible); **G** – *Rhabdinopora?* sp., two early growth stages flattened horizontally, showing quadriradiate development. Original specimens are in the paleontological collection of the University of Sonora. Scale bars = 5 mm (A, C), and = 1 mm (B, D–G).

The graptolite assemblages recorded at horizons H1 and H2 of Unit 5 are dominated by small specimens of *Rhabdinopora* sp. They mostly consist of early growth stages in lateral and discoidal preservation, in the former case usually showing the “pointed” sicula and in the latter case the quadriradiate proximal development (Fig. 2E, F). Small distorted tubaria of conical appearance, with dissepiments obscured by torsion and flattening (Fig. 2D) are also common. Among the numerous specimens recovered, the record of *Rhabdinopora* cf. *canadensis* (Lapworth, 1898) has been established confidently based on the occurrence of specimens with a long undivided nema (Fig. 2B) and slender dissepiments irregularly arranged, with an average stipe width of ca 0.5 mm in dorsal view, and a stipe spacing of about 8–10 mm in mature parts of the mesh.

In addition to the genus *Rhabdinopora*, a triradiate anisograptid with a horizontal tubarium and 4–6 orders of stipes, with variable-spaced dichotomies and lacking dissepiments, was recorded in horizon H2. The most complete tubaria can be seen in dorsal view (Fig. 3A) and, despite the proximal ends not being entirely preserved, it can be identified as *Anisograptus matanensis* Ruedemann, 1937. Other possible *Anisograptus* remains were recorded in H1, represented by poor-quality early stages preserved in lateral view.

Graptolites from Unit 6 are less abundant and determinable than those from Unit 5. The assemblage from horizon H3 includes some small horizontal specimens showing quadriradiate proximal ends (Fig. 2G) as well as somewhat larger horizontal tubaria with a more advanced astogeny, which show diverging stipes without dissepiments. The features of the former are somewhat similar to those of the genus *Staurograptus*, although the short branching divisions allow them to be better identified as juvenile specimens of *Rhabdinopora?* sp. in discoidal preservation. Regarding the larger tubaria (not shown), despite the fact that their proximal

end is not clearly visible in any specimen, its overall morphology allows a provisional identification as *Anisograptus?* sp. until a more complete and better-preserved material is available. Finally, horizon H4 has so far only provided fragments of indeterminable stipes.

Following the biochronological division of the lower Tremadocian on a global scale based on graptolite biozones (Cooper et al. 1998; Maletz 2021; and the recent review by Maletz et al. 2023), the co-occurrence of *A. matanensis* and *R. cf. canadensis* in horizon H2 indicates the lower part of the *A. matanensis* Biozone. If the record of *Anisograptus* in horizon H1 is confirmed by future sampling, the same biozone would begin a few meters below. Otherwise, the mere presence of *R. cf. canadensis* in H1 could also be indicative of the preceding *R. campanulatum* Biozone. Regarding horizon H3, the record of *Rhabdinopora?* sp. and *Anisograptus?* sp. could occur in both the *A. matanensis* and the *R. anglica* biozones, representing in the latter case the youngest graptolites of the local early Tremadocian sequence.

### Concluding remarks

The occurrence of planktic graptolites from the *Anisograptus matanensis* Biozone in east-central Sonora slightly precedes the appearance of the first conodonts from the upper part of the lower Tremadocian *Rossodus manitouensis* Biozone in the Arivechi region, which are succeeded by middle and upper Tremadocian records ranging from *Scolopodus subrex* to *Paroistodus proteus* biozones (Reyes-Montoya 2017; Becuar-Daniels, 2019).

The graptolite assemblage described herein includes two species of *Rhabdinopora* and *Anisograptus* of worldwide distribution, the first of them is representative of a species of the *R. flabelliformis* group, which is recorded in a fully paleo-equatorial area, such as the specimens found in the Bliss

Sandstone of New Mexico (Flower in Taylor and Repetski 1995, 136). Both occurrences of *Rhabdinopora* are unique in the Early Ordovician world if they are projected on the paleogeographical maps of Laurentia (Poole et al. 1995b; Cocks and Torsvik 2011, a.o.). At the same time, the characterization of the *A. matanensis* Biozone (but without *Rhabdinopora*) matches the earliest record of graptolites (“*Anisograptus* Zone”) in classical sections of the Great American Carbonate Bank of Laurentia, such as the base of the Marathon Limestone of Texas and the Goodwin Formation of central Nevada (Erdtmann and Comeau 1980 with earlier references).

The Tremadocian graptolites from Sonora are perhaps coeval with the assemblages found in deeper-water environments in the Tiñu Formation of southern Mexico (see references above). However, the material needs a detailed taxonomic review (it seems to include more than one genus and a single species of *Rhabdinopora*). Paleogeographically, it comes from a terrane (Oaxaquia) that, although accreted to North America, was originally either an insular area in temperate latitudes or was situated in a Gondwanan or peri-Gondwanan position in pre-Silurian times (Landing et al. 2007; Cuen-Romero et al. 2023).

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# The breakup of the L-chondrite parent body 466 Ma and its terrestrial effects – a search for a mid-Ordovician biodiversity event

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## ABSTRACT

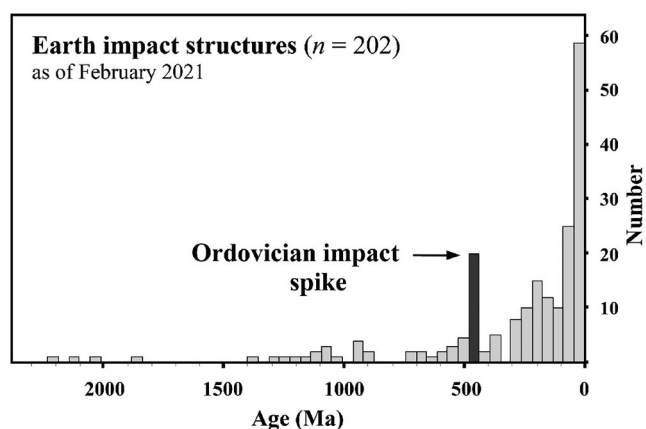
About a third of all meteorites that fall on Earth today, the stony L-chondrites, originate from a major breakup event in the asteroid belt 466 Ma, in the early Darriwilian. This is the largest asteroid breakup in the past three billion years documented by K-Ar gas-retention ages of recently fallen meteorites. There has been a debate whether the breakup had any effects on Earth's biota. Based mainly on brachiopod data from western Russia, some authors have argued for the existence of a major biodiversity 'event' at approximately the time of the L-chondrite breakup. An analysis of the distribution of three fossil groups (conodonts, ostracods and trilobites) across the late Dapingian and early Darriwilian in three sections in southern Sweden shows no evidence of any biodiversity event. The only biotic changes outside a normal trend are those related to a sea-level fall following the arrival of large amounts of dust from the asteroid breakup. We conclude that the Great Ordovician Biodiversification Event represents a sequence of changes over about 20 Myr, coinciding with an asteroid shower from the breakup of the L-chondrite parent body.

## Introduction

During the early Darriwilian, 466 Ma, a 150-km-sized asteroid broke up in the asteroid belt, probably after having been hit by another large asteroid or a comet. This is the largest documented asteroid breakup over the past three billion years. The event still delivers the most common type of meteorites to Earth, the stony L-chondrites. The terrestrial effects of the breakup include a one-order-of-magnitude excess of impact craters of mid-to-late Ordovician age, indicative of an asteroid shower to Earth following the breakup (Terfelt and Schmitz 2021; Schmitz et al. 2022). This is the only resolvable asteroid shower in Earth's impact crater record (Fig. 1). In mid-Ordovician strata, in China, Russia and southern Sweden, a two- to three-order-of-magnitude increase has been recorded in the flux of micrometeorites and extraterrestrial dust to Earth following the breakup (Schmitz et al. 2019). Abundant fossil meteorites recovered during quarrying of mid-Ordovician limestone at Kinnekulle in southern Sweden also attest to the event. In the Hällekis section at Kinnekulle, the onset of the flux increase coincides with the onset of an important sea-level fall, the Täljsten event, possibly related to a mid-Ordovician (short-lived?) ice age triggered by extraterrestrial dust that shaded Earth from some sunlight (Schmitz et al. 2019).

In sections in western Russia, the fossil brachiopod distribution has revealed a so-called biodiversity event in the early Darriwilian, approximately at the base of the *Lenodus variabilis* Conodont Zone (Rasmussen et al. 2007). Since the first dust from the breakup of the L-chondrite parent body, as also reconstructed in the Hällekis section, occurs close to the base of the *L. variabilis* Zone, it has been suggested that the asteroid breakup somehow indirectly triggered the biodiversity event (Schmitz et al. 2008). In order to shed more light on this, we have here compiled detailed biostratigraphic data for three fossil groups in late Dapingian to early Darriwilian sections in Sweden. We compare bed-by-bed the biodata with the registered sea-level changes and the first arrival of extraterrestrial dust from the L-chondrite breakup. Among the sites discussed, there is a depth transect from western Russia (shallowest) to Västergötland (intermediate) and to Scania (deepest), which may allow to discriminate the effects of sea-level changes on the biota.





**Fig. 1.** Histogram that shows the age distribution of terrestrial impact structures. Note the distinct Ordovician spike at ca 470–450 Ma. The impact spike is indicative of an asteroid shower to Earth following the L-chondrite parent body breakup. Presented after Schmitz et al. (2022).

## Materials and methods

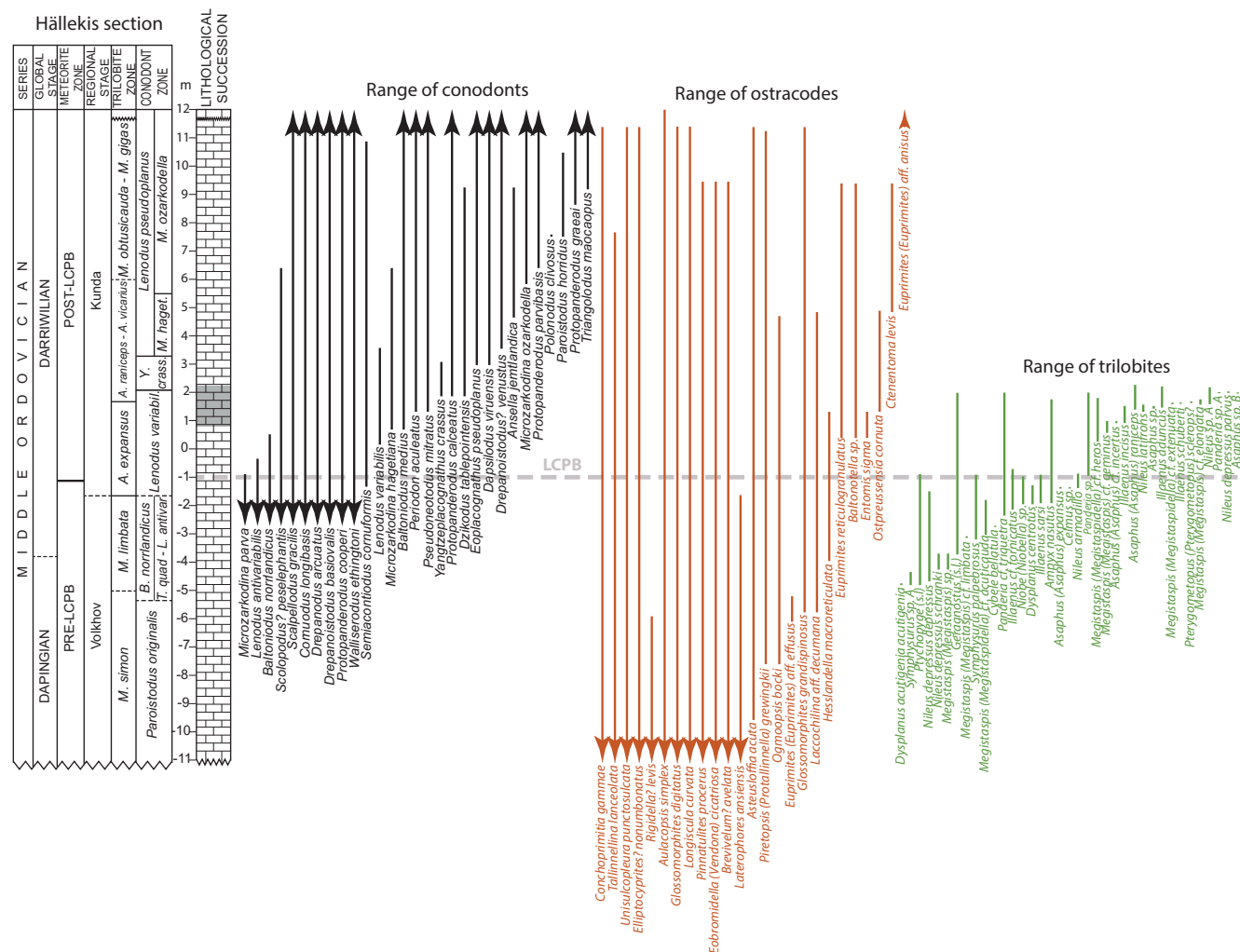
We base our compilations on information from the literature referenced in the captions of the respective plot. The groups and sites considered are ostracods, conodonts and trilobites

in the Hällekis section at Kinnekulle in Västergötland, and conodonts and trilobites in the Fågelsång and Killeröd sections, respectively, in Scania, southernmost Sweden. The timing of the breakup of the L-chondrite parent body has been determined using helium isotopes in bulk sediments, neon isotopes in fossil meteorites and the distribution of L-chondritic chromite in bulk limestone in the sections at Kinnekulle (Schmitz et al. 2019).

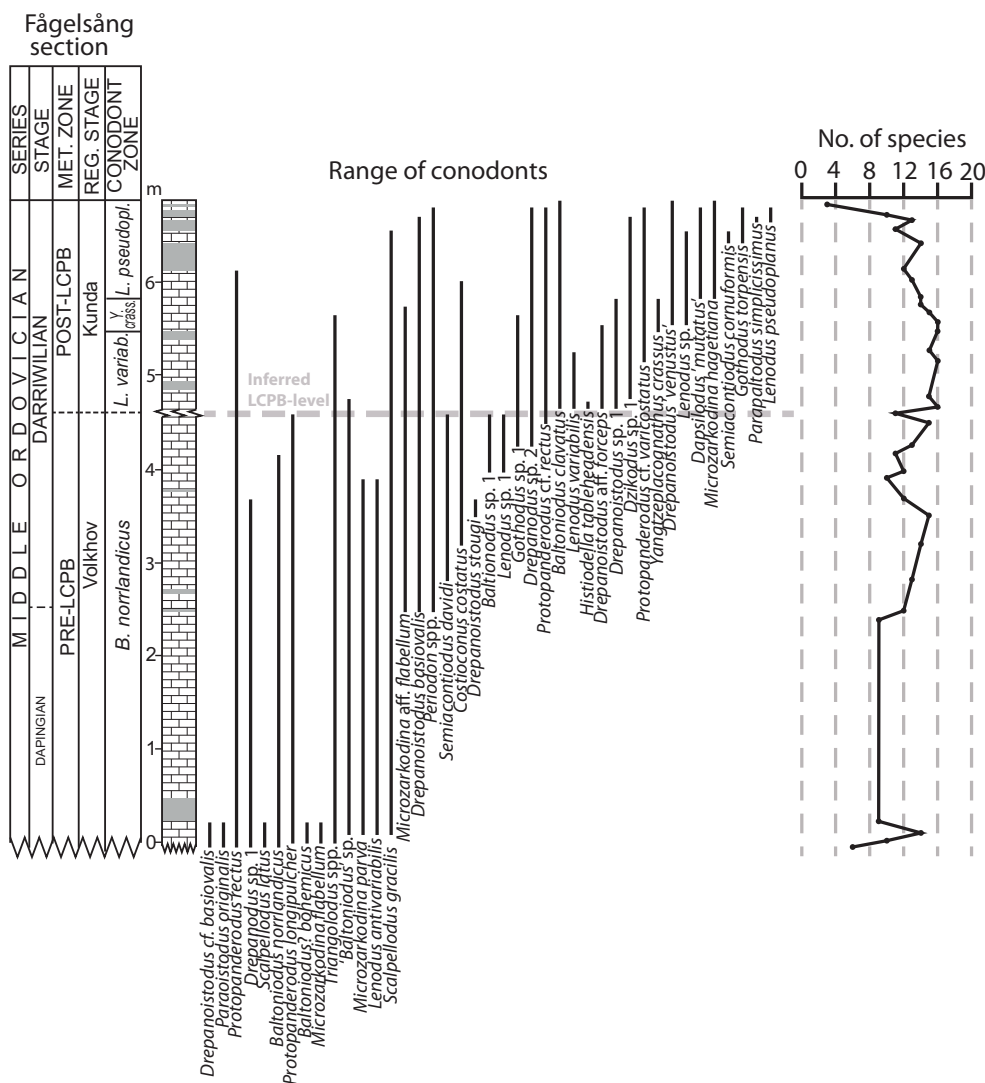
## Results and discussion

Our compilations in Figs 2–4 show smooth and gradual biodiversity changes across the late Dapingian to the early Darrivilian for all three animal groups in all sections. The only ‘event’ is the appearance of some shallow-dwelling species in the Täljsten interval (Zhang 1998; Villumsen 2001; Tinn and Meidla 2001) in the Hällekis section, a feature not seen in the deeper setting at Killeröd and Fågelsång. There is no clear or obvious ‘event-like’ change in biodiversity in any bed over the stratigraphic interval considered.

It appears that the biodiversity event seen in brachiopod distribution in western Russia by Rasmussen et al. (2007) cannot be reproduced in other taxa such as conodonts,



**Fig. 2.** Range and biodiversity data for conodonts, ostracods and trilobites in the Hällekis section, Västergötland, Sweden. The Täljsten interval is marked grey in the lithological log. The stratigraphic position of the L-chondrite breakup (LCPB) is marked with a dashed grey line. Data for conodonts are from Zhang (1998), for ostracods from Tinn and Meidla (2001) and for trilobites from Villumsen (2001). Biostratigraphy is after Lindskog et al. (2019).



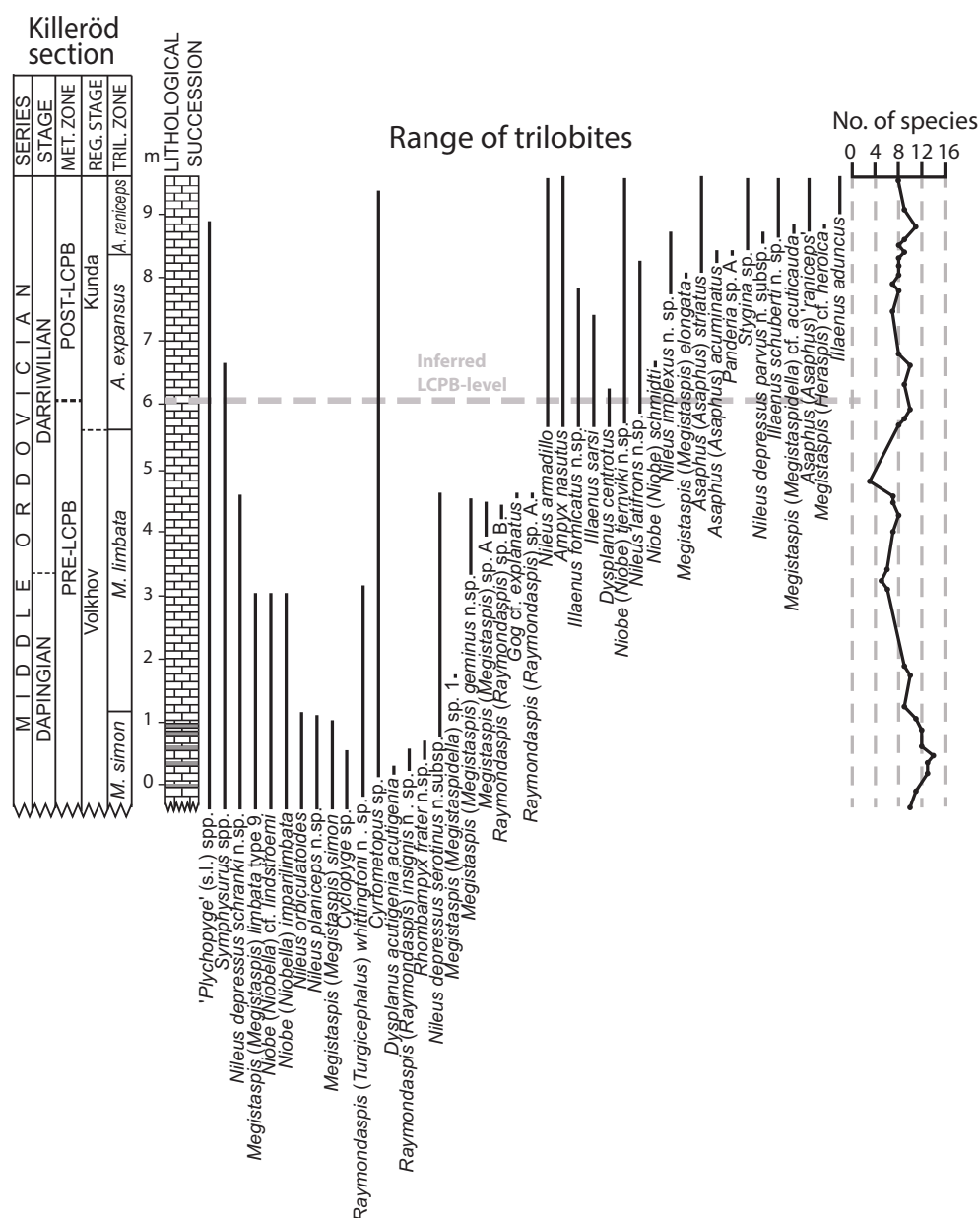
**Fig. 3.** Range and biodiversity data for conodonts in the Fågelsång section, Scania (Stouge and Nielsen 2003). Time of L-chondrite parent body breakup (LCPB) = dashed grey line.

ostracods and trilobites even at a regional scale. No detailed studies have yet been performed of the distribution of brachiopods in the sections in southern Sweden, but we plan such studies in the future. However, there are already reasons to believe that the changes in brachiopod faunas in western Russia may to a large extent reflect a facies shift rather than a true biodiversity event. It is obvious from the available compilations of western Russia brachiopod data that the claimed increase in biodiversity reflects the incoming of several shallow-water species related to a prominent sea-level fall. Our preliminary data suggest that this is the same sea-level fall as the Täljsten event in southern Sweden. A similar sea-level fall is also seen at the corresponding stratigraphic level in many sections worldwide. The onset of the lowstand in the Lynna section in western Russia may coincide with the first arrival of abundant dust from the L-chondrite breakup event. More detailed studies are ongoing to test this hypothesis. We stress that in order to resolve this and similar questions, it is important to adopt a bed-by-bed and section-by-section approach rather than to lump data together and apply various binning and correlation approaches with significant inherent uncertainties that allow great flexibility in arriving at different conclusions.

Although there is no apparent instantaneous biotic event recorded in connection with the breakup of the L-chondrite parent body, other than sea-level related changes, we note that on a more extended time scale the Great Ordovician Biodiversification Event appears to coincide with frequent impacts on Earth by up to kilometre-sized asteroids. This indicates that astronomical processes may somehow have accelerated the diversification process, as originally proposed by Schmitz et al. (2008).

### Conclusions

Our data support the proposal by Servais et al. (2021) that the Great Ordovician Biodiversification Event is not a single event, but an extended sequence of biotic events spanning the period from the early Darriwilian to the Hirnantian. We argue that the early Darriwilian brachiopod event in western Russia may primarily reflect a sea-level fall rather than a biotic event of global, evolutionary significance. We note, similarly to Schmitz et al. (2008), that the ‘extended’ Great Ordovician Biodiversification Event coincides with the period when frequent asteroids from the L-chondrite parent-body breakup hit Earth.



**Fig. 4.** Range and biodiversity data for trilobites in the Killeröd section, Scania (Nielsen 1995). Time of L-chondrite parent body breakup (LCPB) = dashed grey line.

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# Diversification and speciation among Laurentian brachiopods during the GOBE: insights from basinal and regional analyses

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### ABSTRACT

Full understanding of diversity dynamics during the Great Ordovician Biodiversification Event (GOBE) requires analyses that investigate regional and species-level data and patterns. In this study, we combine bedding-plane scale data on brachiopod species counts and shell size collected from the Simpson Group of Oklahoma, USA, with species-level phylogenetic biogeography for three articulated brachiopod lineages that occurred throughout Laurentia. From these data, we ascertain that the primary influences of brachiopod shell size and diversity in the Simpson Group reflect global drivers, notably temporal position and paleotemperature. Similarly, the primary speciation pattern observed within *Hesperorthis*, *Mimella*, and *Oepikina* is the oscillation in speciation mode between dispersal and vicariance, which reflect the connection and disconnection of geographic areas, respectively. Processes that facilitate cyclical connectivity are global to regional in scale such as oceanographic changes, glacial cycles, or tectonic pulses. Therefore, both regional and continental scale analyses reinforce the importance of global factors in driving diversification during the GOBE.

### Introduction

The Ordovician Period is a key interval of diversification and differentiation in the history of marine life. In particular, the Middle Ordovician was a time of accelerated diversification of shelly taxa (e.g., Harper et al. 2013; Wright and Toom 2017; Stigall et al. 2019; Lam et al. 2021). The main pulse of the Great Ordovician Biodiversification Event (GOBE) occurs as an interval of statistically elevated diversification and increase in generic richness during the Dapingian and Darriwilian stages (Kröger et al. 2019; Rasmussen et al. 2019). It is increasingly important to understand how components of global diversity are generated (Stigall 2018), including how processes at local to regional scales influence broader patterns of diversification.

Herein, we examine diversity patterns and reconstruct speciation modes for a group of articulated brachiopods from the Middle Ordovician of Laurentia. Specifically, we combine outcrop-based analyses of diversification in the Southern Oklahoma Aulacogen of the Laurentian mid-continent with a broader multi-basinal phylogenetic biogeographic analysis of select clades. The primary research questions addressed are: (1) to what degree do regional patterns of diversity match patterns from global datasets; and (2) whether speciation in Laurentian brachiopods matches the anticipated patterns of alternating episodes of vicariance and dispersal proposed by Stigall et al. (2017). The first question is assessed using outcrop-level analyses of diversity and shell size, whereas the second question is addressed using phylogenetic

biogeography. Combined, these analyses provide insight into diversification patterns and processes operating within Laurentia during the main pulse of the GOBE.

## Materials and methods

Regional diversity and disparity patterns were assessed via bed-by-bed analysis of articulated brachiopods of the Simpson Group strata of south-central Oklahoma. This succession comprises one of the most complete (biostratigraphically) and best sampled (geochemically) Laurentian sections spanning the GOBE. Specifically, outcrops of the Joins, Oil Creek, McLish, Tulip Creek, and Bromide formations exposed along Interstate 35 and US-77 were targeted for analysis. Each bedding surface was examined and all identifiable brachiopods were counted. Shell width and depth were measured for all specimens with reasonably entire margins. Lithology was also recorded. For diversity analyses, data were aggregated into 10 temporal bins and rarefied diversity was calculated as specified in Trubovitz and Stigall (2016). Trends and variance in shell size through time were analysed using the R package PaleoTS (Hunt 2019) as specified in Hennessey (2023). To test for the impact of local, regional, and global controls on diversity and disparity patterns, a Boosted Regression Model (BRM) was developed using the R package “gbm” (Ridgeway et al. 2020). The BRM incorporated shell size as the independent variable relative to the contributions of lithology, temporal position, diversity (from Trubovitz and Stigall 2016),  $\Delta^{13}\text{C}$  from Simpson Group strata from Edwards and Saltzman (2015) as a proxy for carbon cycle and nutrient conditions,  $\delta^{18}\text{O}$  data from Avila et al. (2022) as a proxy for paleotemperature/salinity, and  $^{87}\text{Sr}/^{86}\text{Sr}$  data from Avila et al. (2022) as a proxy for tectonic activity as specified in Hennessey (2023).

To assess speciation mode and connections between marine basins within Laurentia, species-level phylogenies were developed for three common clades of Middle Ordovician brachiopods: orthids *Hesperorthis* and *Mimella*, and the strophomenid *Oepikina*. A total of 65 species were examined among the three clades and scored for 30, 31, and 32 discrete morphological characters among *Hesperorthis*, *Mimella*, and *Oepikina* species, respectively. Character matrices were analysed using a Bayesian tip-dated phylogenetic analysis conducted using Markov chain Monte Carlo (MCMC) analysis in MrBayes 3.2.7 (Wright 1997; Ronquist et al. 2012). Consensus topologies were timescaled using the R package “paleotree” (Bapst 2012) and biogeographic analysis was conducted in “BioGeoBEARS” (Matzke 2013). Dispersal events were identified when descendent species inhabited additional geographic ranges relative to their ancestors. Vicariance events were identified when descendent species inhabited fewer geographic ranges relative to their ancestors (e.g., Lieberman 2000; Lam et al. 2018, 2021). Data and methods for the phylogenetic and biogeographic analyses are detailed in Censullo (2020).

## Results and discussion

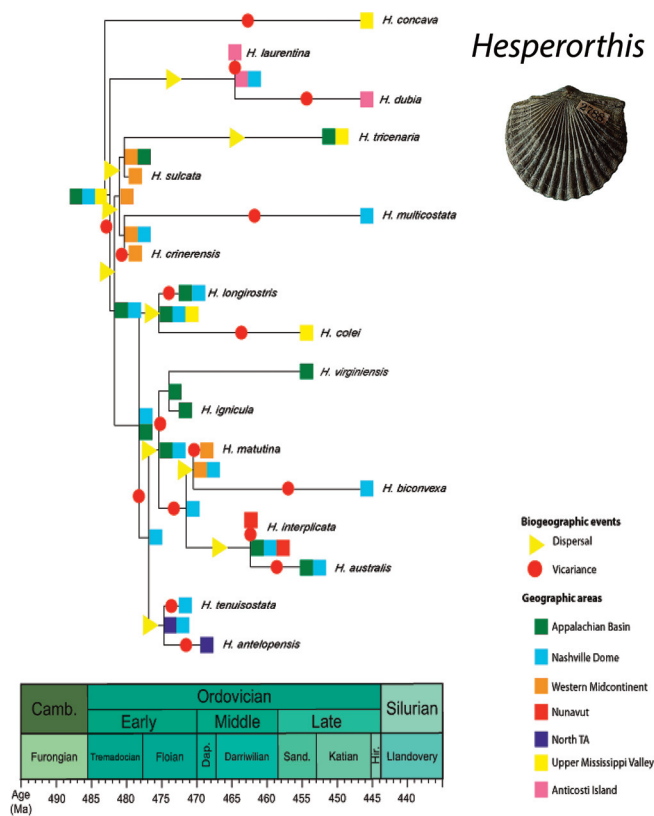
Results of field-based analyses of the Simpson Group brachiopods indicate a rapid increase in species diversity coinci-

dent with increased shell volume. Significantly, these increases are statistically identifiable as related to rapid state changes, rather than long-term directional trends occurring over a million years or more. These coordinated increases are recorded within the lower portion of the Oil Creek Formation, which is correlative with the *Histiodellella sinuosa* and *H. holodentata* conodont biozones. Notably, diversity increases on other paleocontinents, including Baltica and Gondwana, are coincident with the observed diversity increase in Oklahoma (Trubovitz and Stigall 2016; Stigall et al. 2019). The results of boosted regression analysis further indicate that the primary factors influencing shell volume are age (=position in time), paleotemperatures/salinity, and overall diversity. Each of these factors are globally influential. Conversely, local factors such as lithology and basin-specific carbon cycle changes have limited impact on shell volume. Thus, the general picture that emerges is that diversification and ecosystem change was rapid, coincident with similar changes on other paleocontinents, and was primarily influenced by global (age,  $\delta^{18}\text{O}$ , diversity) rather than local ( $\Delta^{13}\text{C}$ , lithology) factors. These results from regional analysis of one of the best preserved Middle Ordovician sections in Laurentia indicate the importance of global environmental changes for driving evolutionary patterns at the regional/local scale within Laurentia during the GOBE.

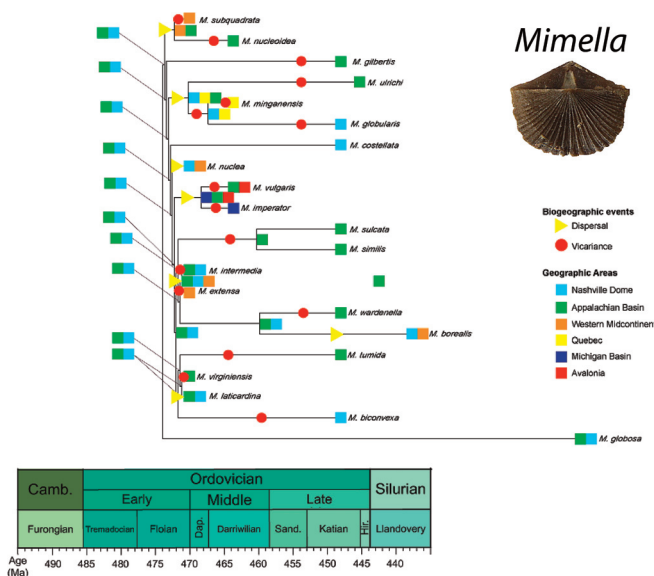
To investigate processes of diversification, we examined how connections vs separations among multiple basins within Laurentia impacted speciation patterns and what environmental factors exerted strong influence on these processes. Diversification rates of *Hesperorthis*, *Mimella*, and *Oepikina* lineages were greatest during the Darriwilian and tapered off during the Late Ordovician. In fact, 89% of observed speciation events occurred during the Early to Middle Ordovician. This pattern of increased diversification, spiking during the Middle Ordovician, is consistent with other marine clades, such as crinoids, graptolites, and bryozoans, which also experienced rapid radiation during this time (Wright and Toom 2017; Stigall et al. 2019).

Speciation within *Hesperorthis*, *Mimella*, and *Oepikina* reflects alternating episodes of speciation via dispersal followed by vicariance events (Figs 1–3), although the frequency of dispersal events vs vicariant events varied among the lineages. A dispersal event followed by a vicariant event, or vice versa, occurred approximately 80% of the time within the genus *Hesperorthis*, 71% within the genus *Mimella*, and 58% of the time in *Oepikina*. Thus, alternation of dispersal and vicariance is a common motif observed within these clades. This alternation supports the BIME (Biotic Immigration Event) biodiversity accumulation model proposed by Stigall et al. (2017), in which alternation between dispersal and vicariance events facilitates speciation through a cyclical process.

Reconstructed dispersal events between basins are consistent with potential dispersal pathways facilitated by ocean currents surrounding Laurentia during the Middle to Late Ordovician (Pohl et al. 2016; Lam et al. 2018). The best fit biogeographic models indicate that founder-event speciation (denoted by the +J added within each model) was an important biogeographic process driving evolution. Basins which



**Fig. 1.** Paleobiogeographic reconstruction of *Hesperorthis* from the BioGeoBEARS analysis. The DIVALIKE+J model, shown here, was the most likely model for the biogeographic evolution of the species of *Hesperorthis* (AIC = 86.44). Dispersal events are indicated by a yellow triangle and variance events by a red circle. Abbreviations: TA – Transcontinental Arch, Camb. – Cambrian, Dap. – Dapingian, Sand. – Sandbian, Hir. – Hirnantian. Modified from Censullo (2020).

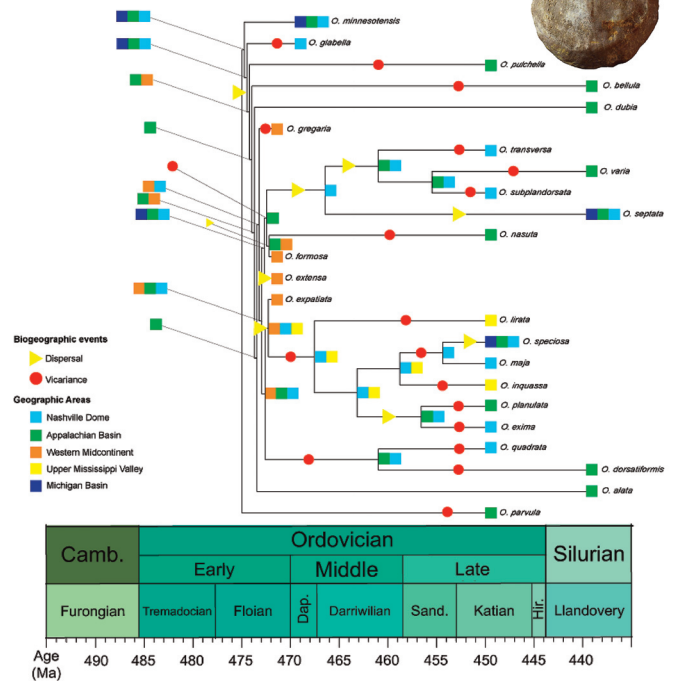


**Fig. 2.** Paleobiogeographic reconstruction of *Mimella* from the BioGeoBEARS analysis. The DEC+J model, shown here, was the most likely model for the biogeographic evolution of the species of *Mimella* (AIC = 95.01). Abbreviations: Dap. – Dapingian, Camb. – Cambrian, Sand. – Sandbian, and Hir. – Hirnantian. Modified from Censullo (2020).

*Hesperorthis*



*Oepikina*



**Fig. 3.** Paleobiogeographic reconstruction of *Oepikina* from the BioGeoBEARS analysis. The DEC+J model, shown here, was the most likely model for the biogeographic evolution of the species of *Oepikina* (AIC = 108). Abbreviations: Camb. – Cambrian, Dap. – Dapingian, Sand. – Sandbian, and Hir. – Hirnantian. Modified from Censullo (2020).

are geographically close would have been connected during intervals of sea-level rise but disconnected following a sea-level fall. Another pattern prevalent through the evolution of these clades is the dispersal to and from the Nashville Dome or Appalachian Basin and the western Midcontinent. Dispersal between these basins, and subsequent dispersal events from the western Midcontinent to northwestern basins, correlates with intracontinental surface currents from prevailing winds (Lam et al. 2018). Reversed dispersal events which brought species from the western Midcontinent east to the Appalachian Basin and the Nashville Dome correlate with larger ocean gyres, such as the Southern Laurentia Current, and the Iapetus Current, which operated around the continent of Laurentia, within the Iapetus Ocean (Pohl et al. 2016).

Sea level fluctuated often during these critical times of speciation during the Ordovician (Pohl et al. 2016; Lam et al. 2018), which would have facilitated the observed pattern of alternating dispersal and vicariance. Sea-level cyclicity has been linked to glaciation potentially as early as the Middle Ordovician (Rasmussen et al. 2016). Cooling ocean temperatures and the formation of glaciers at high latitudes in the Southern Hemisphere caused declining sea level during the Middle Ordovician (Rasmussen et al. 2016). Each genus in this study expanded its range during this time, which may reflect greater potential for brachiopods to occupy previously unavailable niches and regions due to cooling oceans paired with changing surface ocean circulation patterns. Rapidly changing sea-levels would have connected and disconnected adjacent basins, facilitating the alternation of dispersal and

vicariance events, such as the oscillations evident within the lineages of *Hesperorthis*, *Mimella*, and *Oepikina* during the Middle Ordovician. Similarly to the diversification analyses of the Oklahoma basin, these multi-basin scale analyses indicate that global factors, such as climatic cooling and changes in ocean circulation, exerted core influences on regional diversification processes within Laurentia during the GOBE.

## Conclusions

Combining a single-basin, stratigraphically constrained analysis with a multi-basin evolutionarily constrained analysis provides a framework to examine regional vs global diversity dynamics. Within the Southern Oklahoma Aulacogen, diversity and shell volume increased rapidly during the early Darriwilian Stage. This paired increase was primarily influenced by global factors, including temporal position and paleotemperature/salinity, but was not strongly influenced by local factors such as lithology. Notably, speciation events within the *Mimella*, *Hesperorthis*, and *Oepikina* lineages alternated between dispersal (due to connections among geographic areas) and vicariance (due to isolation of geographic regions). Factors capable of producing oscillations in connectivity among basins primarily reflect global influences related to cooling oceans, ice expansion in the Southern Hemisphere, and/or regional tectonics. By integrating these analyses, it is clear that large-scale drivers are important for facilitating local speciation, and thus diversification, within Laurentia during the GOBE.

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# An evo-devo perspective on no Ordovician land plants

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### ABSTRACT

Molecular phylogenetic studies of land plant (embryophyte) origins have begun to tease apart those evolutionary contributions derived from prior algal genes and those *de novo* genes that evolved during a charophyte–embryophyte transition. Applying the concept of genomic *assembly* in plant evolution to the fossil record leads to a paradigm shift in the interpretation of the Ordovician record of land plants. Traditional phylogenetic thinking requires fossil species taxa to occupy nodes on a phylogeny. An evo-devo approach can view character evolution separately from species taxa, freeing up fossil spores and tissue fragments to become clues to underlying developmental pathways or gene regulatory networks. This results in a re-assessment of what is meant by the presence of land plants in the Ordovician landscape. The new model helps to reconcile discrepancies between molecular time-trees and the “missing” record of fossil plants during the Ordovician Period.

### Introduction

In recent years, with the application of phylogenomic techniques to the study of land plant origins, a consensus is now emerging on the Zygnematales as the most closely related group to the Embryophyta (Wodniok et al. 2011; Zhong et al. 2013; Wickett et al. 2014), although on the basis of classical morphological and developmental characters, the Coleochaetales possess synapomorphies today that seem more likely to parallel what we anticipate the last common algal ancestor would have possessed. These include zygospores with resistant walls that contain sporopollenin-like compounds (Delwiche et al. 1989). *Zygnema* and related species also produce zygospores that are known in the fossil record (Hall and McCourt 2017). Thus, it appears that the perennation function provided by a resistant cell wall was transferred in evolution from the algal zygote to the spore wall. Evidence for such a sporopollenin transfer hypothesis (Graham 1984; Hemsley 1994) has been supported by studies of spore development (sporogenesis) in bryophytes (Brown and Lemmon 2011; Renzaglia et al. 2023). Bower (1908), on the basis of comparative developmental morphology of living bryophytes, also saw the evolutionary origin of the plant spore as the initial stage in his interpolational, or antithetic, hypothesis for the origin of the plant sporophyte.

The interpolational hypothesis provides a framework with which to explore an evo-devo model of land plant origins. It begins with the origin of the spore, which is followed by the vegetative plant sporophyte. There is a sequence of origins of developmental pathways which were subsequently incorporated into an evolving genomic complex, out of which came the initial embryophyte. The term “developmental pathways” is vague, but it meant to include both Character Identity Networks (ChINs, Wagner 2014) and structural fingerprints (Tomescu and Rothwell 2022). Studies in the phylogenomics of extant plants and charophyte algae show that these components of the embryophyte genome (the developmental toolkit) that distinguish the embryophytes from their ancestors are a combination of re-purposed (or co-opted) prior algal genes and *de novo* genes that are unique to the embryophytes (Floyd and Bowman 2007; Harris et al. 2022).

### Integrating the Ordovician fossil record within an evo-devo model

Basically, an evo-devo model of the algal-plant transition considers genomic assembly as the underlying evolutionary process by which the transition occurred. The extent to which fossils can be tied to particular ChINs can, then, help to construct an



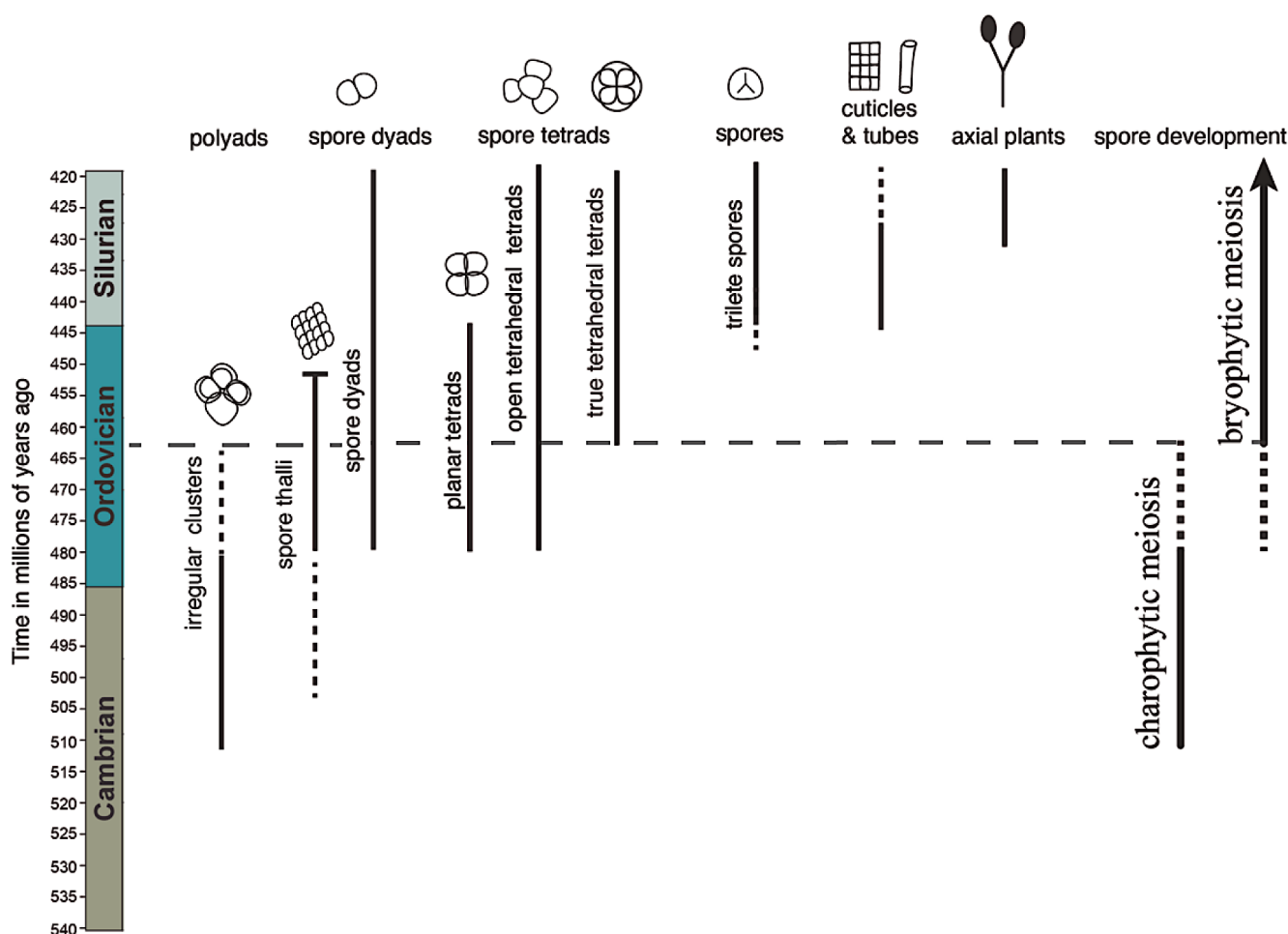
evolutionary timeline of character addition. This frees us to consider the fossil record in terms of the evolution of land plant characters, rather than as species taxa. And, in this way, fossils can be utilized to predict the order in which novel features were added to the evolving embryophytic genome. However, such characters, or features, are limited to a large extent to cells and tissues that are composed of recalcitrant biopolymers that facilitate their preservation in the sedimentary record. These include cryptospores *s.l.*, trilete spores, tracheary elements (TEs) and cuticles. A simple sketch of such a character-based time line is shown in Fig. 1.

The Cambrian cryptospore polyads *Adinosporus* and *Agamachetes*, which persist into the Lower Ordovician, represent the earliest Ordovician occurrences of an evolving subaerial charophytic algal complex (Strother and Foster 2021). These spores occur in packets of enclosed spores that retain their developmental pattern of cell division in the topology of surrounding, resistant walls (Strother and Taylor 2018), patterns that are comparable to reduction division seen in charophyte algae, including *Coleochaete* (Haig 2010, 2015), but not in land plants (Brown et al. 2010, 2015). *Adinosporus* probably represents an early stage in the transfer of sporopollenin from the zygote wall to the spore wall, in which nuclear division is uncoupled from cytokinesis and in

which resistant-walled spores are formed, rather than flagellated zoospores. This later feature is assumed to have occurred in response to perennation in subaerial habitats.

Cryptospore dyads that are indistinguishable from *Dyadospora murusattenuata* Strother and Traverse have their first occurrence in the Tremadocian of Australia (Strother and Foster 2021). *D. murusattenuata* and other species of *Dyadospora* persist throughout the entirety of the Ordovician as they occur in the Katian–Hirnantian of Iran (Ghavidel-Syooki 2016; Ghavidel-Syooki and Piri-Kangarshahi 2021). The morphology of simple dyads makes it treacherous to assume much about their systematic affinities. They occur in the planar, orthogonal spore thalli of *Grododowon*, which clearly demonstrate an algal derivation, but permanent dyads are also known to occur in the sporangia of true land plants as late as the Lochkovian (Wellman et al. 1998; Habgood 2000; Morris et al. 2012).

Tightly adherent tetrahedral tetrads have long been considered the precursors to the trilete spore (Gray and Boucot 1977; Wellman and Gray 2000) and there is little disagreement as to their affinity with the land plants. Both *Tetrahedraletes* and *Cryptotetras* first occur in the Darriwilian and this benchmark is often cited as the fossil basis for the timing of land plant origins. However, more loosely adherent



**Fig. 1.** Fossil record of microfossils related to land plant origins seen as character distributions. The horizontal dashed line represents the conventional origin of land plants based on the first occurrence of tetrahedral cryptospore tetrads. “Spore development” tracks the transition from charophytic spore formation to embryophyte sporogenesis, as recorded in cryptospore polyad topology (see Strother and Taylor 2018).

tetrahedral forms classified as *Rimosotetras* Burgess are morphologically very similar to *Tetraedraletes*, and these are known throughout the entirety of the Ordovician. In a phylogenetic way of thinking, the presence of Ordovician cryptospores that are known to occur in Lochkovian land plant sporangia acts as a proxy for the existence of embryophytes in the Ordovician. However, as pointed out more recently (Strother and Taylor 2018; Strother and Foster 2021), in an evo-devo scenario, isometric spore tetrads, strictly speaking, are proxy evidence for the canalization of an embryophytic form of meiosis (sporogenesis) – not of the existence of the full developmental toolkit that is the genomic basis of embryophytes *per se*. It is entirely possible, even likely, that the first true plant spores/cryptospores were produced in a sporangium that was not attached to an axial sporophyte. This provides a rational basis for why axial plant stems are missing from the subsequent Ordovician rock record. Intriguingly, the single example of an Ordovician (Katian) sporangium (Wellman et al. 2003) shows precisely that – spore masses attached to partial coverings of amorphous organic matter.

Beginning in the Hirnantian, palynological assemblages of non-marine provenance contain scraps of cuticle and a range of tubular organic macerals (*Laevitubulus* and *Porcatitubulus*) (Burgess and Edwards 1991), which have long been considered to be remains of the problematic group Nematophyta Strother (1993). Nematophytes from Lochkovian strata are now considered to be possible lichens (Edwards et al. 2018), and a fungal ecology (Hueber 2001) and physiology (Taylor and Wellman 2009) for these organisms has been proposed. The ties to fungi are very tenuous, however, particularly when it comes to dispersed tubular macerals – none of which possesses any tangible fungal synapomorphies. Niklas and Smocovitis (1983) considered macerated nematophytic thalli of Llandovery age to be conducting cells of a pre-vascular embryophyte, and a recent FTIR analysis of *Nematoplexus* from the Rhynie Chert (Loron et al. 2023) indicated that the organic composition of this Devonian nematophyte reflected a land plant over fungal affinity. An evo-devo model of sporophyte assembly would predict that such isolated tubular macerals are some form of “proto” tracheary elements – apoptotic fluid-conducting cells. The genomic basis for this cell type was later incorporated into the embryophyte genome, where it formed the basis of conducting cells in the developing sporophyte axis.

## Conclusions

The origin of land plants is one of only four cases of the *de novo* origin of complex multicellularity that was achieved through embryonic development (Sebé-Pedrós et al. 2017). As such, it represents an evolutionary transition that was much more complex, and fundamentally different, than any other node in the phylogeny of the Streptophyta, because this transition includes the evolution of development in plants. Fossils which can be traced back to their developmental origin can provide clues about the nature and timing of this evolutionary transition, and the Ordovician is an important

time segment in this regard. If our assumptions about the charophycean affinity of the Cambrian and Early Ordovician cryptospore record are correct (Strother and Foster 2021), then the arrival of tetrahedral cryptospores during the Middle Ordovician is not a record of land plant origins, but is instead an indication of the canalization of meiosis in plant embryogenesis. The reason we do not find plant axes in any Ordovician strata is because the shoot apical meristem (SAM), which is responsible for building a plant stem, did not evolve until the Silurian. This does not, however, preclude the possibility of a thalloid flora at a bryophyte (liverwort) grade of morphological complexity living in a subset of terrestrial settings during the latter half of the Ordovician. The overall similarity, based on wall ultrastructure and morphology, between Ordovician cryptospore dyads and tetrads with similar Silurian taxa supports such a conclusion. However, other likely features of plant development found as fossils, such as dispersed cuticles and proto-tracheary elements, do not appear until very near the end of the Ordovician. This would seem to indicate that the genomic assembly of the embryophytes continued well into the Silurian, culminating in the evolution of the apical meristem and subsequent axial growth by the Wenlock. The Ordovician is a time of cryptospore evolution, but the plant thalli that bore these spores have yet to be recovered in Ordovician strata.

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# Ichnogenus *Trypanites* in the Ordovician of Estonia (Baltica)

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### ABSTRACT

*Trypanites* is a common boring in Ordovician hardgrounds of Estonia (Baltica). The depth of the sedimentary basin and sedimentation rates controlled the distribution of *Trypanites*. The trace-makers' community was diverse and changing over time. Three ichnospecies of *Trypanites* can be distinguished: *T. sozialis*, *T. weisei* and *Trypanites* isp. All three morphotypes can be recognized in the same hardground. It is impossible to distinguish between the different ichnospecies based only on the size of the boring aperture. The depth of early lithification of the seafloor determines the morphological variability seen in *T. sozialis*. The occurrence of elongated borings, such as *T. weisei* and *Trypanites* isp., is related to tropical environments, and their trace-makers strongly preferred substrates with a homogeneous and dense texture. The texture and available volume of hard substrate controls the ichnodiversity of *Trypanites* ichnospecies.

### Introduction

*Trypanites*, a macroboring developed in fully lithified substrates, is common in the Palaeozoic of Baltica. This ichnogenus has been recognized in the Cambrian and has a wide distribution in Ordovician and Silurian carbonate hardgrounds and biogenic substrates (see Toom 2019 and references therein). Five *Trypanites* ichnospecies are regarded as valid. *T. weisei* Mägdefrau, 1932 (the type ichnospecies of *Trypanites*) from the Middle Triassic is more or less straight, oriented perpendicularly to the substrate surface, and has a length/diameter ratio of ca 20–50 (Knaust et al. 2023). *T. solitarius* (Hagenow, 1840) was described from Cretaceous biogenic substrates (Wisshak et al. 2017) and is the smallest (diameter much less than one millimetre) and a relatively long, simple, tubular boring, characterized by a winding course. *T. fosteryeomani* Cole and Palmer, 1999 was erected from Jurassic sediments and is the largest *Trypanites* ichnospecies. *T. mobilis* Neumann et al., 2008 occurs within subspherical bioclasts of Cretaceous to Palaeocene deposits. *T. sozialis* Eisenack, 1934 from the Ordovician and Silurian of Baltica is a short, straight or inclined boring with a small (0.5–15) length/diameter ratio (Knaust et al. 2023).

During the Early Palaeozoic, Estonia was covered by a shallow epeiric sea. Cool-water siliciclastic sediments were deposited in the Cambrian and Early Ordovician. The Middle and lowermost part of the Upper Ordovician succession was deposited in cool- and temperate-water environments and is characterized by a highly condensed succession of carbonates (e.g., Jaanusson 1973; Dronov and Rozhnov 2007). The upper part of the succession is characterized by warm-water carbonates. The sedimentary basin was influenced by changes in sea level, climate, and depositional conditions. The sediments of northern Estonia represent shallow-water settings and those of southern Estonia deeper-water settings (e.g., Nestor and Einasto 1997). Hardgrounds and omission surfaces are numerous and occur frequently. The main impregnation types are pyritic and phosphatic (Põlma 1982; Saadre 1992). Many of the hardgrounds are traceable for considerable distances and are used as markers for the separation of different stratigraphic units.

The aim of this work is to summarize and discuss the distribution patterns of *Trypanites* in the Ordovician of Estonia (Baltica).

### Materials and methods

The study used palaeontological and lithological collections housed at Tallinn University of Technology (GIT) and the University of Tartu. To avoid problems

related to the biogenic substrates, such as symbiotic structures or morphology of borings determined by the skeletal architecture of the host, only *Trypanites* borings from lithic substrates were investigated. A classical method of cutting and polishing rock faces was used to enhance the visibility of borings. Computed tomography (CT) was used to visualize borings hidden inside rocks. Measurements of the length/diameter ratio allowed us to determine borings on the ichnospecies level. Fiji image analysis software (<https://imagej.net/Fiji>) was used to measure specimens from calibrated digital photos. CT scanning was carried out at the Geological Survey of Finland using the GE phoenix v|tome|x s scanner.

The Supplementary material consists of measurements of boring apertures and length-frequency diagrams, it is available at SARV: Geoscience Data Repository (DOI 10.23679/516). Supplementary material 1: Väike-Pakri hardground, Dapingian, cold-water carbonates and Vasalemma hardground, Katian, tropical grain supported carbonates. Supplementary material 2: Sutlema hardground, Katian, pure tropical carbonates.

## Results and discussion

The most common macroboring in Ordovician lithic substrates of Estonia is *Trypanites*, which is recorded from the Tremadocian to the Katian upper boundary. Hardgrounds typically develop in hydrodynamically active shallow environments with low sediment accumulation rates or periods of non-deposition (Christ et al. 2015) and provide a favourable environment for the borers. *Trypanites* occurs in northern Estonia, represented by the shallowest part of the sedimentary basin characterized by a highly condensed succession.

Carbonate hardgrounds from climatically different environments demonstrate a high variability in aperture size and boring depth within a given sample, locality, or stratigraphic unit. Measurements of the length/diameter ratio allowed us to determine borings on the ichnospecies level. Three different morphotypes of *Trypanites* are represented: shallow *T. sozialis*, long *T. weisei*, and course-changing undulating *Trypanites* isp.

*T. sozialis* (Fig. 1A–G, I, O–T) is most abundant, with the earliest finds in the Tremadocian (Fig. 1Q) and the youngest occurrence in the Katian at its upper boundary (Fig. 1T). It occurs in cool-water siliciclastic sediments; in cool, temperate, and warm-water carbonates with coarse-grained and fine-grained textures. The borings demonstrate a high variation in length and diameter (Fig. 1B–D, F, O), but a length/diameter ratio of less than 15 (see Knaust et al. 2023). The trace-maker of shallow *T. sozialis* penetrates bioclasts (Fig. 1F), but may change its boring direction (Fig. 1R, S) to accommodate for variations of the hard substrate. The shape of the borings can be slightly conical, their termination pointed or proboscis-shaped, and some borings demonstrate a slightly enlarged lower portion (Knaust et al. 2023). Specimens from cool- and temperate-water environments (Fig. 1B–D) have a smaller length/diameter ratio than borings from warm-water settings (Fig. 1F, I, N, O). This higher variability is related to slower sedimentation rates (Fig. 1B, C), with these

surfaces separating different lithologies or stratigraphic units (Fig. 1F, N, O).

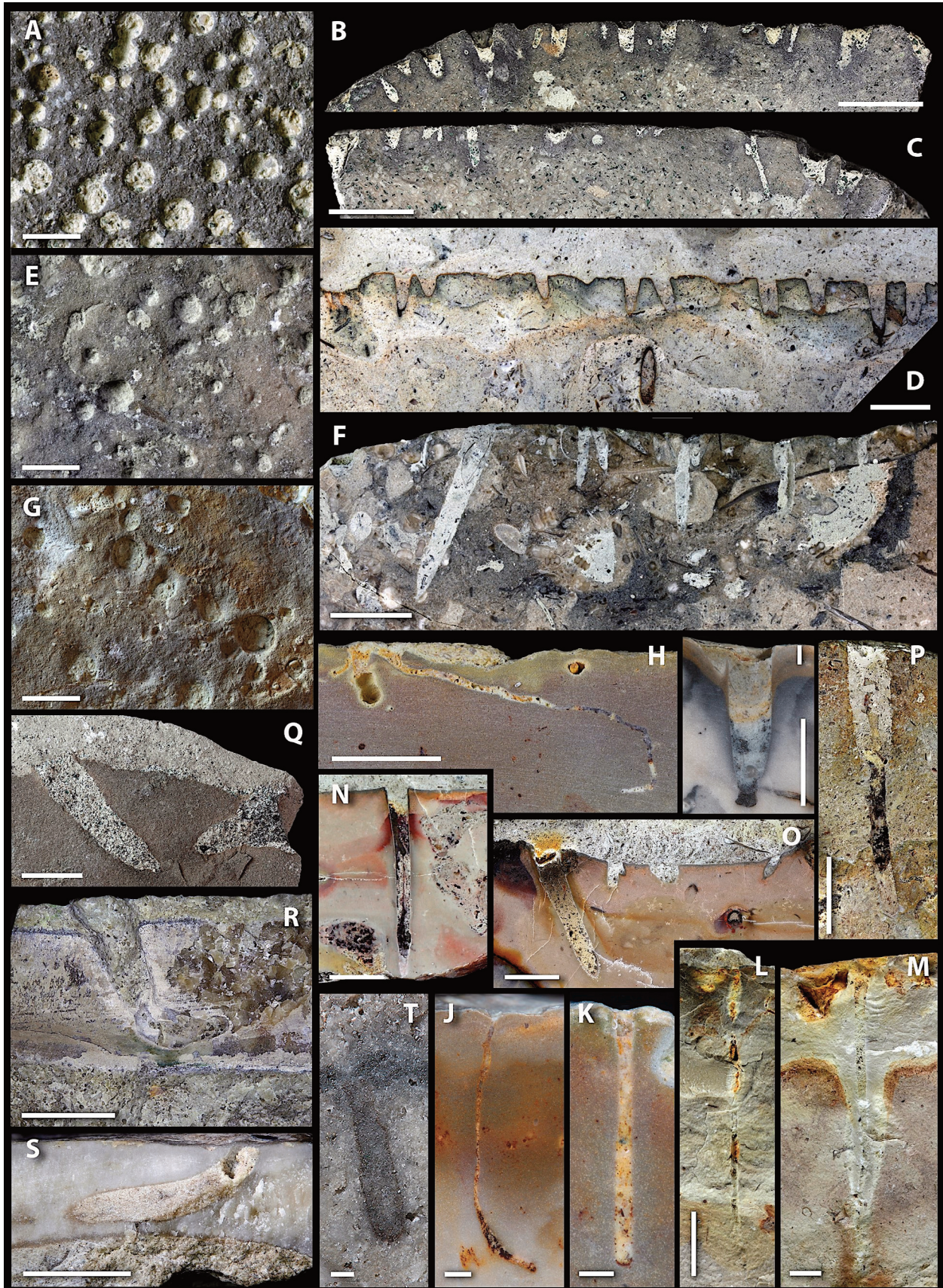
All records of *T. weisei* (Fig. 1K–M) come from the Katian pure tropical carbonates with a very fine texture. The borings are recognizable in a hardground separating the Saunja and Kõrgessaare formations (fms) of the Nabala and Vormsi stages. In addition, the three hardgrounds from the Oandu and Vormsi stages contain *Trypanites* borings with a length/diameter ratio larger than 15 (Figs 1P, 2A, B).

The boundary beds of the Nabala and Vormsi stages (Saunja and Kõrgessaare fms) demonstrate tubular borings with a changing course, small diameter (far less than 1 mm) and a high length/diameter ratio (Fig. 1H, J). This morphotype differs from *T. weisei* in its changing course and small diameter. The borings resemble *T. solitaria*, but due to their presence in lithic instead of biogenic substrate, we currently do not assign it to that ichnospecies.

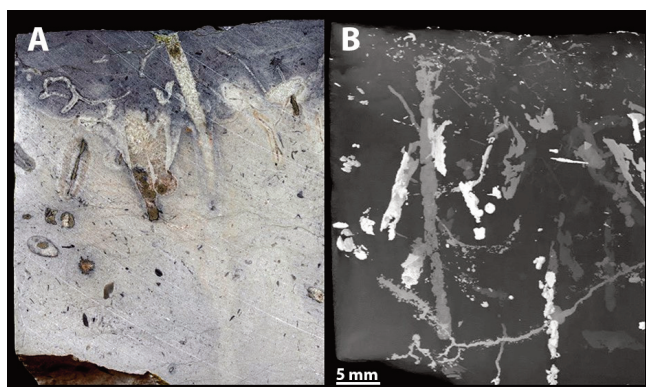
It should be emphasized that all three morphotypes of *Trypanites* are recognized in the same hardground (Fig. 1H–J, M). It is generally assumed that variation in boring diameter suggests several colonization stages of one and the same trace-making species (e.g., Kobluk and Nemcsok 1982; Nield 1984). The length-frequency diagrams of Estonian *T. sozialis* apertures measured in hardgrounds of the cold-water environment with extremely low sedimentation (Suppl. material 1, Väike-Pakri hardground) and in tropical grain-supported carbonates (Suppl. material 1, Vasalemma hardground) show a bimodal distribution and it allows us to assume that more than one species of borers was involved. The diagram of pure tropical carbonates with three *Trypanites* ichnospecies is not following a normal distribution curve (Suppl. material 2, Sutlema hardground). The Estonian hardground material demonstrates that it is impossible to distinguish between different ichnospecies based on the size of their apertures. Since the diagrams do not show a regular distribution, it is likely that a diverse group of bioeroders was responsible for substrate colonization.

The Ordovician was a period of extensive early cementation occurring near the sediment-seawater interface on shallow-marine seafloors (Palmer and Wilson 2004). Early cementation depends on several prerequisites. In the Baltic basin, cyanobacterial films covering sediments played the leading role in the rapid development of hardgrounds in cold- and warm-water sediments (Rozhnov 2018). Borers are the first inhabitants of the hard substrate. *T. sozialis* demonstrates deviations from the direction (Fig. 1R, S), the conical shape and expanded terminations of borings (for details, see Knaust et al. 2023). The trace-makers of *Trypanites* are highly selective in their choice of substrate and are strongly controlled by the hardness and extent of the substrate (e.g., Kobluk and Nemcsok 1982; Nield 1984; Kočová Veselská et al. 2021). More likely, deviations from the normal boring shape are trace-makers' reactions to a decrease in the hardness of the substrate and the volume, and depth of early lithified seafloor determined the high variability of *T. sozialis*.

The finds of elongated borings from the Ordovician of Estonia (*T. weisei* and *Trypanites* isp.) are related to tropical environments and their trace-makers strongly preferred substrates with a homogeneous and dense texture.



**Fig. 1.** *Trypanites* from the Ordovician of Estonia. **A-G, I, N-T** – *T. sozialis* Eisenack, 1934; **A-C** – cool-water carbonates of the Toila Formation (Fm), Dapingian, GIT 381-595, Väike Pakri; **D** – cool-water carbonates of the Vao Fm, Darriwilian, GIT 858-1, Keila River; **E, F** – coarse-grained tropical carbonates of the Pääsküla Member, Katian, GIT 362-95, Vasalemma; **T** – upper boundary of the Adila Fm, Katian, GIT 362-889-2, Reinu quarry; **I, N, O** – pure tropical fine-grained carbonates of the Saunja Fm, Katian; **I** – GIT 881-2-3, Sutlema; **N, O** – GIT 858-2, Aulepa; **Q** – siliciclastic sediments of the Türisalu Fm, Tremadocian, GIT 858-8, Tallinn; **R** – bioclast from the Pakri Fm, Darriwilian, GIT 426-707-1, Muraste; **S** – fragment of coral from the Kõrgessaare Fm, Katian, GIT 520-256-1, Saxby; **K-M** – *T. weisei* Mägdefrau, 1932 in pure tropical fine-grained carbonates, Saunja Fm, Katian; **K** – GIT 881-9-4; **L** – GIT 881-1-2; **M** – GIT 881-1-1, all from Sutlema; **P** – *T. sozialis* overprinted by *T. weisei*, Kõrgessaare Fm, Katian, GIT 362-865, Sutlema; **H, J** – course-changing *Trypanites* isp. in pure tropical fine-grained carbonates of the Saunja Fm, Katian; **H** – GIT 881-9-3; **J** – GIT 881-17-5, both from Sutlema. Scale bars for **B-F, L, M** = 1 cm; **E, G-I, N, O** = 5 mm; **J, K, T** = 1 mm.



**Fig. 2.** Pyritized hardground with *Trypanites weisei* Mägdefrau, 1932, GIT 362-587, Äiamaa drillcore, Katian. **A** – image of vertical section; **B** – X-ray computed tomography 3D reconstruction.

Seawater chemistry and temperature control lithification, and appropriate water temperatures ensure a sufficient supply of carbonate minerals for cementation (Flügel 2010: subtropical and tropical shallow waters, supersaturated with calcium carbonate, contribute significantly to rapid cementation) and it enhanced the formation of surfaces with suitable thickness for the elongated *Trypanites* borings.

## Conclusions

The primary controls on the occurrence of *Trypanites* in the Ordovician of Estonia (Baltica) are the depth of the sedimentary basin and the sedimentation rate. The trace-makers' community was diverse and has changed over time. The texture and volume of the hard substrate controlled the ichnodiversity of *Trypanites*.

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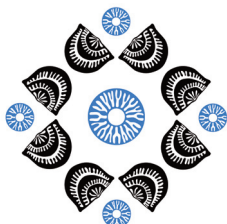
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# Parasite-induced shell damage in brachiopod *Porambonites* (*Porambonites*) *laticaudata* from the Late Ordovician (Sandbian) of Estonia

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## ABSTRACT

A new type of shell damage has been described in Ordovician brachiopods in *Porambonites* (*Porambonites*) *laticaudata*. There is a pair of small pits with somewhat different outline in the shell surface at the anterior commissure of the brachiopod. These pits are oriented in lateral direction, about 40° from the direction of the sulcus on the anterior commissure. Previously known shell damage has resulted from failed predatory attacks by durophagous predators and differ from the shell damage in *P. (P.) laticaudata*. The pits in the shell margin are most likely the result of shell malformation caused by the presence of symbionts. It is plausible that the symbionts of the *P. (P.) laticaudata* benefitted from inhalant currents and were cleptoparasites. The symbionts caused damage to the host brachiopod, which also suggests a parasitic relationship.

## Introduction

Shell damage is common in Palaeozoic brachiopods, whereas most of the shell damage has been interpreted as the result of failed predatory attacks. Damaged shells have been described in lower Cambrian lingulates (Walcott 1912; Zhang et al. 2011; Peel 2014) and Upper Ordovician rhynchonelliform brachiopods (Alexander 1986). Four distinct types of shell repair occur in Late Ordovician brachiopods (Alexander 1986). In addition to predators, parasites also caused malformations in brachiopod shell. The earliest parasite-induced structures have been described from lower Cambrian brachiopods (Bassett et al. 2004; Peel 2014). Macroscopic invertebrate symbionts in brachiopods are sometimes preserved as bioclastrations, which are among the best examples of symbiotic interactions in the fossil record (Bassett et al. 2004; Vinn et al. 2014). The fossil record of all parasitic associations has been analysed most recently by De Baets et al. (2021a, 2021b). Nevertheless, in contrast to predation, parasitic associations involving brachiopods remain poorly known and most evidence so far has been reported from the Palaeozoic (e.g., De Baets et al. 2021a, 2021b). The majority of research has focused on parasitic interactions in bivalve molluscs, with the earliest evidence dating from the Silurian to the Devonian (De Baets et al. 2011). These interactions became more diverse in the Mesozoic and Cenozoic (Huntley et al. 2021).

The aims of this paper are to: 1) describe a new type of shell damage in Ordovician brachiopods; 2) discuss the nature of shell damage; and 3) discuss the ecology of the possible parasitic association.

## Geological background

During the Sandbian, Baltica was located in the temperate climatic zone (Nestor and Einasto 1997; Torsvik and Cocks 2013). The lower Sandbian of Estonia is characterized by temperate carbonates (Dronov and Rozhnov 2007). The Kukruse



Regional Stage (RS; lower Sandbian) contains intercalation of limestone and carbonaceous oil shale (kukersite) layers of various thicknesses deposited on a carbonate platform in normal marine conditions. The Kukruse Age is characterized by a high diversity of both macro- and microfauna in Baltoscandia (Kaljo et al. 2011). Kiipli et al. (2010) suggested that the rise in bioproduction during the Kukruse Age was associated with regional seawater circulation and coastal upwelling. *Porambonites* (*Porambonites*) *laticaudata* was first described from the Kukruse RS (Bekker 1921). The specimen with shell malformation was collected from the Kukruse RS of the Estonian Oil Shale Basin, but its accurate locality is unknown.

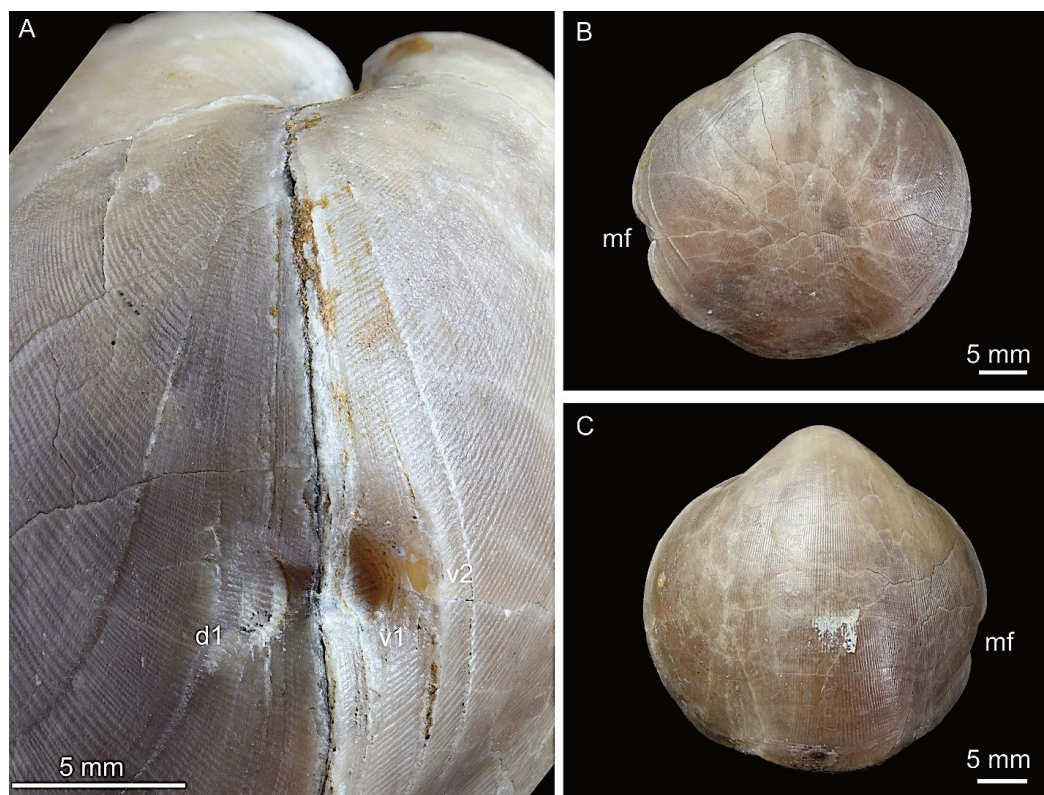
### Materials and methods

Collections 408 (TUG) and 188 (GIT) of *Porambonites* brachiopods from the Kukruse RS, NE Estonia, were searched for signs of bioerosion and shell damage. Only one brachiopod (0.17 %) from the Kukruse RS showed shell damage and no signs of bioerosion were detected. The brachiopod with shell damage was cleaned and photographed with a digital camera (Canon EOS 5DSR). The shell damage was photographed using an apochromatic zoom system Leica Z16 APO. The measurements of the shell damage were obtained from calibrated high-resolution photographs. The studied collections are housed at the Natural History Museum, University of Tartu (TUG), Department of Geology at Tallinn University of Technology (GIT), Estonia, except for the specimen of a figure with shell malformation (Fig. 1), which is deposited at Paleontological Museum of

St. Petersburg State University (Russia), with collection number PMSPU 110-1.

### Results

There is a pair of pits (2.4 and 2.5 mm in diameter) in the shell surface at the anterior commissure of the brachiopod *Porambonites* (*Porambonites*) *laticaudata* Bekker (Fig. 1), but they do not form a mirror image. The pit in the ventral valve has an elliptical outline and its walls are equally steep around its perimeter. There is another less developed and shallower pit slightly posterior to the elliptical one in the ventral valve. The pit in the dorsal valve has a slightly crescent-shaped or semicircular outline with a steep and sharp edge near the commissure, and its bottom on the other side is almost flush with the shell surface. The brachiopod is 36.3 mm high and 37.1 mm wide, corresponding to the size of adult specimens of this species. The dimensions of *P. (P.) laticaudata* in the GIT collection range from 26.3 × 28.4 mm to 42.5 × 45.4 mm. The pits are oriented in lateral direction, about 40° from the direction of sulcus on the anterior commissure. The pits are located almost exactly opposite each other in the ventral and dorsal valves. Both larger pits are about 2 mm deep. The shell surface inside the pits is covered with costae and has a normal appearance besides forming a depression. There is no sign of shell breakage associated with the pits. The frontal edges of the pits are 1.0 mm and 0.5 mm away from the anterior commissure. The anterior commissure is laterally invaginated at the pits. The invagination of the commissure is about 5 mm long and 2 mm deep. The invagination is broad, V-shaped, with a rounded terminus.



**Fig. 1.** Shell malformation (mf) in the brachiopod *Porambonites* (*Porambonites*) *laticaudata* from the Sandbian (Kukruse Regional Stage) of the Estonian Oil Shale Basin. **A** – detailed view of two malformations on both sides of the commissure: v1 – large elliptical pit, v2 – small shell deformation, d1 – large pit; **B** – ventral valve; **C** – dorsal valve.

## Discussion

### Comparison with predatory shell damage in Palaeozoic brachiopods

Scalloped valve damage in brachiopods displays a ‘micro-escarpment’ that is anteriorly or laterally concave to straight but concentrically discontinuous (Alexander 1986). Scalloped valves sometimes have arched fractures positioned contiguously around the former commissure (Alexander 1986). The shell damage in *Porambonites* (*Porambonites*) *laticaudata* has an outline somewhat similar to some scalloped shell damage (Alexander 1986, 275, fig. 3.1–3) but differs in the lack of shell fracture and in the opposite morphology of the pits, where the steepest slope is the anteriormost one. The cleft type of valve damage in brachiopods has a common direction, which is usually approximately parallel to the costae (Alexander 1986, 276, fig. 5). The matching slits in both valves narrow posteriorly and resemble somewhat the lateral invagination in both valves of *P. (P.) laticaudata*, but the latter lacks a slit. Divoted valve damage in brachiopods displays parabolic to chevron-shaped fractures which outline a roughly triangular area of resecreted shell surface that is depressed below the surface posterior and lateral to the fracture (Alexander 1986, 276, fig. 4). The divoted valve damage is least similar to the morphology of the shell damage in *P. (P.) laticaudata*. There is also an embayed type of valve damage in Ordovician brachiopods, which display a meandering or zigzag fracture that outlines a jagged piece of the valve surface that was removed and resecreted (Alexander 1986, 277, fig. 6). The latter damage has no resemblance to the shell damage in *P. (P.) laticaudata*. All shell damage listed above has resulted from failed predatory attacks by durophagous predators and differ from the shell damage in *P. (P.) laticaudata* in the presence of a fracture. Thus, it is unlikely that the shell damage in *P. (P.) laticaudata* was induced by durophagous predators. One should also explore the possibility that such shell damage could result from drilling predation. However, the studied shell damage shows no sharp boundaries characteristic of the drill holes and their elliptical to crescent-shaped outline is also alien to typical drill holes. We can also exclude spontaneous tissue damage, as the resulting shape of shell damage would have had less depth and most likely a more slit-like morphology as well. Mechanical tissue damage (e.g., temporary detachment of mantle) is also unlikely, as it would result in re-attachment of the mantle and the start of a new shell layer, which would leave sharper boundaries, different patterns in ornamentation and cross-sectional profile, and is often associated with a slit-like opening in bivalves.

### Comarginal parasites

The described structures are most likely the result of interference of shell secretion and associated shell malformation caused by the presence of symbionts (compare Kinne (1983) and Mironenko (2016) for cases of modern and fossil shell-secreting molluscs), as there is no indication of shell breakage that would point to predators. Similar shell damage without shell breakage is known from Cambrian brachiopods, where

parasitic epibionts attached to the inside of the commissure produced globose callosities and V-shaped invaginations in the growing margin (Peel 2014). Deep, V-shaped invaginations occur commonly in the comarginal growth ornamentation of larger lingulate brachiopod (*Botsfordia*) specimens from the lower Cambrian of Greenland, but the overall lack of fractures transgressing growth lines indicates that these were not caused by breakage (Peel 2014, 153, fig. 3D, K, N). Similar structures are also present in *Diandongia* Rong from the Cambrian of Southwest China (Zhang et al. 2011, fig. 2C, D) and in *Botsfordia pulcher* Matthew from the middle Cambrian of New Brunswick (Walcott 1912, pl. LXII, fig. 5i). In addition to brachiopods, similar marginal invaginations occur in the operculum-like *Mobergella holsti* (Moberg) from the lower Cambrian of Sweden (Bengtson 1968, fig. 16B). The lack of shell breakage makes these structures similar to the ones in *P. (P.) laticaudata*, but the elliptical shape of the pits in the latter does not resemble the shape of the shell damage in lower Cambrian *Botsfordia* from Greenland or in other Cambrian brachiopods. Thus, the shell damage in *P. (P.) laticaudata* was likely made by a different organism than the damage in Cambrian lingulates and *Mobergella*. It is also more discrete and rarer than other malformations reported in brachiopods and attributed to disease (Zong and Gong 2022). Zhang et al. (2020a) described a drilling in a rhynchonelliform brachiopod from the Katian of Central China. Even if we cannot see inside the shell damage in *Porambonites*, it differs from drillings (e.g., Deline et al. 2003) in not being smooth (ornamentation present), in the larger size, the clear inward deflection of the shell material and the presence of the deformations on both valves.

Encrusting worm-like organisms on brachiopods have been interpreted as cleptoparasites as early as stage 4 of the Cambrian (Zhang et al. 2020b), but these interactions were much more numerous (47.79% of the 429 sampled brachiopods were encrusted). Worm-like organisms have also been implicated in various other brachiopod shell deformations or internal structures in the Palaeozoic (Chatterton 1975; Basset et al. 2004; Baliński and Sun 2010; Vinn et al. 2014), as well as in the Mesozoic (Kiel 2008) or modern brachiopods (Rodrigues 2007).

The shape and depth of the pits in *P. (P.) laticaudata* indicates that the trace maker was likely not a worm-like animal which would have needed a deeper hole, but something similar to a small sea anemone in the body plan. If the trace maker fed on small food particles in sea water, it could have benefitted from the feeding currents of the host brachiopod. Based on the ecological studies of modern brachiopods, it is now commonly accepted that brachiopods have separate inhalant and exhalant feeding currents (LaBarbera 1984). The inhalant water currents are located on both sides of the shell, and the exhalant water current is located in the central part of the shell. Thus, it is possible that the symbionts of the *P. (P.) laticaudata* benefitted from inhalant currents and were cleptoparasites, as suggested for Cambrian worm-like encrusters (Zhang et al. 2020b). The symbiont-caused damage to the host brachiopod suggests also

parasitic relationship. As the culprit remains unknown, but all points to a parasitic interaction, with support for negative effects on the afflicted individual, we assign it to category 3 (i.e., the symbiont caused definite harm to the host, but it may have also been beneficial to the host in other ways) in the sense of the De Baets et al. (2021a).

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# Ordovician stratigraphy of the Junee–Narromine Volcanic Belt in central New South Wales, Australia: conodont studies and regional correlations

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### ABSTRACT

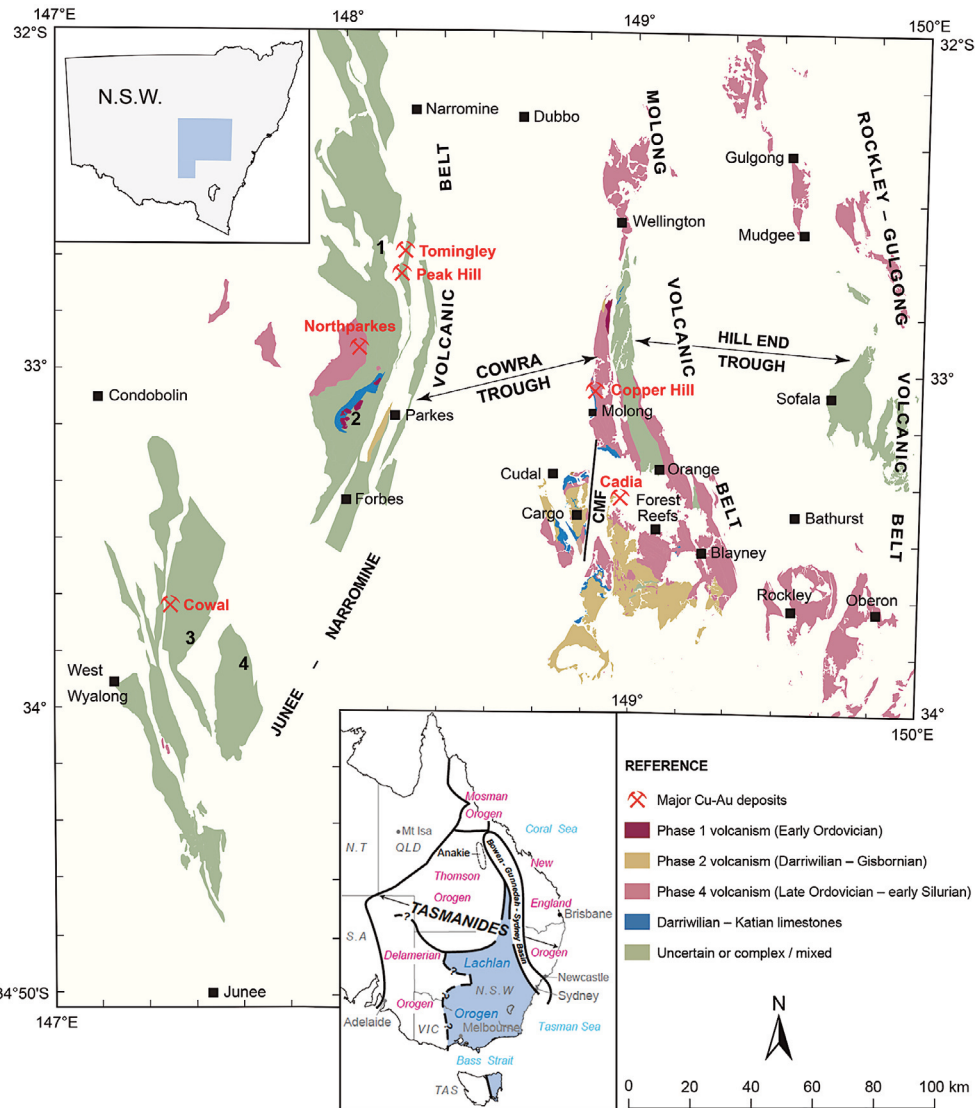
This contribution reviews the newly revised biostratigraphy of Middle–Upper Ordovician marine shelf successions from the Junee–Narromine Volcanic Belt in central New South Wales, based on conodont studies from four areas covering the northern, central and southern sectors of the Belt. Seven conodont biozones ranging from the middle Darriwilian (*Histiodella holodontata*–*Eoplacognathus pseudoplanus* Biozone) to the lower Katian (*Taoqupognathus blandus* Biozone) are recognized in the Billabong Creek Formation exposed in the Gunningbland area. This includes the first known biostratigraphic succession in Australia that extends continuously from the middle Darriwilian to the basal Sandbian. These new data are crucial for a better understanding of the geological evolution of this region in central New South Wales, and for the enhanced correlation of Ordovician rocks throughout the Macquarie Volcanic Province, which hosts substantial porphyry Cu–Au mineral deposits.

### Introduction

In central-western New South Wales, the Ordovician to the earliest Silurian Macquarie Volcanic Province occupies the eastern part of the Lachlan Orogen (Fig. 1). It is characterized by a distinctive association of porphyry intrusions, mafic extrusive rocks and volcanoclastic rocks hosting several large porphyry Cu–Au deposits. The Macquarie Volcanic Province is subdivisible into three linear N–S oriented belts separated by contemporaneous deep-water quartz-rich clastic rocks of turbiditic origin. The Junee–Narromine Volcanic Belt (JNVB) is the westernmost belt and consists of >16 discrete igneous complexes within its ~200 km north–south strike (Fig. 1). Establishing a well-calibrated biostratigraphic and chronostratigraphic framework is essential for constraining the temporal and spatial distribution of these igneous complexes and their associated volcanic and volcanoclastic strata. Four magmatic phases are recognized within the Macquarie Volcanic Province (Percival and Glen 2007), with phases 3 and 4 in the Upper Ordovician hosting most of the economic mineralization and being the most prospective for further porphyry Cu–Au exploration (Glen et al. 2007; Zhen et al. 2022). Detailed study of the Ordovician biostratigraphy in the JNVB is crucial, as throughout most of the Middle and Upper Ordovician well-developed marine shelf sedimentary facies are in close association with volcanic facies (Simpson et al. 2005). During the Middle and Late Ordovician, the region now preserved as the JNVB was covered by a shallow tropical sea in which scattered volcanic islands were distributed. Carbonate sediments forming algal and coralline limestones were deposited on narrow shelves fringing the emergent volcanic edifices and were surrounded by siliciclastic sediments that extended offshore into turbidites and submarine fan systems of deep-water settings (Percival et al. 2023).

### Revised biostratigraphic framework

Our ongoing studies of the Ordovician conodont biostratigraphy within the JNVB focus on: 1) documentation of the Late Ordovician faunas recovered from an unnamed subsurface formation within the Mingelo Volcanics, intersected in several drill holes located immediately west and northwest of Peak Hill in the northern sector



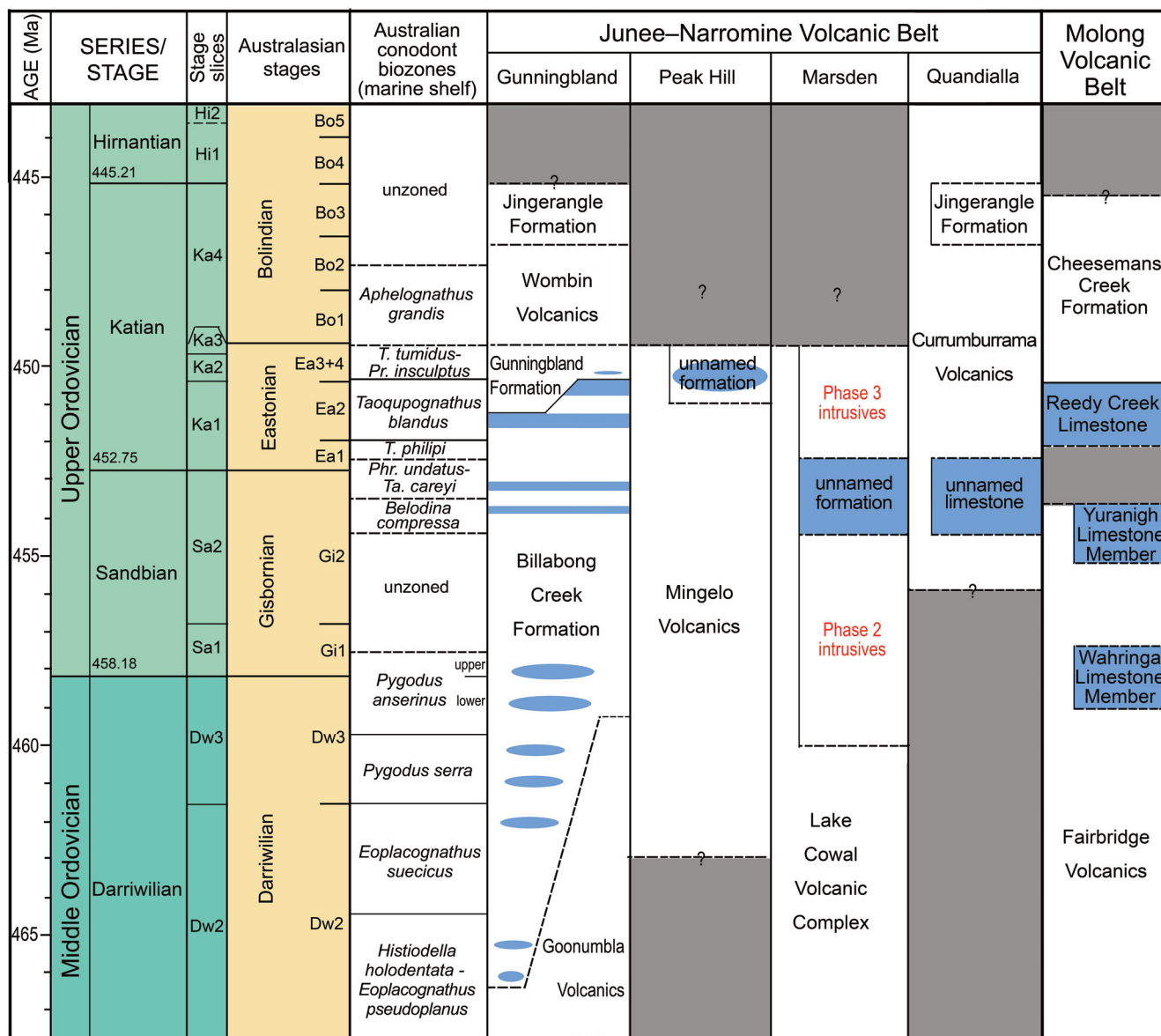
**Fig. 1.** Map of central New South Wales in eastern Australia showing the four study areas (1 – area immediately W and NW of Peak Hill, 2 – Gunningbland, 3 – Marsden prospect, and 4 – Quandialla) in the Junee–Narromine Volcanic Belt, the major mining sites of Ordovician porphyry copper–gold deposits, and distribution of Ordovician rocks in the three main volcanic belts of the Macquarie Volcanic Province that occupies the eastern part of the Lachlan Orogen (modified from Percival et al. 2023).

(Zhen et al. 2022); 2) re-examination of the Darrivilian and Late Ordovician conodonts from the Billabong Creek and Gunningbland formations in the Gunningbland area west of Parkes (Pickett and Percival 2001; Zhen and Pickett 2008; Zhen, Percival and Smith, unpublished new data); 3) study of limestones within the Lake Cowal Volcanic Complex in the Marsden prospect southeast of the Lake Cowal Gold Mine (Percival et al. 2006) and 4) investigation of a late Sandbian to earliest Katian conodont fauna recovered from an unnamed subsurface formation within the Currumburrama Volcanics of the Quandialla area in the southern sector (Zhen and Percival, unpublished new data). These studies have generated significant new data supporting regional correlations with much improved precision (Fig. 2). More specifically, seven conodont biozones from the middle Darrivilian to the lower Katian are recognized in the Billabong Creek Formation in the Gunningbland area, which represents the first biostratigraphic succession in Australia extending continuously from the middle Darrivilian to the basal Sandbian.

### Conodont biofacies

The Middle and Late Ordovician conodont assemblages are preserved in a range of depositional settings reflecting varying water depths. The middle Darrivilian conodont fauna is dominated by *Erraticodon balticus* (44.2%) and *Kirkupodus tricostatus* (36.7%), with *Protopanderodus* species being less common. Based on the abundance of *E. balticus* in the fauna, Zhen and Pickett (2008) interpreted it as representing a shallow-water near-shore facies, consistent with the lithology. Higher in the Billabong Creek Formation, late Darrivilian (Dw3) assemblages are dominated by *Periodon aculeatus* (43.2%), with less common *Pygodus* species (10.9%) and *Ansella robusta* (5.6%), indicative of deeper-water settings in the intermediate to distal shelf.

Upper Ordovician samples are dominated by the species of *Belodina* and *Panderodus*, which inhabited a range of water depths but tend to be more abundant in shallow-water shelf settings. However, the relatively common occurrence of *Phragmodus undatus* in several samples is significant, as this



**Fig. 2.** Correlation of the Middle–Upper Ordovician marine shelf carbonate (in blue) successions from the Junee–Narromine Volcanic Belt in central New South Wales with contemporaneous succession of the northern Molong Volcanic Belt between Molong and Wellington. For localities, refer to Fig. 1.

species characterizes the *Ph. undatus* biofacies, indicative of deep-water settings (Zhen and Webby 1995; Zhen and Percival 2017). This mixture of depth-dependent biofacies may reflect steep volcanic island gradients. In the Peak Hill district of the northern JNVB (Zhen et al. 2022), an early Katian conodont assemblage (*T. blandus* Biozone) has a much higher percentage (45%) of *Ph. undatus*, supporting a more off-shore deeper-water setting (*Ph. undatus* biofacies) for this fauna.

### Regional correlations

In the central sector of the JNVB, the Billabong Creek Formation has a maximum estimated thickness exceeding 320 m and is represented by discontinuous exposures in the Gunningbland area, located about 20 km west of Parkes (Fig. 1). Conodont studies confirm that this formation spans a stratigraphic interval from the middle Darriwilian to the lower Katian. Seven conodont biozones are recognized, from the early middle Darriwilian (*Histiodela holodentata-Eoplacognathus pseudoplanus* Biozone) to the earliest Sandbian (upper

*Pygodus anserinus* Biozone) age, and from the latter part of the late Sandbian (*Belodina compressa* Biozone) to the early Katian (*Taoqupognathus blandus* Biozone) age (Fig. 2). This conodont succession correlates precisely with the biozonation established in the Upper Ordovician of the Molong Volcanic Belt further east (e.g., Zhen and Webby 1995; Zhen et al. 1999, 2004) in central New South Wales, and in the Gordon Limestone Group of western Tasmania (e.g., Zhen et al. 2010; Zhen and Percival 2017).

In the northern sector of the JNVB, a conodont assemblage of early Katian age (*T. blandus* Biozone) and a succeeding coral and stromatoporoid assemblage, corresponding to the *Taoqupognathus tumidus-Protopanderodus insculptus* conodont Biozone of middle Katian age, were reported from carbonate intervals intersected in three drill holes immediately west and northwest of Peak Hill. These limestones represent the northernmost record of the fossiliferous Ordovician marine shelf successions currently known from the JNVB (Zhen et al. 2022; Fig. 2). In the southern sector of the JNVB,

Percival et al. (2006) reported a conodont assemblage of latest Sandbian to earliest Katian age (*B. compressa* to *Ph. undatus-Tasmanognathus careyi* Biozone) from a carbonate unit intersected in drill core sections located near Marsden, about 20 km SSE of the Lake Cowal Gold Mine (Fig. 1). A Late Ordovician (late Sandbian, *B. compressa* Biozone) conodont assemblage was recently found in a carbonate unit intersected in drill hole CBMD006 located near Caragabal, about 20 km further SE (Zhen and Percival, unpublished new data).

## Conclusions

The refined biostratigraphy of carbonate facies within the Billabong Creek Formation in the Gunningbland area west of Parkes comprises seven conodont biozones within a stratigraphic interval extending from the middle Darriwilian (*Histiodelia holodentata-Eoplacognathus pseudoplanus* Biozone) to the lower Katian (*Taoqupognathus blandus* Biozone). This includes four successive conodont biozones representing the first biostratigraphic succession in Australia that extends from the middle Darriwilian to the basal Sandbian. New biostratigraphic data from several Ordovician units, including the Northparkes Group, Mingelo Volcanics, Lake Cowal Volcanic Complex, and Currumburruma Volcanics, provide much improved precision for their correlation within phases 2 and 3 in the mineral-rich Macquarie Volcanic Province. This study contributes to an enhanced understanding of the geological evolution of the Macquarie Volcanic Province by interpreting the interplay between volcanic activity and carbonate deposition.

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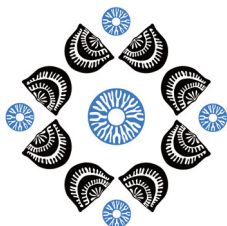
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# Age of the Ordovician sedimentary succession in Lumparn Bay, Åland Islands, Finland

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Depression of the ancient Lumparn meteorite impact structure in the Åland Islands is partly infilled with the lower Palaeozoic sediments, lying presently below sea level. The Cambrian and Ordovician sedimentary cover is distributed in the area of 15 km<sup>2</sup>, with a total thickness of up to 70 m. The Ordovician carbonate rocks of this site, known by the erratic boulders and by the drilling project in the late 1950s, are particularly interesting because of the isolated distant position of this outlier from other distribution areas of the Ordovician sediments preserved in the Baltoscandian Palaeobasin. Ordovician sections in the Lumparn Bay are composed of two distinct lithological units. The older, argillaceous wackestone-packstone unit has been traditionally named 'Orthoceras limestone' or 'Orthoceratite Limestone', and the younger micritic limestone unit is addressed as 'Östersjö Limestone' (or 'Baltic Limestone').

Here we present new data on ostracod biostratigraphy and stable carbon isotope chemostratigraphy derived from three old drillcores from the Tranvik area of the Lumparn Bay. The comparison of ostracod distribution with its succession in Estonia generally supports the previous Darriwilian and Sandbian age interpretations for the Orthoceras Limestone. Considering the ostracod distribution together with earlier acritarch and conodont datings, stable carbon isotopic data and limestone lithology, the Orthoceras Limestone unit might correspond to the Kunda, Aseri, Lasnamägi, Uhaku, Kukruse, Haljala, and Keila regional stages (RSs). The Östersjö Limestone comprises almost the entire Katian, corresponding to the Rakvere, Nabala, Vormsi and Pirgu RSs in the Baltoscandian stratigraphic chart. The uppermost sample yielded the most abundant and diverse assemblage of ostracods that suggests it to correspond to the Vormsi or lower-middle Pirgu (late Katian) RSs.

The global Middle Darriwilian Carbon Isotopic Excursion (MDICE) and Guttenberg Carbon Isotopic Excursion (GICE) as well as the Katian Rakvere and Saunja carbon isotopic excursions are recorded in the studied succession. The  $\delta^{13}\text{C}_{\text{carb}}$  bulk rock curve of the Orthoceras Limestone shows a positive excursion up to 1‰ in the lower part of the interval followed by a negative excursion up to -1‰ in the middle part and another positive excursion reaching 2‰ in the upper part of the interval. This curve resembles well the carbon isotope curve from the Darriwilian and Sandbian in the core sections of the Hiiumaa Island, NW Estonia, and could be interpreted as the MDICE and the rising limb of the GICE.

The  $\delta^{13}\text{C}$  curve of the Östersjö Limestone interval shows two positive excursions. The lower one comprises most likely the peak of the Rakvere Excursion (Rakvere RS) in Estonia, which is also supported by the ostracod data. The upper carbon isotopic excursion may represent the Saunja Excursion correlated with the upper part of the Nabala RS.

The ostracod biofacies characterized by faunal associations of both the Orthoceras and Östersjö limestone units, and the lithological succession of these units suggest more similarities with the Estonian Shelf facies (North Estonian Confacies) than Scandinavian Basin facies of the Baltoscandian Palaeobasin.





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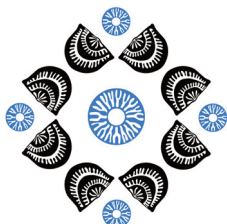
Late Ordovician, Prague Basin, cephalopod,  
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# Three-dimensionally preserved siphuncle in an actinoceratid cephalopod from the late Katian of Bohemia

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The Ordovician to Carboniferous cephalopods of the order Actinoceratida (Teichert, 1933) are distinguished from all other cephalopods by their large siphuncles, which typically contain heavy, calcareous deposits enclosing a complex system of canals. These peculiar structures were already recognised in the 19th century, but it was only in the 20th century that they were properly described and interpreted in a more systematic manner with respect to the phylogeny and palaeoecology of the group. In the present study, we investigate a uniquely preserved actinoceratid cephalopod from the late Katian part of the Králův Dvůr Formation (Prague Basin, Central Bohemia), in order to address the magnificent works of C. Teichert, R. H. Flower, M. Wade and H. Mutvei. The specimen, tentatively assigned to the ormoceratidan genus *Adamsoceras*, consists of four isolated fragments of the siphuncle (nine siphuncular segments) and small remains of phragmocone chambers. All original calcareous parts of the conch were dissolved during diagenesis and fossilisation processes, while the spaces left by decayed soft tissues were filled with pyrite (secondarily converted into limonite). In other words, the specimen is a cast of the axial canal, radial canals and perispatium, plus some remains of phragmocone chambers. Cavities inside the cast mirror the shape of dissolved endosiphuncular deposits and ectosiphuncle; nothing is preserved of the outer shell wall and septa. The remains of phragmocone chambers are diagenetically flattened, but the siphuncle is undeformed, supposedly because it was protected against compaction by the extensive endosiphuncular deposits and possibly by the filling of the endosiphuncular canals with pyrite.

The preservation of the specimen enabled the application of the micro-CT scanning. This non-destructive method has proved invaluable for studying fossils that cannot be otherwise studied using standard oriented sectioning. It also enabled the construction of a virtual model of the specimen, which facilitated the investigation of the siphuncular structure in 3D. Preliminary results show that the endosiphuncular deposits grew unevenly, resulting in highly irregular shapes and distribution of the radial canals, and an irregularly flattened form of the central canal. The flattening of the central canal is interpreted as reflecting the dorso-ventral plane of symmetry of the siphuncle. Furthermore, the endosiphuncular structures did not form symmetrically and their appearance depends on the selected median section. This suggests that the distinction between several types of endosiphuncular systems *sensu* Teichert and Flower and the taxonomy derived from these distinctions might be, at least in some actinoceratids, artificial, resulting from studying specimens in 2D median sections.

The studied specimen represents the only unequivocal actinoceratid from the Ordovician of the high-palaeolatitude Prague Basin. Since actinoceratid cephalopods were abundant during the Ordovician mainly in low-palaeolatitude carbonate environments, the presence of this specimen in the Prague Basin supports previous indications of a faunal connection between the high and low palaeolatitudes during the late Katian age.



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# Ordovician conulariid monospecific assemblages (Czech Republic, Morocco)

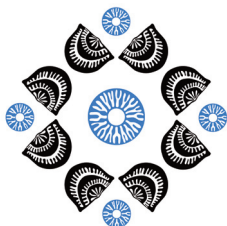
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A recently discovered locality of the Katian age near Erfoud (Morocco) supports an assumption that at least some conulariids lived preferably in monospecific associations. Thousands of skeletons belonging to *Archaeoconularia consobrina* (Barrande, 1867) were documented in an extensive accumulation within a 20 cm thick calcareous sandstone bed containing also rounded intraclasts of fine-grained sediments. The specimens are well exposed on the top surface of the bed due to weathering. The specimens have the same prevailing orientation throughout the entire bed. The preservation and distribution patterns of these conulariids suggest a parautochthonous origin of the accumulation that was likely deposited after a single, high water-energy event, such as a storm or turbidite flow.

The same taphonomic situation was recently described for *Anaconularia anomala* (Barrande, 1867) from a Sandbian site in the Czech Republic and for *Archaeoconularia* cf. *consobrina* (Barrande, 1867) in a different Sandbian site in Bohemia, Czech Republic. Thus, the monospecific conulariid assemblages with abundant specimens seem not to be exceptional. Such mass occurrences of conulariids are similar in (1) alignment of specimens along the prevailing current direction, (2) limited content of other faunal elements, and (3) the presence of intraclasts and the sandstone matrix. These taxa are interpreted as originally inhabiting an off-shore environment below the storm wave base, with erected skeletons firmly attached to the sandy bottom at some calm places, or more probably deeply anchored in sand with the apical part (similar mode of life has recently been shown in fan mussels, which are often accompanied by algae forming sea meadows). During a single catastrophic event, conulariid skeletons were first broken off. This resulted in prevalence of the rounded schott ending in the apical region of the specimens. The apertural endings, including lappets, were destroyed during rapid transport prior to final deposition as aligned monospecific mass accumulations.

It is worth noting that some localities, especially those in Morocco, yielded mass accumulations, with tests densely covered by diverse epibionts like brachiopods and edrioasteroids, while others are typified by undisturbed skeletons without attached epizoans or traces of attachment scars. All these taphonomic and palaeoecological aspects, as well as association with mass occurrences of algae, are subject to further study.



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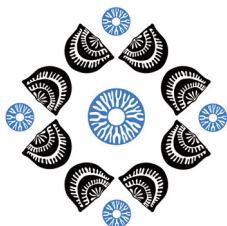
Upper Ordovician, fossil assemblages,  
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# Subway into the Ordovician (Prague Basin, Czech Republic)

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In the Late Ordovician, the Prague Basin was located at the high-latitude northwestern shelf of Gondwana. This period was characterised by profound environmental changes and ended by one of the most severe mass extinctions, which was caused by climatic changes. Although the end-Ordovician extinction is closely related to the Hirnantian glaciation, biodiversity started to decrease already in the late Katian. Decrease in temperatures and sea level drop are the main factors that affected these biodiversity changes.

During the last years, construction of the new subway line D in Prague has provided a unique opportunity to study different aspects of the Upper Ordovician and Silurian of the Prague Basin. These tunnels have provided detailed information about the succession of fossil assemblages, facies variability and actual thicknesses of the upper Katian and Hirnantian formations (upper part of the Bohdalec, and entire Králův Dvůr and Kosov formations) in this part of the basin.

Our study is based on material and data from several sites. We studied drill cores from vertical boreholes drilled from the surface and also horizontal boreholes drilled from the tunnel faces. The richest material came from an interim storage of excavated material near pitheads. In total, almost 700 m of sections in the tunnels were investigated. As the preliminary geological exploration was carried out by various companies in connection with subway construction, intensive excavation and mining took place in several locations at the same time, and the frequency of our research activities and site visits were limited. Therefore, our palaeontological and stratigraphical research was focused mainly on the Bohdalec Formation (upper Katian). The succession is, however, tectonised, apparently incomplete, and repetition of some parts cannot be excluded. The actual thickness of the investigated part of the Bohdalec Formation excavated so far is slightly less than 140 m (December 2022). The unit is dominated by fine-grained siliciclastics (dark grey shales and siltstones), except for the Michle Facies in the uppermost part of the Bohdalec Formation. This facies consists of calcareous sandstones alternating with siltstones and thin shaly interbeds. The section is regarded to be deposited in an offshore setting below the storm wave base.

The Bohdalec Formation in the studied section is fossiliferous, and the abundance of fossils and composition of their associations are variable. Some subsections are typified by reduced fossil content. However, we also recorded several stratigraphical intervals (a few metres in thickness) with distinctly enriched fossil assemblages, notably with echinoderms, bryozoans, cnidarians, planktic graptolites, and sessile dendroid graptolites that are extremely rare anywhere else. Deposits of these specific intervals accumulated during gradual slowdown periods during the subsidence of the Prague Basin, which resulted in a decrease in the sedimentation rate and were followed by uplift, causing local shallowing. Also, global events, such as climatic and sea level fluctuations, influenced these changes of fauna and facies.



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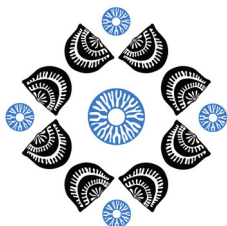
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# The ichnologic signature of deep-sea colonization during the Ordovician radiation

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The fossil record of deep-marine environments is notoriously poor in comparison with that of their shallow-marine counterparts. Notably, deep-marine deposits are typically host to diverse and abundant trace-fossil assemblages, providing evidence of the ancient deep-sea benthos. To analyze the early colonization of the deep sea, we constructed a global dataset of trace-fossil occurrences from a survey of Ediacaran–Devonian stratigraphic units. This analysis highlights the importance of the Ordovician radiation as a pivotal time in the colonization of the deep sea. Ediacaran deep-marine trace fossils consist of very simple trails and burrows. Global and alpha ichnodiversity, as well as ichnodisparity, were extremely low. Nonspecialized grazing trails reveal the exploitation of microbial mats. These strategies persisted in the Cambrian, although with an increase in ichnodiversity (both global and alpha) and ichnodisparity. An increase in the complexity of morphologic patterns, as illustrated by the undermat mining ichnogenus *Oldhamia*, is apparent during the Cambrian. The face of the deep sea started to change during the end of the Cambrian and beginning of the Ordovician with the protracted expansion of farming and trapping strategies. The main architectural designs of deep-marine trace fossils (e.g. regular networks, delicate spiral burrows, guided meandering graphoglyptids) were established in the deep sea by the Early Ordovician, recording the first appearance of the *Nereites* Ichnofacies. Lower to Middle Ordovician deep-marine ichnofaunas are moderately diverse, and fodinichnia commonly dominates rather than graphoglyptids. A significant ichnodiversity and ichnodisparity increase occurred in the Late Ordovician–early Silurian, with ichnofaunas recording higher proportions of graphoglyptids and evidencing the establishment of a deep-marine ecosystem of modern aspect. The distinction between the *Nereites* and *Paleodictyon* ichnosubfacies, with the former characterized by the dominance of feeding traces in muddy turbidites and the later by the dominance of graphoglyptids in sandy turbidites, can also be tracked back to the Ordovician radiation. This trend of increased colonization of the deep sea continued through all the Silurian and the Devonian. However, colonization of carbonate turbidites may have lagged behind that of siliciclastic turbidites. The progressive increase in abundance and diversity of graphoglyptids resulted in an increased role of gallery biodiffusers. This faunal turnover in the deep sea was coincident with an increase in oxygenation in slope and base-of-slope settings, which is thought to have been a driver of Ordovician biodiversifications. The formation of permanent open burrows in the deep sea may have increased bioirrigation in the uppermost zone of the deep-sea sediment, therefore increasing ventilation and potentially generating a feedback loop between bioturbation and oxygenation, with the endobenthos engineering its environment.



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# Chitinozoan nomenclature and databases

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In 1930, Alfred Eisenack suggested the term 'chitinozoan' for a microfossil group that he discovered from erratic boulders on the Baltic Sea coast. They are known from the Early Ordovician until the end of the Devonian and have a broad paleogeographic distribution in marine deposits. Even though they are useful biostratigraphy markers, their biological affinity is unknown. Several theories have been proposed through the years, with the most widely accepted to date being that they are the eggs of soft-bodied metazoans. Nevertheless, some studies suggest that chitinozoans are fossils of individual microorganisms (protists) rather than of metazoan origin.

The aim of this contribution is to summarize the advantages of the current chitinozoan classification and analyze the status quo of the current chitinozoan databases in order to make the classification less subjective and data more accessible.

Since the beginning of their study, chitinozoan workers have used a binominal taxonomy describing genera and species based on morphological features. In 1999, Florentin Paris and co-authors introduced a revised suprageneric classification regulated by the International Code of Zoological Nomenclature (ICZN), which proved very efficient and has since been followed by all workers on this group.

According to the ICZN, the concept of 'species' is the only one that refers to an actual population or entity and all higher categories are abstract entities. This means that any feature can be selected to separate the genera and families. In chitinozoans, scanning electron microscope (SEM) images are used to distinguish morphologic features such as the vesicle, aperture, neck, and ornamentation. These main characteristics were used as the basis of classification. The category of 'Order' is not regulated by the ICZN; however, in 1972, Eisenack proposed the useful subdivisions of 'Operculatifera' and 'Prosomatifera' that have been maintained until today. This classification gives stability to the nomenclature, prevents overlap of generic descriptions, and provides a framework for phylogenetic analysis. It was highlighted by the authors of this classification that a computer-assisted system of identification could be developed if a digital taxonomic database were available.

There are several databases with the potential to be useful for chitinozoan taxonomic classification. *ZooBank* is the official registry of the ICZN. It records nomenclatural acts and includes the original descriptions of new scientific names and their publications. For occurrence-based paleontological records, the *Paleobiology Database* and the *Geobiodiversity Database* are extremely useful. Both have an intuitive and simple interface for the user to see the taxa distribution and taxonomic information. These three databases complement each other, but they either have few chitinozoan records or lack complete taxonomic information. There is a desktop taxonomic database *CHITINOVOSP* for chitinozoans, designed by Florentin Paris, which has proven to be useful but needs to be purchased. Achab et al. developed in Canada another chitinozoan database *CHITINOS* that is not currently used. The most complete and useful chitinozoan database at present seems to be *CHITDB*, where browsing and searching for chitinozoan taxa, samples, sections, references, and SEM images is simple. However, it is focused only on material from the Baltic region. Databases such as the *Encyclopedia of Life*, the *Catalogue of Life* and the *World Register of Marine Species* lack chitinozoan records but they are collaborative and provide free global access to knowledge. This collaborative formula seems to be efficient enough to have a trusted digital source of information.

Since at present the taxonomic classification of chitinozoans is no longer under discussion and it has proven to be workable, the following step for chitinozoan researchers would be to have a complete database. We believe that a collaborative effort should be made as there are only a few specialists in the area nowadays. It is not crucial which database should be completed, but it should be useful, as complete as possible, and freely accessible. In particular, we believe that the Baltic *CHITDB* database is an excellent starting platform to achieve that goal in the near future.



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# Biogeographic dynamics of graptolite species during the end-Ordovician mass extinction in South China

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Spatial and temporal analysis of geographical biodiversity dynamics and reconstruction of species distribution areas are essential for revealing the patterns of evolution of graptolites and their survival strategies during bio-events. Over 800 occurrences of graptolites representing 84 species from five graptolite biozones (GB) through the interval of the end-Ordovician mass extinction (from the late Katian *Dicellograptus complexus* GB up to the early Rhuddanian *Akidograptus ascensus* GB) coming from 60 localities in South China were integrated for this study. All earlier identifications of taxa were updated following a unified taxonomic scheme and their distribution presented in a biozone-level stratigraphic correlation framework.

The distribution areas of 26 species occurring in the study interval were reconstructed using GIS software whereby the convex hull areas and maximum distribution distances were calculated. Based on variations in geographical distribution and the relationship with the end-Ordovician mass extinction, graptolite species can be divided into three evolutionary types: the background extinction type, the mass extinction type, and the origination type. The first and second types belong to Diplograptina, and the third one belongs to Neograptina. The analysis of the reduction rate in the geographic distribution of diplograptid species shows that the extinction event not only hit the mass extinction type taxa, but also impacted those of the background extinction type. It also shows that the original distribution area of selected species is not directly related to their extinction risk. Changes in distribution areas of the graptolite species indicate the replacement of neograptids for diplograptids during the end-Ordovician mass extinction.

To study patterns and changes in the spatial distribution of graptolite fauna, quantitative analyses of species-level  $\alpha$ -,  $\beta$ -diversity, and occurrences were performed. Our results demonstrate that the end-Ordovician extinction mainly affected graptolites in the offshore and low-energy areas. Meanwhile, the extinction not only led to a sudden decline in the total diversity, but also resulted in a significant change in the composition and geographic differentiation of the graptolite fauna. Cluster analysis demonstrates that, before the extinction, the graptolite fauna showed two different geographic clusters, which resulted from the hydrodynamic conditions rather than from the distance to the coastline. After the extinction, the fauna became highly similar all over the study area, from nearshore to offshore and from high-energy to low-energy environments, which were mainly comprised by widespread, eurytopic species all over South China.



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# Ordovician conodonts from the Ban Tha Kradan area, Western Thailand

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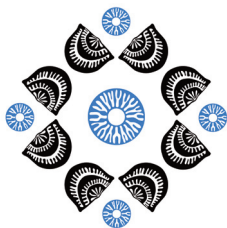
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During the Ordovician period, Western Thailand was part of the Sibumasu Block. Most studies on Ordovician conodonts in this region have focused on the Thong Pha Phum area, where the *Triangulodus larapintinensis* Range Zone of Floian and *Aurilobodus leptosomatus* Range Zone of Darriwilian have been documented.

In this study, conodont samples were collected from two sections in the Ban Tha Kradan area of Western Thailand: from the Wat Mong Krathae (WMK) and Nautiloid Site Geosite (NSG) sections. In total 24 conodont samples were collected from the WMK section, all from the Tha Manao Formation characterized here by laminated and cross-bedded thin- to medium-bedded limestones. From the NSG section only three conodont samples were processed, one of them from the Tha Manao Formation and two from the revised Pa Kae Formation, which consists of thin- to medium-bedded laminated limestones and stylonitic limestones.

Eleven Ordovician conodont species representing nine genera are documented and illustrated from the Ban Tha Kradan area for the first time. The species identified are *Baltoniodus* cf. *alobatus* (Bergström), *Cornuodus longibasis* (Lindström), *Drepanoistodus pitjanti* (Cooper), *Drepanoistodus* cf. *pitjanti* sensu (Zhen et al. 2021), *Erraticodon patu* (Cooper), *Protopanderodus nogamii* (Lee), *Plectodina* sp., *Scabbardella altipes* (Henningsmoen), *Scolopodus striatus* (Pander), *Triangulodus larapintinensis* (Crespin), and *Triangulodus* sp. In the WMK section, the *Scolopodus striatus* Assemblage Zone can be recognized in the Tha Manao Formation. Roughly, it corresponds to the eponymous assemblage zone in the northwestern peninsular Malaysia.

Furthermore, the upper part of the Tha Manao Formation in the NSG section as identified earlier has been revised and assigned to the Pa Kae Formation, based on the lithostratigraphic features. Considering the occurrences of cephalopod *Sinoceras chinense* (Foord) and conodont *Baltoniodus* cf. *alobatus*, as well as on the recognition of the Guttenberg Carbon Isotope Excursion (GICE) in the lowermost part of the formation, the revised Pa Kae Formation in Western Thailand has a similar temporal range as that of the Pa Kae Formation in the southern peninsular Thailand. Thus, the Tha Manao Formation in Western Thailand is assigned to the upper Floian or Darriwilian, and the conformably overlying Pa Kae Formation to the Sandbian–lower Katian.



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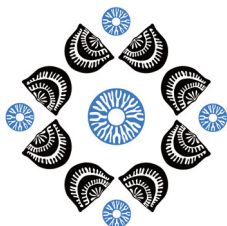
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# Lower–Middle Ordovician brachiopods from the Eastern Cordillera of Peru: biostratigraphical and palaeobiogeographical significance

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Lower–Middle Ordovician brachiopods are well known from the Central Andean Basin of Argentina and Bolivia, but relatively little data comes from its northern prolongation in the Altiplano and the Eastern Cordillera of Peru. Here we present information about brachiopods collected from the San José Formation (Fm) from several sections located at the northeast of the Apurímac River valley in the surroundings of Kimbiri city in the Eastern Cordillera. From northwest to southeast the sections and their locations are: Libertad, in the mountain trail between this hamlet and the city of Pichari; Catarata and Nueva Alianza, in the mountain trail between Oroya and the last hamlet; and Kimbiri (K), in the trail parallel to the Kashiroveni stream north of the village of Kimbiri Alto. In these localities the San José Fm lies unconformably on Neoproterozoic rocks, reaching the maximum thickness of about 700 m. This shale-dominated formation comprises a biostratigraphically almost complete succession of the upper Tremadocian to lower Sandbian strata and contains graptolites, trilobites, brachiopods, molluscs, echinoderms and ostracods, as well as some conodonts and other microfossils. The upper part of the San José Fm is unconformably overlain by a thick sandy and diamictic succession, known as the Kimbiri Fm. About 30 fossiliferous levels have been found in the San José Fm in the Kimbiri section, nine of which contain identifiable brachiopod remains and most of them are precisely constrained by graptolites. The lowermost brachiopod-bearing fossiliferous bed (K-03) occurs about 115 m above the base of the section, being assigned to the *Baltograptus minutus* Graptolite Biozone (GB) (upper Floian, FI3) and containing a single specimen of a small indeterminate orthid. Stratigraphically higher in the formation, the next two assemblages in the beds K-07 and K-11, containing also upper Floian graptolites, provided *Paralenorthis immitrix*. This species was originally described from the San Lucas locality of the Bolivian Eastern Cordillera, from rocks tentatively correlated with the upper Floian–lower Darriwilian. It also occurs in the San José Fm in the Inambari River section located in the Peruvian Eastern Cordillera, ca. 250 km to the east of Kimbiri, in the interval corresponding to the upper Floian–Dapingian(?). Sandstones occurring about 40 m higher, in the fossiliferous bed K-12, yielded a slightly more diverse assemblage composed of *Mollesella planidorsalis*, *P. immitrix* and an indeterminate orthid. *M. planidorsalis* is characteristic of the Loma del Kilómetro Member of the Suri Fm in the central Famatina Range, correlated with the Floian to middle(?) Dapingian based on the occurrence of conodonts of the *Prioniodus elegans*, *Oepikodus evae* and *Baltoniodus navis* conodont biozones. Less than 10 m higher, the sandstones of the bed K-13 only yielded two poorly preserved unidentifiable specimens of *Ahtiella*. Slightly higher, in the bed K-15 just below the *Holmograptus lentus* or *Didymograptus artus* GB, a more diverse assemblage is dominated by a new species of *Phragmorthis* as well as by *P. immitrix*; additionally it contains few specimens of *Ahtiella zarelae* and a new species of *Dalmanella*. *A. zarelae* was exclusively reported from the San José Fm at the Inambari River section. From this level upwards, the brachiopod assemblages become homogeneous in the Kimbiri section (but dominance changes) and co-occur with graptolites of the *Didymograptus artus* GB (middle Darriwilian, Dw2). For instance, in the bed K-16 a new species of *Dalmanella* becomes predominant. The bed K-17 yielded only *P. immitrix*. The highest sampled bed with brachiopods (K-21) is dominated by *A. zarelae* and a new *Phragmorthis* species, *P. immitrix* is still present and unidentifiable specimens of *Christiania* occur. This particular assemblage occurs about 30 m below shales of the *Nemagraptus gracilis* GB (lower Sandbian, Sa1). The brachiopod occurrences cited above improve the knowledge of the late Early Ordovician–early Middle Ordovician faunas of the Peruvian Eastern Cordillera and emphasize strong connections of this region with the Bolivian Eastern Cordillera and Argentinian Famatina Range during that epoch. Additionally, the occurrence of *Phragmorthis* suggests connections with several low-latitude terranes and palaeocontinents, such as the Mayo Terrane, Laurentia, Baltica, and South China.





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# Ordovician Bryozoa of Estonia

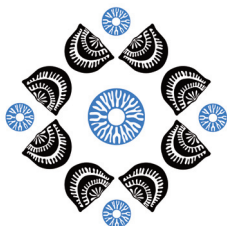
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Bryozoans are one of the most important groups of fossils found in the Ordovician deposits of Estonia. Bryozoa comprise sessile colonial, filter-feeding animals, many of which possess hard carbonate skeletons of different morphology. The bryozoan faunas of the Ordovician of Estonia were studied early by famous naturalists such as Karl Eduard von Eichwald and Władysław Dybowski. Later, in the 20th century, many palaeontologists, among them Ray Bassler, Hendrik Bekker, and Ralf Männil, devoted extensive studies to the Ordovician bryozoans of Estonia. Soviet and Russian specialists contributed to the knowledge about this important group of fossils with numerous publications. The Ordovician deposits bearing abundant and well-preserved bryozoans are well exposed and often easily accessible. Therefore, the Estonian bryozoan faunas are much better studied than the contemporary assemblages of Sweden or Norway.

Few representatives of this phylum appeared in the sediments of the Lower Ordovician, but then the group experienced a rapid diversification. The current evaluation of the data (published and based on the results of our own research) on the distribution of bryozoans in the Ordovician (Tremadoc–Hirnantian) deposits of Estonia revealed 194 species of 90 genera. The most diverse bryozoan group is trepostomes, with 77 species of 36 genera. The Sandbian and the Katian show the highest species richness of bryozoans, with 92 and 112 species, respectively. During the Hirnantian, bryozoans in Estonia experienced an immense diversity drop, with only a few species passing through the Silurian. This pattern mirrors the global development of bryozoan faunas during the Ordovician.

Ordovician bryozoans of Estonia have been found in diverse environmental settings. The best-known deposit containing excellently preserved bryozoans is kukersite. This oil shale was formed in shallow subtidal shelf conditions, and contains more than 60 bryozoan species. Another famous bryozoan locality is the reefs of the Vasalemma Formation (Katian), exposed in the Vasalemma quarry. The bryozoans found in the Ordovician deposits of Estonia reveal a great variety of growth forms adapted to different biotopes of the sea bottom. The sizes of bryozoans vary immensely within the same assemblages. Some massive trepostomes such as *Diplotrypa petropolitana* attained heights of up to 20 cm, whereas species such as the cyclostome *Kukersella borealis* developed colonies less than 0.5 mm in diameter.



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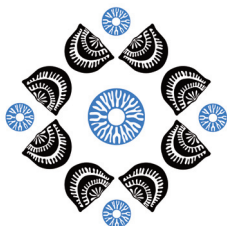
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# Upper Ordovician chronostratigraphic correlation between the Appalachian and Midcontinent basins

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Study of a subsurface core (named F688) from northern Indiana provides integrated data sets linking Katian chronostratigraphic records of the Appalachian and Midcontinent basins. The F688 core shows a variety of shallow- and deep-water facies containing numerous, well-preserved and zonally significant fossil species and diagnostic chemostratigraphic patterns. The succession belonging to the Cincinnati Regional Stage in the F688 core is 210 m thick. Detailed benchtop examination of the succession revealed several phosphatic intervals, rich brachiopod faunas, multiple graptolitic horizons, and at least two tephtras. Elemental analysis was conducted at 60 cm spacing quantifying lithofacies composition. Based on these results, the succession was assigned to six previously defined lithostratigraphic units (Kope, Waynesville, Liberty, Whitewater, Elkhorn, and Fort Atkinson formations). This lithostratigraphic succession shares components with both the Appalachian and Midcontinent basins, suggesting deposition near their shared margin. Twenty samples yielded abundant, well-preserved, low-diversity conodont assemblages with long-ranging taxa that clearly demarcate the position of the Ordovician–Silurian boundary at the top of the succession in the core. More than fifty palynologic samples, targeting graptolite-bearing intervals, were processed for chitinozoans and produced important new insights. The Kope Formation contains the chitinozoan species *Belonechitina kjellstromi*, *Hercochitina downiei*, and *Clathrochitina* sp. nov., co-occurring with a graptolite assemblage suggestive of the *Geniculograptus pygmaeus* Zone. Samples from the overlying Waynesville Formation produced graptolites indicative of the upper *G. pygmaeus* to *Paraorthograptus manitoulinensis* zones co-occurring with the long-ranging chitinozoan species *Belonechitina micracantha* and *Plectochitina spongiosa* as well as several new species of the genera *Tanuchitina* and *Hercochitina*. Higher in the core, the Liberty, Whitewater, Elkhorn, and Fort Atkinson formations yielded chitinozoan species characteristic of the upper Katian biozones of Anticosti Island and Nevada, such as *Tanuchitina anticostiensis*, *Hercochitina longi*, and *Eisenackitina ripae*. Results of  $\delta^{13}\text{C}_{\text{carb}}$  analysis reveal partial preservation of the Kope, Waynesville, and Elkhorn excursions. A tephtra in the rising limb of the Waynesville Excursion yielded needle-shaped clear zircons that will provide a high-precision U-Pb age. The Fort Atkinson Formation is overlain by the Brassfield Formation containing Silurian conodonts and  $\delta^{13}\text{C}_{\text{carb}}$  values suggesting an Aeronian age.

Chronostratigraphic data from our study of the F688 core resolves longstanding uncertainty about correlations between strata of Katian Age in the Appalachian and Midcontinent basins. Integration of core F688 with our other regional chronostratigraphic data in the Midcontinent Basin demonstrates that the Fort Atkinson Formation of the Indiana and Illinois subsurface is age equivalent to the Fernvale Formation of Tennessee, Arkansas, and Oklahoma. Across this area, the Fernvale is overlain by graptolitic shales of the uppermost *P. manitoulinensis* to basal *Dicellograptus complanatus* graptolite zones. By contrast, the type Fort Atkinson Formation of Iowa is interpreted to occur completely within the younger *D. complanatus* Zone. These regional correlations taken as a whole suggest that the uppermost Katian (all of Ka4) and all but the uppermost Hirnantian are missing throughout much of the Appalachian Basin. By contrast, the Midcontinent Basin contains a much more complete upper Katian and Hirnantian succession. Our comprehensive approach is correcting temporal miscorrelation and providing robust chronostratigraphic context for study of biogeochemical events, which will further enable us to disentangle proxy data and identify the processes that drove the Katian diversity peak and culminated in the Late Ordovician mass extinction.



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# Late Ordovician gastropods from the Zhaolaoyu Formation in the southwestern margin of the North China Platform

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The Ordos Basin is located in the western part of the North China Platform and is the second largest sedimentary basin in China; the basin has a huge thickness of the Early Palaeozoic marine deposits, especially the Ordovician ones. The Zhaolaoyu Formation is distributed in the Fuping area of the southern Ordos Basin, where brachiopods, gastropods, graptolites, sponge spicules and ichnofossils are abundant. Ordovician gastropods are abundant, widespread and well known from different palaeocontinents across the world and are important for the study of biogeography and palaeoenvironments of the Ordovician.

However, gastropods from the Ordovician in the Ordos Basin of North China have been rarely documented. The Early to Middle Ordovician of gastropod fauna from the Zhouzishan area, Inner Mongolia, western Ordos Basin, is dominated by the discoidal gastropods with a three to four whorls. Twelve genera of gastropods from the Ordovician of the western and southern Ordos Basin were documented, all with larger spire angle and up to four whorls. Since then, no other Ordovician gastropod fossils have been reported from the Ordos Basin. Herein, we reported and illustrated a gastropod fauna from the Late Ordovician in the Ordos Basin of North China. All gastropod specimens were preserved as internal moulds, which were manually picked from the residues after the samples were chemically dissolved in buffered acetic acid (5–10%). The fauna was recovered from the Zhaolaoyu Formation at the Zhaolaoyu section, Fuping County and consists of several species: *Hormotoma* sp., *Lophonema* sp., *Lophospira* sp. and *Lophospira* cf. *sinensis*. This fauna is dominated by high-spined gastropods with more than five whorls and provides an important supplement to the palaeontological information of the studied area.



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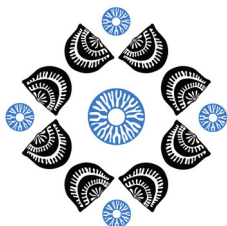
diversity, biogeography, Cambrian, Ordovician, statistics

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# A methodological scheme to analyse the early Palaeozoic biodiversification with the example of echinoderms

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The early Palaeozoic biodiversification is the most significant radiation of marine ecosystems of Earth's history, starting with the appearance of invertebrate organisms near the Precambrian–Cambrian boundary and followed by a significant diversification during the Great Ordovician Biodiversification Event (GOBE). The apparently sudden appearance of major phyla of metazoans during the earliest Cambrian (i.e., the 'Cambrian Explosion', c.a. 540 Ma) has been considered by many as corresponding to an 'explosive' process that took place during a very short time interval. Similarly, the GOBE has been considered as a short spectacular global event triggering a massive biodiversification during the early Middle Ordovician (c.a. 470 Ma). However, it appears that both 'events' have been more intensively studied in a few locations, creating multiple gaps, and thus a bias, in the biodiversity datasets. For example, the 'Furongian gap' (late Cambrian) is clearly an artefact in the Paleobiology Database (PBDB), which includes mostly data from North America and Western Europe. These geographic areas were more intensively sampled and recorded in the PBDB than others (e.g., China), separating the 'Cambrian Explosion' and the GOBE artificially, whereas the Geobiology Database (GBDB), which is focused on data from eastern Asia, records a more gradual increase of the global diversity during the early Palaeozoic.

These diversity curves are indeed not truly global but reflect patchy data from different palaeocontinental margins. Moreover, the evolution of global biodiversity is mostly estimated only in two dimensions (taxonomic richness *versus* time) and spatial distribution is rarely assessed. The organisms might have occupied the Earth's surface heterogeneously because of constraints on their ecological niches, generating 'diversity hotspots' that were recorded in some databases and not in others.

We want to test whether global 'explosions' of diversity ever occurred, or instead a single, but very complex, long-term evolutionary process took place over space and time, starting in the late Precambrian and lasting throughout most of the early Palaeozoic, with changing 'diversity hotspots' at different palaeogeographical locations. To do so, we use echinoderms as a model and we propose a protocol to (1) assess the validity of diversity curves based on data currently available online, and (2) analyse the spatio-temporal evolution of their diversity (i.e., generic richness) in the Cambrian and the Ordovician.

We first compare echinoderms diversity curves between the PBDB, the GBDB and an original database built from a comprehensive synthesis of the literature, with a temporal resolution at the scale of the stratigraphic stage. Then, we gather the three datasets to build a synthetic database that includes a revised taxonomy. To avoid fake spatio-temporal diversity peaks and hotspots, we define comparable stratigraphic units in terms of temporal range and gather sampled sections that refer to the same locality (e.g., the Montagne Noire).

We will present the comparison of the diversity curves between the three databases and the details of the whole methodological protocol.



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# The Ordovician System: From overlapping unit stratotypes to Global Boundary Stratotype Sections and Points

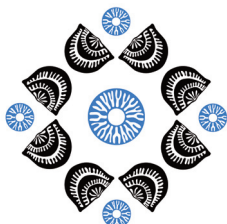
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For nearly a century the Ordovician System was hidden as Murchison and Sedgwick tussled over the overlapping ground between their Silurian and Cambrian systems. The Ordovician is, in fact, one of the longest of the geological periods, characterised by major magmatic and plate tectonic activity; the roles of microcontinents and volcanic archipelagos were significant in shaping the Ordovician planet and the evolution of its biotas, associated with an immense biodiversification, significant fluctuations in climate and sea levels, and the first Phanerozoic mass extinction of marine invertebrates. The period was unique in being thalassocratic; epicontinental seas had a wider reach than during any other geological period. The land areas were restricted to isolated microblocks of archipelagos of various sizes with low relief, with rivers traversing gentle gradients, carrying sparse terrigenous material seaward. It is an ancient world with few parallels elsewhere in the Phanerozoic, and little in common with Holocene ecosystems and environments. The Ordovician System was introduced by Charles Lapworth as a solution to the stratotypes of overlapping units loosely defined by Adam Sedgwick for the Cambrian and by Roderick Murchison for the Silurian. Following a period of intensive research into all the key regions of the globe, unit stratotypes in the type areas of England and Wales have been replaced by seven global stages and three series based on Global Boundary Stratotype Sections and Points, enhancing the definition of these chronostratigraphic units and facilitating global correlation. As a consequence, the biological and geological events during the period can be recognised, and the magnitude and significance of originations and extinctions understood. A global synthesis of successions in Europe (*Geological Society, London, Special Publications, 532*) and the rest of the world (*Geological Society, London, Special Publications, 533*) has emphasised the importance of a universal language for Ordovician chronostratigraphy and its dividends.



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# Siphonotretoid brachiopods – a thorny problem

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Siphonotretoids are presently placed within the subphylum Linguliformea and the class Lingulata, where they constitute a small, relatively short-lived superfamily and order, appearing near the end of the mid-Cambrian, with most forms becoming extinct near the end of the Late Ordovician, but with some rare forms ranging through the Silurian and even into the early Devonian. It has been noted previously that siphonotretides are very different from all other lingulates in shell structure, ontogeny and ornamentation, and may have diverged from other lingulates already during the early Cambrian. Findings of exceptionally preserved 'soft-shelled' possible early stem-group setigerous representatives such as *Acanthotretella* in the Burgess Shale and the Chengjiang fauna have strengthened this view. Exceptionally preserved siphonotretides from Iran clearly show that they are provided with organic setal structures associated with spines, and similar setal structures are known from stem brachiopods, such as *Micrina* and *Mickwitzia*, as well as from some later true rhynchonelliforms. Evidence for preserved setal structures is now also recorded from the Cambrian–Ordovician boundary beds in Wyoming. In the Ordovician, the spinous structures include complex branching forms, such as the widely distributed *Alichovia*, and *Siphonotreta* itself has clear evidence of branching spines. The branching spines probably also contained setal structures, and similar forked setae are known from living annelids.



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# Distinguishing borings and burrows in intraclasts

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Hardgrounds are surfaces of syndementarily cemented carbonate beds that form at or near the seafloor. They are concentrated in particular periods of the geological record and their presence is closely linked to main climatic and biological events. For example, it has been proposed that early lithification of carbonate sediments facilitated the substantial increase of biodiversity during the Great Ordovician Biodiversification Event. Thus, identification of hardgrounds forms an integral component in documenting both geological and evolutionary events in the early Palaeozoic.

Recognition of hardgrounds, including early Palaeozoic examples, is often not straightforward, usually because they lack encrustations and/or bioeroded grains and clasts. Due to the homogeneous texture of micrite, often bioeroded grains and clasts are hard to find and thus cannot be used for hardground identification. Hiatal surfaces, due to omission, are frequently associated with the development of hard substrate. Hiatal surfaces and hardgrounds are often characterised by occurrences of attached organisms, encrustations, truncation and signs of bioerosion. Borings are key evidence in investigations of hardground development. The unequivocal identification of borings is done through identification of the crosscutting relationship between the proposed boring and a hard substrate such as lithoclasts and/or shells. However, morphological criteria are difficult to use when trying to identify borings or burrows in a homogeneous substrate. Bioeroded hardgrounds and burrows with a micrite halo/lining are subjects to fracturing and reworking, resulting in accumulations of intraclasts in flat-pebble conglomerates (FPC). The recognition of borings and broken burrows with a halo can be challenging in FPC. Using trace fossils preserved in situ and in FPC in the late Cambrian carbonates of North China, we established a set of criteria for distinguishing borings from burrows with a halo in FPC. Features such as the relative volume of burrows and borings versus the host pebble and the number of traces per pebble, the cross-cutting relationship with laminae of different colour, and the presence of pyrite or glauconite encrustations can all be used for the recognition of borings. However, examination of the crosscutting relationship and encrustation are not sufficient on their own. Our results suggest caution by defining borings in FPC, particularly as syndimentary deformation of burrows with a halo in the late Cambrian FPC can create structures similar to borings.



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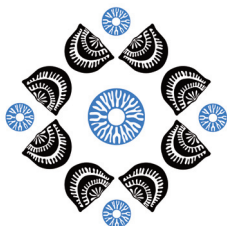
# Coupled extinction–regression episodes revisited in mid-oceanic settings for comparative extinction study during the Palaeozoic in view of non-bolide extraterrestrial causes

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Major change in the Earth's surface temperature appears to be the most critical and universal factor for inducing coevally multiple kill mechanisms for organisms during the global environmental change episodes. Among the major extinction events during the Phanerozoic, the end-Ordovician episode shares almost the same environmental background with that of the end-Guadalupian (middle Permian). These two major extinction-relevant episodes, however, occurred respectively before and after the mid-Palaeozoic botanical revolution, i.e., the first mass development of land plants/forests. Owing to the enhanced terrestrial photosynthesis, the atmospheric CO<sub>2</sub> content decreased irreversibly from ca. 2800–800 ppm in the Ordovician down to 400–300 ppm in the Permian. This highlights an apparent contradiction between the end-Ordovician glaciation and distinctly high atmospheric pCO<sub>2</sub>, which may suggest that one or more agents on global scale were likely responsible for the prominent global cooling besides atmospheric pCO<sub>2</sub> with respect to the greenhouse effect. The same conundrum is much clearer in the cases of Proterozoic snowball Earth events.

Ancient mid-oceanic sedimentary rocks, i.e., deep-sea cherts and atoll carbonates on top of seamounts, are valuable in recording the average regional/global changes of past oceanic domains without receiving tectonic disturbances along continental margins. The Permian mid-oceanic deep-sea cherts and paleo-atoll carbonates in South-West Japan were deposited in the mid-Panthalassa superocean that occupied nearly 70% of the Earth's surface (the rest 30% by Pangea). The latest research results from these unique sedimentary archives in Japan are introduced with particular focus on the hiatus-bearing sea-level drop and a unique signature of extraordinarily high <sup>3</sup>He enrichment in the extinction-relevant interval. These new lines of evidence imply non-bolide extraterrestrial agent for driving global cooling/sea-level drop. Comparative discussion with the end-Ordovician episode may open a new window for extinction study.



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# The earliest known stromatoporoid and its contribution to reef construction

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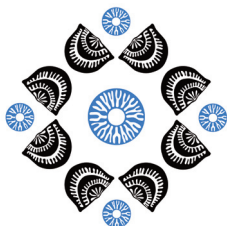
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Stromatoporoid-type hypercalcified sponges are known to have contributed to the global reef system since the late Middle Ordovician until their major disappearance in the latest Devonian. However, the timing of their appearance and how the earliest stromatoporoids were incorporated into the reef ecosystem remains a mystery. A stromatoporoid taxon was previously reported from the lower Floian of South China, but this example limitedly occurs within the cryptic space of a lithistid-*Calathium* reef and has negligible importance in reef construction, unlike the later stromatoporoids that formed the major reef frameworks during the Palaeozoic.

In this study, we describe the earliest known definitive stromatoporoids and the reefs constructed by them in the upper Tremadocian to the lower Floian of South China. The reef framework is dominated by various growth forms of stromatoporoids – ranging from laminar, domical, bulbous to digitate morphologies – that alternate with other organisms such as the calcimicrobe *Girvanella* and stalked echinoderms. Stromatoporoids have played a significant role in frame-building and binding associated with other reef components, contributing to the construction of a complex reef community similar to those found in the late Middle Ordovician and onwards.

In South China, late Cambrian microbial-dominant reefs were rapidly substituted by newly-emerging metazoan reef-builders in the Early Ordovician, such as lithistid sponges, quasi-sponge *Calathium*, bryozoans, echinoderms, the problematic *Pulchrilamina* and stromatoporoids. This is in contrast to other palaeocontinents where lithistid-microbial reefs dominated throughout the late Cambrian and Early Ordovician, with *Calathium* being incorporated in the Early Ordovician. This finding supports the idea that there was regional heterogeneity in reef evolution during this critical time of the Great Ordovician Biodiversification Event.



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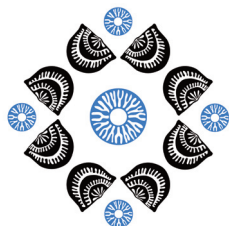
Middle Ordovician, Prague Basin, Bohemia,  
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# Preservation of fossils in the Šárka Formation (Darriwilian, Czech Republic)

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The Šárka Formation is a well-known, fossiliferous Ordovician deposit in Bohemia. It has been targeted by fossil collectors since the 19th century due to the excellent preservation of many fossils. As a result, mainly well-preserved and interesting specimens have been deposited in collections. Many fragments, typical fossil accumulations but also complete specimens belonging to common taxa, have been ignored because they were considered poorly preserved compared to others. That is why some palaeoecological and taphonomical aspects of faunas are insufficiently represented in the existing collections.

The Šárka Formation is early to middle Darriwilian in age and reflects an overall deepening of the Prague Basin, an Early Palaeozoic peri-Gondwanan basin, with a relic of its fill situated roughly between Plzeň and Prague as a part of the Teplá-Barrandian unit in Central Bohemia, Czech Republic. The Šárka Formation is typified by the prevalence of grey to dark grey shales that are 50 m thick in the south-western part of the basin and up to 300 m in the north-eastern part of it. Locally, these shales contain levels with predominantly siliceous nodules. Both, shales and nodules, are fossiliferous, but fossils demonstrate different modes of preservation, primarily resulting from different degrees of compaction accompanied by other processes such as the dissolution of shells.

The highly diverse fauna in the formation is dominated by trilobites. Rhynchonelliformean brachiopods, bivalves, gastropods, cephalopods, ostracods, hyoliths, and echinoderms are very abundant; other groups such as conulariids, monoplacophorans, rostroconchs, machaeridans, and graptolites are less frequent. The fossils occur as isolated specimens, in clusters, or in larger concentrations of transported shells on the bedding planes. Fossils, the shells of which were originally composed of several parts (trilobite exoskeletons, bivalve molluscs, crustaceans, hyoliths, etc.), are often disarticulated. Disarticulated parts of skeletons are mostly complete, with a low degree of fragmentation. This is the prevailing mode of preservation, but some localities yielded also abundant complete trilobites. In general, allochthonous material transported to short distances prevails in the Šárka Formation.

*Preservation in shales.* The fossils in shales are variably compacted. Specimens of the groups producing organic protective structures, such as graptolites, range from predominantly flattened to relief when pyritized. The material of phosphatic shells (phyllocarid crustaceans, linguliformean brachiopods, conulariids) is usually preserved, primarily deformed depending on its solidity, and secondarily slightly flattened. Calcareous shells are often dissolved and the fossils cracked. Although primary cracking also occurs, many shells are collapsed indicating their deformation due to the sediment compaction before dissolution of a shell during late diagenesis.

*Preservation in nodules.* Nodules are of early diagenetic origin and fossils in them are preserved in full relief because they were protected from compaction. All deformations of fossils, such as cracking, can be considered primary, i.e. formed before the nodule formation. Only phosphatic shells occur in the nodules, organic and calcareous shells are not preserved with only minor exceptions. Thus, the dominating preservation mode of fossils in the nodules is as internal and external moulds or only external moulds with a cavity inside. However, there is one special type of internal mould, which has been known for a long time but ignored because of its 'worse' preservation. This is related to many articulated brachiopods and bivalves but often also to some parts of trilobites, hyoliths and gastropods. It is formed by a porous spongiform material, sometimes forming irregular structures resembling the crumble. This taphonomic feature, unique for the nodules, represents a specific type of preservation. It can fully or partly fill in the cavities inside the closed two-valved shells, some enrolled trilobites, adapical parts of hyolith conchs, and gastropod shells but also glabellae, axes, or other parts of trilobites. This preservation is therefore common in enclosed spaces of shells where the presence of organic substances, especially remains of tissues can be expected to occur even after their burial in the sediment. Subsequent decay of tissues in an open geochemical system, such as inside a muddy substrate that is a precursor of shales, would not be traced under normal conditions due to the migration of matters. The nodules were apparently of a very early diagenetic origin and their formation ceased the migration system of decaying tissue substances. The products of these processes remained *in situ* and fossilized in the form of the 'taphonomic crumble', which has a considerable potential for several research directions.



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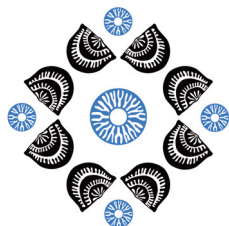
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# Diversity and spatial turnover of bryozoan assemblages in the reefs of the Vasalemma Formation (Late Ordovician), Estonia

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The reefs of the Vasalemma Formation, late Sandbian, Late Ordovician, of northern Estonia contain an exceptionally rich and abundant bryozoan fauna. They are an example of contemporaneous bryozoan-rich reefs known from around the world, representing the peak diversification interval of this group during the Ordovician. The diversification is associated with global climatic cooling and increasing atmospheric and sea water oxygenation. However, the mechanisms that led to the bryozoan diversification are poorly known. Here we estimate the bryozoan richness ( $\alpha$  and  $\gamma$  diversity) and turnover ( $\beta$  diversity) at the level of samples, reefs, and formations in the Vasalemma Formation. The resulting richness and turnover values differ among the three observational levels and hence are scale dependent. A pattern with lowest between-reef turnover and relatively high between-sample turnover could be detected, reflecting high small-scale (within reef) heterogeneities in lithology and original bryozoan habitat. This is consistent with the hypothesis that small-scale substrate heterogeneity was the most important diversification driver in the Vasalemma Formation.



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# Global palaeogeographical implication of acritarchs in the Upper Ordovician

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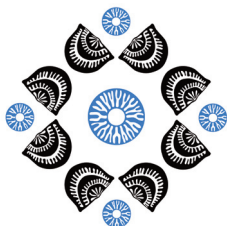
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The Early–Middle Ordovician peri-Gondwana and Baltica acritarch provinces are easily recognizable, illustrating a clear provincialism of global phytoplankton. However, acritarch assemblages have been reported to become increasingly similar towards the Late Ordovician, revealing a general cosmopolitanism, although, based on more recent studies, their assemblages from Laurentia and Baltica are reported to be rather different from those from peri-Gondwana. In this decade, new acritarch assemblages reported from South America, the Baltic region, Iran and Siberia, as well as the new material from South China and Tarim, provide additional data that help to understand the palaeobiogeographical distribution and evolution of phytoplankton during the Late Ordovician in more detail.

The binary dataset was compiled based on published information from about 120 localities in South China, the Middle East, North Africa, South America, India, Bohemia, Avalonia, Laurentia, Baltica, North China, Tarim and Siberia. This dataset was used for Cluster Analysis (CA), Nonmetric Multidimensional Scaling (NMDS), and Network Analysis (NA) to understand acritarch palaeogeography in the Late Ordovician. Re-evaluation of the global palaeobiogeographical distribution of acritarchs revealed their clear provincialism also during the Late Ordovician, particularly in the Katian. The Late Ordovician acritarch provinces were related to global climatic zones. The highly diverse acritarch assemblage normally existed around 30° in the Southern Hemisphere, which is similar to the latitudinal diversity gradient model proposed by Zacaï et al. (2021) for the Late Ordovician. The total diversity of acritarchs was highest and their palaeobiogeographical differentiation strongest in the Katian. The higher acritarch diversity recorded in this time interval may have resulted from their clearly developed provincialism. Acritarch diversity decreased rapidly at the end of the Ordovician, evidently due to the Late Ordovician Mass Extinction (LOME). The relative proportion of endemic taxa in the assemblages in different regions was very high during the main part of the Late Ordovician. However, as a consequence of the LOME, the relative proportion of cosmopolitan taxa increased in the Hirnantian and became higher than in the Sandbian and Katian. Acritarch assemblages from different plates (regions) reacted to the LOME differently and exhibited various diversity trends.



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# Late Ordovician beachrock as a far-field indicator for glacial meltwater pulse

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Understanding ancient climate changes is hampered by the inability to disentangle trends in continental ice volume from records of relative sea-level change. As a unique coastal deposit in tropical and subtropical regions, beachrock has been proved to be reliable for constraining the glacial meltwater signal and thus the total volume of land-based ice in Quaternary. However, beachrock is rarely recognized in the fossil record due to (a) the two-dimensional distribution of beach deposits, as opposed, for example, to extended platform sediments, and (b) the fact that specific environmental conditions are required in order to lithify sediments directly on the beach. By combining the stratigraphic architecture with petrography of characteristic carbonate cements, we demonstrate the first known occurrence of Ordovician beachrock in the Tarim Block, northwestern China. According to biostratigraphic data, a middle Katian (Upper Ordovician) palaeokarst surface is capped by carbonate conglomerate beachrock and this is suggesting a significant relative sea-level rise in late Katian. The beachrock can be correlated with widespread subaerial exposure surfaces and a pronounced stratigraphic gap within the Katian in northwestern Tarim. We suggest that the beachrock 'fingerprinted' a strong melt-water pulse in high latitudes after a short-lived Katian glaciation, which has not received much attention in scientific papers so far.



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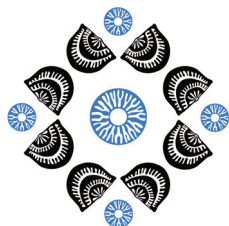
# When lingulid brachiopods became infaunal(?) – perspectives from the morphological and anatomical information

Yue Liang<sup>a,b</sup>, Luke C. Strotz<sup>a</sup>, Timothy P. Topper<sup>a</sup>,  
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Morphology usually serves as an effective proxy for functional ecology, and the evaluation of morphological, anatomical, and ecological changes allows for a deeper understanding of the nature of diversification and macroevolution. Lingulid (Order Lingulida) brachiopods were diverse and abundant during the early Palaeozoic, but decreased in diversity over time, with only a few genera of linguloids and discinoids present in modern marine ecosystems, frequently referred to as 'living fossils'. The dynamics that drove this decline remain unclear and it has not been determined if there is an associated decline in morphological and ecological diversity. We applied geometric morphometrics to reconstruct global morphospace occupied by lingulid brachiopods through the Phanerozoic, with results showing that maximum morphospace occupation was reached in the Early Ordovician. At this time of peak diversity, linguloids with sub-rectangular shells already possessed several evolutionary features common to all modern infaunal forms such as the rearrangement of mantle canals and reduction of the pseudointerarea. The end-Ordovician mass extinction had a differential effect on linguloids, disproportionately wiping out those with rounded shells whilst forms with sub-rectangular shells survived both the end-Ordovician and the Permian–Triassic mass extinctions, with post-extinction faunas predominantly composed of infaunal forms. For discinoids, both morphospace occupation and epi-benthic life strategies remain consistent through the Phanerozoic. Analysis of the morphospace occupation of lingulids over time, taking into account their body size, anatomical features and ecological changes, suggests that the reduced morphological and ecological diversity observed in modern lingulid brachiopods reflects evolutionary contingency rather than deterministic processes.



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# The morphological disparity, ecological evolution and palaeobiogeography of Palaeozoic hyoliths

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Christian B. Skovsted<sup>a,b</sup> and Zhifei Zhang<sup>a</sup>

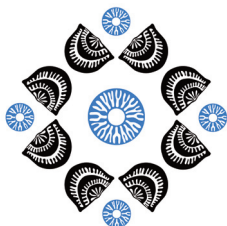
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Hyolitha is a group of extinct invertebrates, the most dominant benthic animals within the Cambrian evolutionary fauna and forming a part of the Palaeozoic evolutionary fauna. Hyoliths are generally divided into two groups, Orthothecida and Hyolithida. They originated in the Terreneuvian and experienced a rapid diversification during the Cambrian Explosion but reached a diversity bottleneck during the Cambrian extinction (Sinsk Event). Hyoliths were characterised by low disparity beginning from the Ordovician and got extinct in the Permian. Factors that affected the evolutionary pattern of Palaeozoic hyoliths from the early domination period up to extinction are poorly known. Herein, we collected material on 148 Palaeozoic hyolith genera from around the world and documented their key morphological characters and distributions. Combined with the phylogenetic analysis based on a matrix of morphological characters, the nonmetric multidimensional scaling (NMDS) using the Paleontological Statistics Software Package, and palaeobiogeographical data, we intended to analyse the biodiversity changes during the evolutionary history of hyoliths and uncover the influence of morphological selectivity in different palaeoenvironments, from the Cambrian to the Permian.

Our results showed that the Cambrian taxa occupied quite a different morphospace compared to that of the Ordovician–Permian assemblages. The morphology of the early Cambrian hyoliths was mainly simple, comprising long conical weakly ornamented tubes. They radiated worldwide during the Cambrian 'Epoch 2', reaching high disparity and diversity, but faced a disadvantageous situation after the mid-Cambrian. The younger genera with strong ornamentation usually showed low diversity and provincialism during the Ordovician. The morphological shift from a simple conical tube morphology with weak ornamentation (orthotheccids of the early Cambrian) to a complex morphology with distinct venter and dorsal pyramidal conch and strong ornamentation from the late Cambrian up to the Permian reflects ecological evolution of the hyoliths. This was accompanied by a change of their feeding habits from active deposit-feeding to passive suspension/filter feeding and change in conch configuration from rheophilic to non-rheophilic.



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# Impoverished fossil association in the lowermost Sandbian of the Prague Basin (Czech Republic)

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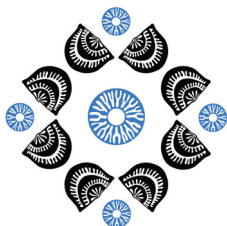
The Darriwilian to the earliest Sandbian Dobrotivá Formation is a sedimentary unit in the Prague Basin (Czech Republic). It conformably overlies the Šárka Formation that formed during GOBE (Great Ordovician Biodiversification Event), during the rapid worldwide increase of faunal diversity. The fauna in the Šárka Formation is rich and reflects the first of the two Ordovician diversity maxima observable in the Prague Basin. The character and diversity patterns of the faunas of both, the Šárka and Dobrotivá formations are similar in many aspects.

Recently, a section of the Dobrotivá Formation, exposed in a low terrain step in Ejpovice, in a village situated halfway between Rokycany and Plzeň, yielded three bulk samples each in size of several cubic metres; more than twenty tons of rock material was extracted. Each of the samples represented a thickness of 1 m of the section. Lithologically, the samples consist mainly of micaceous black shales locally containing infrequent phosphatic nodules. Thousands of specimens were recorded during a detailed study. This dataset was supplemented with information about distributional patterns influenced by taphonomical effects.

Stratigraphically, the succession in this locality belongs to the uppermost Dobrotivá Formation, to the *Cryptograptus tricornis* Biozone. All fossil groups present (hyoliths, molluscs, brachiopods, phyllocarid crustaceans, trilobites, graptolites, and some other minor groups) as well as ichnofossils were studied in detail using semi-quantitative analysis of relative abundances. Combined with taphonomic aspects they were used in paleoecological interpretations, in analysis of diversity and abundance patterns, and in characterisation of faunal associations in each sample.

The fauna at Ejpovice is species-depleted in comparison with the overall diversity within the Dobrotivá Formation. The most abundant fossil groups at this locality, such as graptoloids, cyclopygid trilobites and phyllocarids, are pelagic. However, each of these groups is strongly dominated by specimens of one or two species. Sessile benthic taxa are rarer and their preservation is often fragmentary. Some groups such as conulariids, and taxa such as trilobites of the genus *Placoparia* or brachiopods of the genus *Paterula* are extremely rare at Ejpovice although they are abundant and widespread in the Dobrotivá Formation.

Based on the lithology and fossil associations, deeply dysoxic to anoxic conditions with weak currents prevailed near the bottom at Ejpovice. The fauna is mainly allochthonous and most of the organisms are regarded to be concentrated in postmortal accumulations. Its impoverished composition is typified by prevailing cyclopygid trilobites and graptoloids. The abundance of graptoloids is the highest compared to all other localities of the Dobrotivá Formation in which graptoloids are usually rare or absent. Such considerable differences in abundance of graptoloids in sections of coeval strata are typical for many other Upper Ordovician formations in the Prague Basin.



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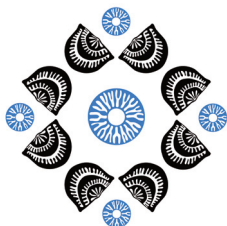
trace fossils, asaphids, olenids,  
marginal-marine environments,  
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# Trilobite expansion into estuarine environments during the Ordovician radiation

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Trilobites have traditionally been considered fully marine. Through the integration of ichnological, palaeobiological and sedimentological datasets within a sequence-stratigraphic and stratigraphic palaeobiology framework, we challenge this assumption. This analysis is based on the study of incised fluvio-estuarine valley deposits from the Furongian Tilcara Member (TM) and the latest Furongian Pico de Halcón Member (PHM) of the Santa Rosita Formation, the early late Tremadocian Cardonal Formation (CF), and the Dapingian–Darrivillan Alto del Cóndor Formation (ACF), from Cordillera Oriental of northwest Argentina. These valleys were incised into wave-dominated shallow-marine strata and filled with transgressive deposits that accumulated in tide-dominated estuaries. Whereas the TM lacks any body or trace fossil evidence of the presence of trilobites in estuarine settings, the other three units reveal that trilobites were able to inhabit these settings. The PHM and CF are host to trilobite trace fossils in outer estuarine facies, both containing various ichnospecies of *Cruziana* (e.g., *C. omanica* and *C. semiplicata* in the TM) and *Rusophycus* (e.g., *R. latus* in both units). In addition, the PHM also contains body fossils of the olenid trilobite *Neoparabolina frequens argentina* in the same deposits in which the trace fossils are preserved, as well as from middle estuarine facies. The ACF displays trilobite trace fossils of the *C. rugosa* group in inner, middle, and outer estuarine deposits, illustrating further landward incursions. This unit also contains body fossils of the asaphid trilobite *Ogyginus* sp. Accordingly, our data indicate two attempts of landward exploration via brackish water: phase 1 in which the outer to middle portion of estuaries were colonized by olenids (Furongian–early late Tremadocian) and phase 2 involving exploration of the inner, middle, and outer estuarine zones by asaphids (Dapingian–Darrivillan). Our study indicates that these trilobites were tolerant to salinity stress and able to make use of the ecological advantages offered by marginal-marine environments migrating up-estuary, following salt wedges either reflecting amphidromy or as euryhaline marine wanderers. It is suggested that tolerance to salinity stress arose independently among different trilobite groups as a result of the broad array of behaviors and adaptations of trilobites during the Ordovician radiation. We speculate that the assumption that all trilobites were stenohaline may have resulted in the misinterpretation of some tide-dominated estuarine deposits as fully marine.



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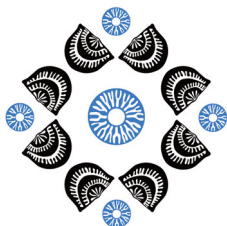
Darriwilian–Katian, stable isotopes, climate, chemostratigraphy, Siberia, Baltica

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# Ordovician climate changes in the northern subtropics: The $\delta^{18}\text{O}$ record from the Tunguska Basin, Siberia

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Oxygen isotopes from bioapatite (conodonts) have been used for several decades to reconstruct the Palaeozoic climate history. During the Ordovician, conodont-based  $\delta^{18}\text{O}_{\text{phos}}$  studies have revealed a general cooling trend throughout the system. The  $\delta^{18}\text{O}_{\text{phos}}$  data from Estonia confirm this long-term shift but also demonstrate that against the background of a generally cooling climate in the pre-Hirnantian, the Late Ordovician was quite unstable, with several episodes of sea surface temperature (SST) decrease and increase of different magnitude and duration. In the sedimentary sequence, these cooling events are reflected by major sea-level lowstands. Several of these are also recognizable in the Tunguska Basin of Siberia. We have recently studied the  $\delta^{18}\text{O}_{\text{phos}}$  record from two Middle and Upper Ordovician sections in Siberia. Comparisons of the results with data from the Baltic region have revealed differences but also some similarities in the  $\delta^{18}\text{O}_{\text{phos}}$  trends, even though these two regions were located on different palaeocontinents, Siberia and Baltica. Both were geographically separated and display different Early Palaeozoic histories with respect to their environmental conditions. Siberia was located in low equatorial latitudes from the Cambrian onwards and remained there through the Ordovician and Silurian, whereas Baltica drifted from high southern latitudes to low latitudes from the late Cambrian and reached the southern subtropics in the Late Ordovician (late Sandbian–early Katian).

Despite Siberia's location at low northern subequatorial latitudes, the upper Middle (starting from the Darriwilian) and the Upper Ordovician in the Tunguska Basin are assumed to be represented by cool-water deposits (various calcareous siltstones with interbeds of micritic and/or bioclastic limestone). The onset of cool-water conditions is explained by plate-tectonic reorganization, resulting in the upwelling of cold oceanic waters along the southern margin of the palaeocontinent and their penetration into the epicontinental seas. Our  $\delta^{18}\text{O}_{\text{phos}}$  data generally fluctuate around 17.5‰ (VSMOW), indicating that SST was relatively stable. This general state is interrupted by six cooling episodes, but unlike in Baltica, no general trend of SST change in any direction (decrease or increase) is evident. In the Baltic region, a general cooling trend prevailed, and SST decreased continuously during the pre-Hirnantian Late Ordovician. In addition to this general trend, seven cooling events (CE) are observed, named (from the oldest upwards) the Late Kukruse, Haljala, Keila, Early Nabala, Vormsi, Early Pirgu, and Middle Pirgu CEs. Comparison of the  $\delta^{18}\text{O}_{\text{phos}}$  curves from the Tunguska and Baltoscandian basins shows that five of these CEs are reflected by brief intervals of higher  $\delta^{18}\text{O}_{\text{phos}}$  values also in the former one. The Keila CE is identified in the lower Mangazea Formation (Fm), the Early Nabala CE in the upper Mangazea Fm, and the Vormsi CE in the uppermost Mangazea Fm. In addition, the Haljala CE probably corresponds to an interval in the lowermost Mangazea Fm and the Early Pirgu CE to a small  $\delta^{18}\text{O}_{\text{phos}}$  peak in the lowermost Dolbor Fm. The most pronounced CE in Siberia is recorded in the upper Darriwilian, in the lower Ust'Stolbovaya Fm, and apparently reflects the Middle-Darriwilian Ice Age. The recognition of the same CEs in successions on two different palaeocontinents is clear evidence that they are not some regional phenomena but the result of global climatic perturbations.

The recently acquired  $\delta^{18}\text{O}_{\text{phos}}$  data allow an improvement in the dating of the Siberian strata and their correlation with successions on other palaeocontinents. Previously, the MDICE, Upper Kukruse Low, GICE, and an interval probably including Rakvere (KOPE) and Saunja carbon isotopic events (CIE) were recognized in the Siberian  $\delta^{13}\text{C}_{\text{carb}}$  record. Now, the position of the Keila CE just below an increase in  $\delta^{13}\text{C}_{\text{carb}}$  in the Tunguska Basin confirms the identification of this CIE as GICE and allows the correlation of this level (lower Baksian Regional Stage) with the Keila Regional Stage in Estonia. In addition, the prolonged CIE between the Early Nabala and Vormsi CEs as identified in the Tunguska Basin apparently corresponds to the Saunja (Waynesville) CIE. This also means that the small peak in the  $\delta^{13}\text{C}_{\text{carb}}$  curve below this CIE correlates with the Rakvere CIE.



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# Palaeozoic carbon isotope excursions and carbonate component analysis

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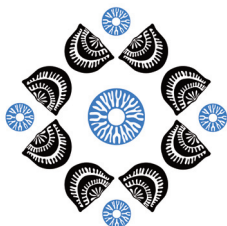
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Palaeozoic carbonate  $\delta^{13}\text{C}$  studies have mainly focused on bulk rock analysis in chemostratigraphic correlations and palaeoenvironmental interpretations, assuming limited isotopic heterogeneity of samples. Particular attention has been paid to positive  $\delta^{13}\text{C}$  excursions, which likely reflect climatic events. However, several studies have provided isotope data from different rock components demonstrating significant sample-scale variation of  $\delta^{13}\text{C}$  values.

We describe the isotopic and elemental composition of individual components in carbonate rocks and analyse which components carry the primary depositional isotopic signatures and which components have been isotopically reset by diagenetic processes. The comparison of bulk rock and component-specific data allows us to assess the reliability of isotopic data used in environmental reconstructions and offers an opportunity to better reconstruct magnitudes of  $\delta^{13}\text{C}$  excursions and related dynamics of seawater dissolved inorganic carbon.

Here we focus on the Hirnantian Isotopic Carbon Excursion (HICE) at the end of the Ordovician period and the Mid-Ludfordian Carbon Isotope Excursion (MLCIE) during the late Silurian period. Previous bulk rock studies have demonstrated the occurrence of the HICE in multiple Estonian drill cores corresponding to the Porkuni Regional Stage. The HICE samples from the Kamariku, Karinu, and Otepää drill cores were subsampled by micro-drilling, and isotope analysis of individual components was done by isotope-ratio mass spectroscopy (IRMS). Limited sample-scale heterogeneity and good correspondence with bulk rock  $\delta^{13}\text{C}$  values are seen in micritic carbonate samples, whereas different bioclastic and cement components in wackestone and grainstone samples exhibit up to 4% range of  $\delta^{13}\text{C}$  values with some components having  $\delta^{13}\text{C}$  values up to 3% higher than the bulk rock values. Lithologically heterogeneous grainstone from the Otepää core shows  $\delta^{18}\text{O}$  variability as much as 3‰ and ooids carrying the lowest, most overprinted values.

Isotope results obtained by the Secondary Ion Mass Spectrometry (SIMS) on MLCIE samples from Lithuanian Vidukle drill core show up to 5% range of  $\delta^{13}\text{C}$  values, and some values are up to 4% higher than the bulk rock values. A similar range can also be seen in  $\delta^{18}\text{O}$  values. Our results demonstrate that multi-component wackestone and grainstone samples from HICE and MLCIE intervals are isotopically heterogeneous and that heterogeneity needs to be accounted for in reconstructions of the past carbon cycle and  $\delta^{13}\text{C}$  curves.



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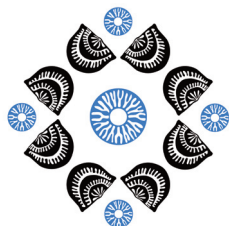
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# Ordovician scientometrics

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Scientometrics is a tool for studying the development of science to observe and analyse patterns that emerge from it. Our aim is to elucidate how the Ordovician has been studied through the years, through the perspective of the published papers, the main topics related to it and how researchers have collaborated along the years, studying Ordovician rocks.

The proposition of a new System 'between' the Cambrian and Silurian rocks was made by Charles Lapworth, researcher at University of Birmingham, by 1879. Only by 1988 the Tremadocian rocks were recognized as Ordovician (and not Cambrian) by the International Union of Geological Sciences (IUGS).

This work uses the OpenAlex database, which contains most of the scholarly information available with metadata of a larger portion of published material in several forms and includes records into that period. In its comprehensiveness, it competes with commercial databases such as Dimensions, Web of Science and Scopus. For all the analysis, we have used a version of OpenAlex included in the Google BigQuery platform available through a public link. The scientometric analysis starts by filtering the papers from the database containing the word 'ordovician' in their titles or abstracts (when available). That selection resulted in 30259 works with publication years ranging from 1871 to 2022. There is a nearly quadratic growth with oscillations starting at 1 and a peak of 1090 works in the year 2009.

As the next step, using information about co-authorship of papers, it is possible to collect the information on author affiliations. This way we establish connections among the institutions in a network. The network reveals that geographically close institutions tend to be more collaborative within one time period.

Chinese institutions are closely connected such as the Chinese Academy of Sciences and China University of Geology. Another group is English speaking countries outside the United States such as the Australian National University and British Geological Survey. There are two large groups that interconnect these first two groups: European and North American institutions represented by the largest – Lund University, National History Museum, Uppsala University. These institutions appear foremost when filtering the network for more than 200 connections (co-authored papers).

Going into further detail, one can see a network with over 100 connections showing Chinese Oil Research Institutions closely linked to their universities. Also, the Chinese institutions connect directly to the European institutions such as Czech Geological Survey and University of Bergen. British universities such as Bristol, Leicester and Durham further serve as a connection point between North America and Europe.

When the connections are split into 30-year time periods, it is possible to note the geographical growth in the Ordovician studies, spreading from traditional centres of knowledge into areas where new universities and institutes are created. In the first two periods of three decades, institutions present no connections.

Starting from 1933 to 1962, three of them appear collaborating: Florida State University, Rice University and Shell Oil. In the period from 1963 to 1992, 412 institutions were connected. For that period, the United States Geological Survey, Geological Survey of Canada, and the Chinese Academy of Sciences come out as hubs of collaboration.

In the last period, 1978 institutions are connected. Recent years show a significant presence of Ordovician studies linked to the oil industry, to the point that, when connected to the higher productivity, oil research institutes dominate the network of connections in the Chinese hub, now linked together around the Chinese University of Geosciences. The British Geological Survey is the most important focal point between Europe, through the National University of Córdoba, and North America, through the Ohio State University.



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# An Ordovician ostracod palaeopsychrosphere?

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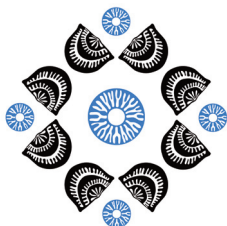
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Ostracods are tiny bivalved crustaceans with a fossil record extending into rocks of the Lower Ordovician. They occupy almost all aquatic environments today, from the ocean abyssal planes to damp forest leaf litter. Their stratigraphical record suggests they had diversified into a wide range of marine and non-marine habitats already during the Palaeozoic. Through the Ordovician, ostracods are mostly known from marine shelf depositional settings. These are mostly podocope ostracods that appear to have had a benthic mode of life like their modern counterparts; myodocope ostracods, though known from the Ordovician, likely became pelagic only in the Silurian. As they are considered benthic, and possessed no pelagic larval stage, Ordovician podocope ostracods have been widely used as key biogeographical index species for much of the early Palaeozoic.

A fundamental question in the oceanographic evolution of ostracods is: when did a psychrosphere evolve (a fauna inhabiting cool waters below the thermocline)? A psychrospheric ostracod fauna in the Ordovician would question some of their biogeographic utility, given that such taxa might have a much wider dispersal capability than more shallow shelf faunas. Here we describe a new ostracod fauna from a palaeotropical South China plate setting, preserved in Upper Ordovician mudstones and siltstones from northern Vietnam. The fauna contains taxa endemic to the South China palaeoplate, but also yields several taxa at the generic level that are known from European and North American Ordovician settings. We discuss whether these latter taxa might be indicative of a more widely dispersed deeper marine psychrospheric Ordovician ostracod fauna, and the implications this would have on traditional biogeographic models. We also discuss other possibilities for these apparently more cosmopolitan taxa, including homeomorphy, previously unknown palaeogeographical connections, and the possibility of pelagic podocope taxa.



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# The late Katian Elkhorn event: precursor to the Late Ordovician mass extinction

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The late Katian Elkhorn event is a biogeochemical perturbation preceding the Late Ordovician mass extinction (LOME) with an exceptional record in the United States (U.S.). Results of our recent studies in this interval allow revised temporal ordering to strata across multiple basins providing insights into the magnitude of environmental disturbance and associated processes and feedbacks. The record of the Elkhorn event spans portions of the Appalachian and Midcontinent basins in the eastern U.S. and the Williston Basin and Cordilleran margin in the west. Our work focuses heavily on the Midcontinent Basin in particular, as it shares many characteristics of size, tectonic setting, and lithofacies with the Baltic Basin, providing the potential for resolving global signatures of the event.

In its type-area, the Cincinnati Series ends with the Elkhorn event. The succession is marked by shallowing from subtidal to marginal marine facies, capped by a karstic sequence boundary. Our new conodont data demonstrate that an overlying white to pink crinoidal grainstone package, previously assigned to the basal Silurian “white” Brassfield Formation near the Ohio-Indiana state line, is in fact Upper Ordovician. Further,  $\delta^{13}\text{C}_{\text{carb}}$  values in this unit are elevated, in line with later phases of the Elkhorn event (2% more positive than reported Rhuddanian values). These findings support a correlation of the grainstone interval with the Fernvale Formation of central Tennessee. To the east, much of the northern Appalachian Basin was overfilled with widespread marginal marine to terrestrial red beds by the onset of the Elkhorn event, while the Midcontinent Basin to the west remained relatively sediment starved. In the southern Midcontinent, the mid-Elkhorn event sequence boundary was overlapped by ironstone deposition (lower Fernvale Formation). The ironstones are overlain by sparry and hematitic grainstones with localized bioherms. In Arkansas, where the Fernvale is thickest (>30 m), the sparry phase gives way upward to manganese carbonates and bioherms. Across the region, the Fernvale is, in turn, cut by a sequence boundary, suggesting a yet higher Katian sequence, and is perforated by paleokarst pockets that are filled and overlain by upper Katian (Ka4) sediments. This sequence boundary is overlapped by black shales and the thickest (>10 m) phosphorite of the Ordovician at the end of the Elkhorn event.

Previous studies have suggested age equivalence of the Elkhorn and Paroveja  $\delta^{13}\text{C}_{\text{carb}}$  excursions in Laurentia and Baltica. Despite the attraction of aligning the latest Richmondian and Pirgu regional stages, our data sets demonstrate that this is a miscorrelation. Critical to this revision are new integrated biostratigraphic and chemostratigraphic data sets in a transect from the margin of the Appalachian Basin into the Midcontinent Basin. The new data reveal that the Elkhorn Shale and Fernvale Formation are overlain by the Brainard and laterally equivalent Sylvan, and Mannie shales. These shale successions contain graptolites of the *complanatus* and *pacificus* zones. Thus, the Elkhorn event occurred in the latest *manitoulinensis* Zone, suggesting correlation with the Baltic Moe  $\delta^{13}\text{C}_{\text{carb}}$  excursion.

Our extensive new data sets provide regional chronostratigraphic correlation of strata deposited during the Elkhorn event. When temporally ordered, these records provide evidence for high amplitude sea level oscillations, major redox fluctuations, and reef pulses that demonstrate the waxing and waning of continental ice sheets on Gondwana and the spread of oceanic anoxia only a few million years before the LOME. These findings further call into question traditional models of rapid glaciation during a long-lived greenhouse state as the sole driver of the LOME and emphasize the need for new integrated Upper Ordovician research initiatives to better characterize Katian events.



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# Recent advances in the Ordovician stratigraphy of the Baltic Palaeobasin and Tornquist margin of Baltica

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Ordovician rocks are widely distributed in the Baltoscandian region as well as in Poland, Belarus, Ukraine and Moldova. The Ordovician studies in this area were initiated in the 19th century in the outcrop belt in northern Estonia. The strata are well accessible here and fossils and sedimentary structures are excellently preserved. Further south, in other countries, the succession is lying progressively deeper (up to 2500 m) in the subsurface, except for limited exposure in Ukraine. The thickness of the Ordovician within the Estonian outcrop area reaches about 100 m but exceeds 200 m in several parts of the subsurface area. Since the 1960s, several Ordovician correlation charts have been compiled for this area. Recent developments in the stratigraphy are summarised in the volume 'A Global Synthesis of the Ordovician System: Part 1' (*Geological Society, London, Special Publication*, 532).

The system of bio-, litho- and chronostratigraphic units is highly detailed in the area. The regional stages defined in Estonia were introduced for the western part of the East European Platform in the 1980s. The correlation of the regional succession to the global stratigraphic standard is generally well constrained, although it still needs to be refined in some details. A novel element of the stratigraphic standard, the isotopic zones, is based on secular variations of stable carbon isotopic composition of bulk carbonates and allows amendments to the correlation of strata.

The application of a regular timescale is based on a well-dated system of biostratigraphic marker levels that were traced into the Baltic Palaeobasin and further to the south. The dated boundaries were tied to the regional succession mainly based on the correlation of conodont, chitinozoan and graptolite zones, but also using chemostratigraphic events.

Correlation of formations to the chronostratigraphic standard in ten subregions (North and Central Estonia, South Estonia together with West Latvia and West Lithuania, Kaliningrad Region, East Latvia, Central Lithuania, East Lithuania together with northwestern Belarus, southwestern Belarus, West Volyn and Podillya together with East Volyn and Moldova) is summarised in an emended correlation chart. Development of the subregional correlation charts was well coordinated before the 1990s and the charts were based on a unified nomenclature of lithostratigraphic units for major facies zones that crossed the national borders. Trends in the development of nomenclature and correlation of formations have been different in different countries after 1991. This resulted in increasing differences in nomenclature and rank of lithostratigraphic units in subregions and led to an increase of the number of subregions. The development towards a more detailed stratigraphic classification in Lithuania has elevated the rank of many former units (several formations are now ranked as superformations, etc.). In 2011, a completely new system of formations and members replaced the formerly applied standard in the Kaliningrad Region.

The climatic history of the region presented in papers of the last decades is modified in the light of the newest results of isotope-geochemical studies on Baltoscandian sections, which do not support the idea of gradual warming throughout the Middle and Late Ordovician in the region. The global cooling trend was also influencing Baltica despite the continental drift towards the lower latitudes.

The richly fossiliferous regional succession has been extensively studied, but analyses with a broader view have been sparse. According to the general understanding, backed by data on different fossil groups, the main origination episodes in the early Darriwilian and Darriwilian–Sandbian transition led to the peak of regional diversity in the early Sandbian. Remarkable extinction events known from the early Darriwilian, early Sandbian and early Katian are expressed to a different degree in different fossil groups. The major extinction event in the latest Katian–Hirnantian, which impacted all major invertebrate groups, has been ascribed to the Hirnantian glaciation, the related glacioeustatic sea-level fall and the repeated rapid rearrangement of facies. A recovery that started in the latest Ordovician was relatively slow. Significant spatial differences in the dynamics of biodiversity within the eastern Baltic area and between this area and Scandinavia are considered partly due to uneven data coverage.



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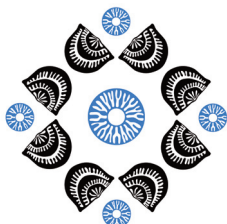
halite, carbonate, trace elements,  
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# Drivers of the Late Ordovician Mass Extinction: redox, volcanism, atmospheric oxygen/carbon dioxide and/or glaciation

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The Late Ordovician marks an epoch of substantial change during Earth's geologic history. It documents the first mass extinction event of the Phanerozoic, which wiped out a plethora of marine genera. Though signatures of the extinction event are quite evident on the species level, there are many underlying uncertainties as to which factors drove the near destruction of Ordovician marine life. The exact causes and contributing factors of the Late Ordovician Mass Extinction (LOME) are highly debated. Previous studies propose processes such as redox shifts, volcanism, deep-water anoxia, low atmospheric oxygen, or excess CO<sub>2</sub> as significant influencers.

In this study, we utilized a multi-archive/proxy approach in reconstructing paleoenvironmental, stratigraphic, chronologic, and diagenetic signatures of halite and carbonate sequences from two localities containing the Ordovician–Silurian boundary. Our preliminary findings suggest that an abrupt, multi-pulsed glaciation was probably the main driver of the LOME. However, the exact duration, intensity, and number of cooling pulses are still up to interpretation and will require additional geochemical work to paint the entire picture.

Samples were obtained from two localities of similar low paleo-latitudes. Marine halite and carbonate were obtained from the upper Ordovician Red Head Rapids Formation, Hudson Bay Basin, Canada. Another suite of halite was collected from the Ordovician/Silurian Mallowa Salt Formation, Canning Basin, Western Australia.

The diagenetic integrity of Red Head Rapids halite and carbonate were assessed through strontium isotope analysis. Since the strontium isotope remains in equilibrium with seawater, we can cross-analyse the preservation potentials of both marine archives. All sample results lay within the  $\pm 0.00006$  ‰ natural variation of <sup>87</sup>Sr/<sup>86</sup>Sr measured in modern marine counterparts, providing evidence of primary material and accurate paleo-interpretations.

Trace element chemistry study was conducted on halite samples from both localities. Previous studies suggested that the spikes of Hg, Mo, and U concentrations signify the aftermath of a greenhouse event that triggered the expansion of deep-water anoxia. Furthermore, heightened volcanic activity led to significant greenhouse gas emissions and produced a period of warming. Instead, our halite Hg, Mo and U concentrations are extremely low, many below detection limits, which correspond to glacial signatures of an icehouse. Interpretation of the sedimentary cerium anomaly of the Red Head Rapids and Mallowa salts also revealed characteristics of an oxygenated marine environment, with all calculated values below the threshold, typical of anoxia.

Rigorous halite fluid inclusion analysis was conducted to qualitatively distinguish between primary and secondary material based on size, shape, orientation, and multiple growth patterns. Microthermometry homogenization temperatures derived quantitative distinctions between primary and secondary fluid inclusions of preserved and altered material, respectively. Paleotemperatures of primary fluid inclusions exhibited oscillations that were evident of daily/seasonal variation of inter- and/or glacial times, averaging approximately  $24.2^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$  for the latest-Ordovician–earliest-Silurian. Apart from minor fluctuations, we noticed up to four major cooling pulses associated with the major glaciation characterizing the latest-Ordovician–earliest-Silurian time.





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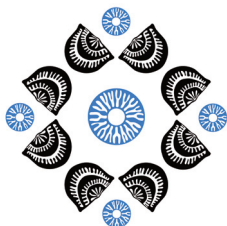
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# Changes in shelf phosphorus burial during the Hirnantian glaciation and its implications

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The Late Ordovician mass extinction occurred during an icehouse interval, accompanied by the glaciation of the supercontinent Gondwana, which was located at the South Pole at that time. As suggested by sequence stratigraphy of near- and far-field sedimentary successions as well as stable oxygen isotope studies, ice sheets reached their maximum extent in the late Hirnantian *M. persculptus* graptolite zone. As a result, the global sea-level dropped significantly during the Hirnantian Glacial Maximum (HGM). This led to exposure and erosion of sediments on the tropical shelves of Laurentia and Baltica. Where shelves remained submerged, water depths were probably very shallow.

Local redox proxies, such as I/Ca ratios or iron speciation, indicate that shelf environments were well oxygenated. At the same time, stable uranium isotopes, measured on shallow-water carbonate samples, indicate a global expansion of the seafloor overlain by anoxic water. This implies that the observed increase in anoxia was confined to the open ocean and that there was a redox gradient between coastal and oceanic environments. Unfortunately, the lack of Late Ordovician deep water sedimentary records makes it impossible to directly measure open-ocean redox conditions. In general, Late Ordovician deoxygenation is in stark contrast to other oceanic anoxic events of the Phanerozoic, which occurred during greenhouse conditions and are associated with rising water temperatures.

Under present interglacial conditions, with a relatively high sea-level, it is estimated that about 70% of the nutrient phosphorus delivered from the continents is retained in shelf sediments. Hence, shelf environments act as a nutrient filter. However, during times of low sea-level, this filter is switched off due to the bypassing of incoming riverine dissolved load through river canyons. As a result, excess phosphorus is released into the open ocean leading to eutrophication. This has previously been proposed for the Last Glacial Maximum (LGM) and is supported by geochemical data. We suggest that this scenario may also be applicable to the HGM and serve as an explanation for increasing anoxia during cold climatic conditions.

To test this, we measured phosphorus concentrations across the HGM on carbonate samples collected from two low-latitude successions (Ruisseau aux Algues on Anticosti Island and Valga-10 core section from Estonia, both interpreted as shelf environments). To eliminate the detrital, non-reactive phosphorus fraction, we used the SEDEX sequential extraction method, which allows to separately measure reactive ( $P_{\text{react}}$ ) and organic phosphorus ( $P_{\text{org}}$ ). In order to evaluate the burial efficiency of phosphorus, we determined total organic carbon (C) concentration and calculated  $C/P_{\text{org}}$  and  $C/P_{\text{react}}$  ratios.

We observe a decreasing trend in  $P_{\text{react}}$  towards the HGM and a minimum during the subsequent initial transgression. Low  $C/P_{\text{react}}$  and  $C/P_{\text{org}}$  in the range of the Redfield ratio indicate efficient burial under oxygenated conditions. Therefore, we can rule out that phosphorus regeneration, which is stronger under anoxic conditions, caused the observed minimum. This means that  $P_{\text{react}}$  is a direct measure of primary productivity and phosphorus burial.

Using the  $P_{\text{react}}$  data and an estimate for the shelf area, we modelled the global burial flux of phosphorus into shelf sediments. Due to the overall reduction in shelf area during the HGM and the low  $P_{\text{react}}$  contents, the modelling suggests that the shelf burial flux was approximately halved. If the phosphorus input had remained constant across the interval, which is reasonable given that the erosion of exposed shelf sediments compensated for a reduction in continental weathering during the cold and arid climate, the excess phosphorus would have entered the open ocean stimulating primary productivity. Ultimately, enhanced productivity would have resulted in a high organic matter sinking flux and oxygen depletion by aerobic respiration. In summary, our data and modelling support the proposed scenario of an inefficient nutrient filter.



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# Echinoderm Lagerstätten from high-latitude Gondwana – filling the gap in the Ordovician diversification of the phylum

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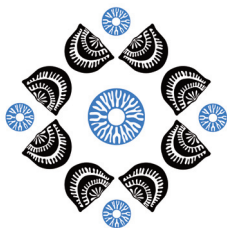
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The phylum Echinodermata is a major component of marine ecosystems since the first appearance of echinoderms in the Cambrian. Like other metazoan phyla, echinoderms underwent two major evolutionary pulses in early Palaeozoic times: the Cambrian Explosion and the Ordovician Radiation. In the Ordovician, the exploitation of new ecological niches triggered an exponential diversification of the phylum, leading to its highest morphological disparity and class-level diversity (about 18 classes compared to only five extant classes) of the whole Phanerozoic. However, the precise spatio-temporal patterns of the Ordovician Radiation of echinoderms remain poorly known, owing to geographical and taphonomic biases. Over two centuries, the sampling effort was mostly focused on faunas from Europe and North America, providing a wealth of information on crinoid- and/or blastozoan ('cystoid')-dominated low-latitude assemblages from Avalonia, Baltica and Laurentia. Moreover, echinoderm Lagerstätten, bearing fully articulated skeletal elements, provide valuable snapshots of past communities but are rare in the rock record because echinoderm endoskeletons disarticulate into many calcite plates shortly after death. Recent discoveries of several new Ordovician Lagerstätten from high-latitude Gondwana, i.e., the Czech Republic (Barrandian area), France (Armorican Massif, Montagne Noire) and Morocco (Anti-Atlas, Meseta), provide a unique opportunity to fill the existing knowledge gap regarding the Ordovician diversification of the phylum. Echinoderm assemblages from high-latitude areas are dominated by asterozoans, blastozoans and stylophorans, with very few crinoids, unlike those from low-latitude regions. By comparing and combining these two sets of information, it is possible to coherently frame the early diversification of echinoderms in space and time.



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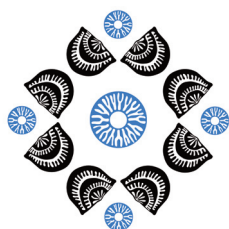
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# Towards a revised Sandbian conodont biozonation of Baltica

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One of the key objectives of the studies proposed by the Ordovician Subcommittee is the improvement of regional stratigraphy for further advancements in global correlation. The results of this work can be found in numerous updates and reviews published in the recent *Geological Society, London, Special Publications* 'A Global Synthesis of the Ordovician System'. Several of these papers refer to the Baltic Ordovician conodont biozones. While different schemes share many common features, their correlation with stages and biozones differ in detail. Considering the recent developments in the studies of the Sandbian stratigraphy in the Baltoscandian region, it is possible to complement the current conodont biozonation.

*Pygodus anserinus*, *Amorphognathus tvaerensis* and *A. superbus* conodont zones are recognized in the Sandbian Stage in Baltica. The lower boundary of the stage is located within the *Pygodus anserinus* Zone, and the main part of the stage corresponds to the *Amorphognathus tvaerensis* Zone. In Scandinavia, the upper boundary of the stage correlates with a level within the *A. superbus* Zone or lies in a conodont-poor interval in the eastern Baltic region. The lower boundary of the *A. inaequalis* Subzone is tentatively correlated with the base of the Sandbian in Scandinavia but is located in the uppermost Darrivillan in the eastern Baltic region. In both areas, the *A. tvaerensis* Zone is subdivided into the *Baltoniodus variabilis*, *B. gerdae* and *B. alobatus* conodont subzones.

The *A. inaequalis* Subzone – in some cases indicated as a zone – has been included in the regional stratigraphic charts for more than a decade. However, so far, *A. inaequalis* (Rhodes) has been reliably identified and also illustrated only from Avalonia, i.e. outside the palaeocontinent Baltica. A recent restudy of collections from the Fjäckå main section and the Smedsby Gård drillcore (both from Sweden), as well as from several Estonian sections, did not prove the occurrence of *A. inaequalis* in these areas.

The *A. tvaerensis* Zone comprises almost the whole Sandbian, both in Scandinavia and the eastern Baltic areas. During this long age, the morphology of the P and M elements of *A. tvaerensis* (Bergström) gradually changed, and elements of distinct morphology appeared and were assigned to a new species, *Amorphognathus viirae* Paiste, Männik et Meidla, 2022, in the upper part of the range of the species. In succession, *A. viirae* appears in the upper part of the *B. gerdae* Subzone. Currently, *A. viirae* has been identified in numerous Estonian sections, as well as in the Fjäckå main section and the Smedsby Gård drillcore in Sweden. Based on published figures, it occurs evidently in the Mójcza Formation of the Holy Cross Mountains (Poland) and the Black Knob Ridge section in Oklahoma (USA), in the GSSP for the base of the Katian Stage.

*A. inaequalis* has also been reported and an eponymous zone identified in two other sections located on the palaeocontinent Baltica, in the Bliudziai-150 drillcore (Lithuania) and the Kovel-1 drillcore (Ukraine). During the restudy of collections from these sections, no elements of *A. inaequalis* were found in either of them. The earliest recorded elements of the genus *Amorphognathus* have been assigned to *A. tvaerensis*, and the specimens from the upper range of this species reidentified as *A. viirae*.

Analysis of the new material and revision of previous collections has revealed problems related to the Sandbian conodont biozonation of the palaeocontinent Baltica and demonstrated the need for its updating. The new proposed zonation excludes the *A. inaequalis* Subzone, as the occurrence of its nominal taxon on the palaeocontinent Baltica could not be proved. Additionally, a new unit, the *A. viirae* Zone, has been included in the zonation. It corresponds to the upper part of the former *B. gerdae* Subzone, which is now treated as a zone. Also, all subzones based on the succession of *Baltoniodus* species have been elevated to the rank of zones.



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# The earliest Ordovician trace fossils *Cruziana* and *Rusophycus* from Baltica

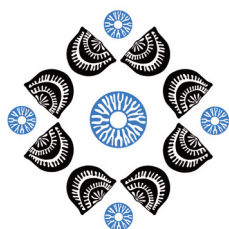
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Trace fossils of the ichnogenera *Cruziana* and *Rusophycus* are described for the first time from the Lower Ordovician of Baltica. These specimens were found from the upper Tremadocian–lower Floian glauconite sandstone of the Leetse Formation in the Leetse and Uuga cliffs on the Pakri Peninsula, North-West Estonia. The one from the Leetse locality was collected already in the 19th century but was hidden in museum collections. On this piece of rock, together with the *Rusophycus*, brachiopods *Leptembolon lingulaeformis* and *Thysanotos siluricus* occur. They indicate that the sample comes from the strata corresponding to the *Thysanotos siluricus* Brachiopod Biozone of the Hunneberg Stage. Different lithology of the two newly discovered loose slabs with trace fossils found under the Uuga cliff indicates that, most probably, they originate from different levels of the glauconite sandstone exposed in this section. One of them is heavily pyritized and yields a contact surface with the underlying beige argillite of the Varangu Stage with fragments of the graptolite *Kiearograptus supremus* and some undescribed acrotretid and other linguloid brachiopods. The second, less strongly lithified slab contains abundant fine debris of thin-shelled unidentifiable linguloid brachiopods and probably comes from a higher level. Earlier studies of conodonts revealed that the *Prioniodus elegans* Conodont Zone is missing in the Uuga section, thus narrowing down the possible interval of origin of these ichnotaxa to the *Paroistodus proteus* zone.

Interestingly, these two slabs preserve the dissimilar pattern of grouping and orientation of the multiple *Rusophycus/Cruziana* traces giving some idea about the ethology of trilobites who probably left these traces. The earliest trilobites in the Ordovician succession of Estonia are recorded from the Mäeküla Member, the uppermost part of the Leetse Formation, from an interval where calcareous component first appears in the sediment and thus also the trilobites with their calcitic exoskeleton are preserved. The only trilobites recorded from the Mäeküla Member of the Leetse Formation in these two localities are specimens of *Paramegistaspis leuchtenbergi* who could have been the trace maker with its macropygidium being of similar size to its cephalon if the second slab would come from the same interval. However, there are more candidates, mainly isoteline trilobites with similar characteristics which are preserved in older but calcareous succession in Sweden and Norway.



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# Upper Ordovician hardgrounds – from localized surfaces to global biogeochemical events

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Upper Ordovician hardgrounds display a spectrum of complexity reflecting a range of local to global-scale processes. Hardgrounds are cemented seafloor surfaces typically marked by the presence of encrusting taxa and borings. Many hardgrounds show evidence for successive episodes of colonization by hard substrate specialists and are associated with localized evidence of seafloor erosion such as overhangs and reworked concretions. They commonly show trace amounts of pyrite and dolomite cements indicating an association with sulfate reduction. The most widespread hardgrounds are highly complex and unravelling their history provides insights into global biogeochemical events.

The Curdsville and Kirkfield hardgrounds in the Appalachian Basin (Kentucky and Ontario) represent relatively simple end members of the hardground spectrum. They covered 10s to 100s km<sup>2</sup> and formed relatively quickly during the early Katian. They display both planar to sub-planar and hummocky to topographically complex surfaces (cm-scale) and contain highly diverse encrusting echinoderm faunas. Study of these surfaces yields important insights into the evolutionary history of encrusting communities.

By contrast, the slightly younger hardground at the top of the Galena Group (Ka1) is a surface that is present throughout most of the Midcontinent Basin (>7.5 × 10<sup>5</sup> km<sup>2</sup>). It is an example of a highly complex surface that was repeatedly modified by erosion and mineralization. Near the eastern margin of the basin in Indiana, the capping Galena hardground is pinnacled with cavity-filling sharpstone clasts, phosphate grains and bored crusts, iron ooids, and pyritic impregnated surfaces. It is overlapped by graptolitic shales of the Kope Formation (Fm) (Ka1) indicating an unconformity of approximately 1 m.y. To the west, in Illinois, the Kope Fm is erosionally truncated and the hardground is directly overlain by graptolitic shales of the Waynesville Fm (Ka3), where the unconformity expands to nearly 4 m.y. Toward Iowa, the hardground is overlapped by meters of phosphorite. Taken together, these observations reveal that the capping Galena Group hardground reflects a complicated history of repeated subaerial exposure, karsting, and marine flooding by a dysoxic to anoxic water mass with fluctuating redox conditions, similar to the age equivalent hardground at the base of the Fjäckå Shale in the Baltic Basin.

Thus, hardground studies provide important insights for resolving the temporal continuity of the Upper Ordovician rock record and unravelling processes that controlled carbonate precipitation and dissolution and the evolution of sea floor communities. Some simple hardgrounds may have formed through random exhumation of cemented sediments on the sea floor through the effects of storm scour. However, their clustering into certain portions of the Upper Ordovician suggests that processes that affected sea water chemistry may also be involved. The most complex surfaces reflect major environmental perturbations with large amplitude sea level oscillations and redox changes that in some cases generated rare-earth enriched phosphorites.



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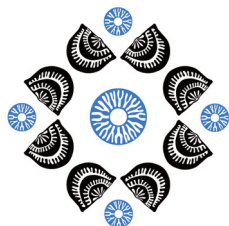
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# The Late Ordovician extinction conundrum

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The Late Ordovician mass extinction (LOME) has long been known for its association with the Hirnantian glaciations. Two extinction pulses seem to reflect global cooling and warming, respectively. The effects climate change had on Ordovician life are well documented through palaeontological evidence, several geochemical proxies and further simulated in modelling scenarios. Preceding the Hirnantian extinction interval was a phase of prolific faunal migrations in notably the later parts of the Katian. Well-documented evidence shows that low-latitude faunas dispersed to high latitudes, and taxa that had previously been endemic to particularly Baltica and South China, suddenly began to appear in Laurentia. These events, referred to as the Boda warming event and the Richmondian invasion, have been suggested to reflect a biotic response to warmer climate indicating that the onset of the subsequent Hirnantian icehouse marked a considerable environmental shift from the latest Katian warming phase.

Whereas a lot of focus has been on untangling the selective effects of the two Hirnantian extinction pulses on different clades, less focus has been on what led to the transition from the Middle Ordovician biodiversity rise to the dispersal phase seen during the Katian. It appears that most clades did not – during any point of time in the Ordovician – surpass the richness levels they had achieved by the earliest Katian. Rather, a plateau was established when all metazoan clades are compiled together. This could suggest that extinction rates began to increase relative to originations. Either a threshold was reached by the early Katian prohibiting ecosystems to expand, or an extinction pulse occurred that decimated overall biodiversity accumulation. Two lines of evidence suggest the latter to be the case. Firstly, several new clades became hugely diverse by the Katian. These include bryozoans, crinoids, rugose and tabulate corals, as well as molluscs such as bivalves and gastropods, and show that obviously increased ecosystem complexity with, for instance, more epifauna and tiering occurred. Secondly, large richness datasets compiled from all metazoan clades differ from biodiversity curves based on individual clades in that they show a drop in richness already by the earliest Katian (as opposed to the classic two-pulsed Hirnantian scenario). This discrepancy has long been an overlooked conundrum that arguably has been ascribed to the larger datasets having been temporally less well-resolved. However, these new multiclade Ordovician biodiversity curves are – in some cases – resolved down to the scale of millennia, and they still depict this large fall in richness levels during the early Katian. As this pattern is observed across vastly dispersed regions, it is arguably a true signal depicting a global extinction pulse that precedes the two classic Hirnantian extinction waves by several million years.

If such a three-phased ‘extended-LOME’ interval is to be corroborated, it would imply a considerably different extinction scenario from the classic Hirnantian one. For instance, most of the Katian would then have to be viewed as being part of a protracted survival phase. In such a scenario, the global dispersal of faunas during the Boda and Richmondian events could reflect faunas adapting to changing climatic and environmental conditions during not just the classic Hirnantian icehouse–greenhouse scenario but as part of a prolonged phase culminating with the Hirnantian extinctions. It would further entail a new perspective on the possible mechanisms driving this long extinction phase. Several extinction determinants, both intrinsic and extrinsic may be culprits, but it is hard to overlook the apparent correlation between the start of this ‘extended-LOME’ phase and some of the largest volcanic eruptions known in Earth’s history. Future better temporally resolved research into both the interplay between life and the environment during the earlier parts of the Late Ordovician hopefully will shed more light on this fascinating mass extinction event.



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# Where are all the Ordovician sea cucumbers (Echinodermata)?

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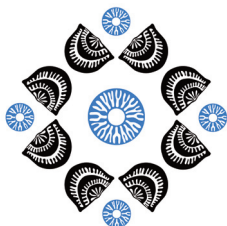
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The Ordovician Period witnessed the first evidence of appearance of all modern echinoderm clades as well as it is the most concentrated interval of echinoderm diversity in Earth's history. This knowledge is largely based on reports from Baltica, Avalonia, Laurentia and Gondwana. However, the Ordovician record of sea cucumbers (Holothuroidea) and their allies, like echinoids and ophiocystioids (Echinozoa), is sparse and patchy. The earlier published Cambrian or Ediacaran records of echinozoan echinoderms (e.g., sea cucumbers) are based on misinterpreted specimens of other phyla. Neither the origins of the Echinozoa nor the split of holothuroids from ophiocystioids or echinoids are properly understood. One reason for this is the fact that less than 100 (articulated) Ordovician specimens of sea urchins, sea cucumbers and ophiocystioids have been recovered worldwide so far.

In general, fossil remains of the Holothuroidea are limited to (1) innumerable microscopic and/or mesoscopic ossicles of the body wall, (2) five distinct calcareous plates which supported the anus in some (more highly evolved) sea cucumber groups, and (3) a total of usually ten radial and interradial elements of the calcareous ring surrounding the pharynx. The latter represents a synapomorphy for the entire group and is important in the higher-level group systematics. In addition, to date, there are only about two dozen known Phanerozoic localities (Konservat-Lagerstätten and obrution deposits) that have yielded (4) articulated body fossils of holothurians.

Few attempts have been made to use disarticulated fossils of Echinodermata to understand the distribution, diversity and early radiation of Holothuroidea, Echinoidea and Ophiocystioidea. Only during the last two decades, advanced micropalaeontological and macropalaeontological techniques have been combined to investigate these understudied echinoderm groups in greater detail. This will help to gain further understanding about the Early Palaeozoic echinozoan echinoderms.

In this presentation, a short overview of known holothurian finds (mostly from Baltica) is given.



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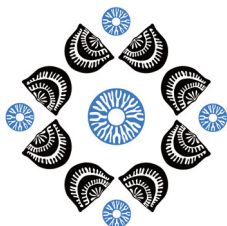
Ordovician, Baltica, palynomorphs,  
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# Middle–Late Ordovician organic-walled phytoplankton from Sweden: diversity and early radiation

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The Borensult-1 core, drilled in the vicinity of Motala, east of Lake Vättern in south central Sweden, comprises a well-dated and nearly complete succession of marine marly carbonates deposited relatively close to land. The 34 core samples analyzed for palynology encompass the upper part of the Darriwilian (Furudal Limestone), the entire Sandbian (Dalby Limestone, the Kinnekulle K-bentonite and the lower Skagen Limestone) and the lower part of the Katian (Skagen Limestone). The age of this interval is well-constrained to the late Darriwilian (Stage slice Dw3)–early Katian (Stage slice Ka1), based on conodonts and <sup>206</sup>Pb/<sup>238</sup>U dating of volcanic ash deposits.

The samples yielded predominantly marine organic-walled phytoplankton, mainly acritarchs, with subordinate chitinozoans, scolecodonts and fragments of graptolites. Sparse terrestrial palynomorphs, represented by cryptospores and trilete spores, were also found in 23 of the samples.

A total of 154 acritarch species corresponding to 53 genera were identified, as well as low percentages of abnormal forms (teratological forms) of acritarch species at some levels. The stratigraphic distribution of genera and species allowed for three palynological assemblages to be distinguished: Assemblage A of a late Darriwilian age, Assemblage B of a Sandbian age (further subdivided into sub-assemblages B1 and B2), and Assemblage C dated as Katian.

Genera such as *Baltisphaeridium*, *Ordoviciidium*, *Pachysphaeridium* and *Orthosphaeridium*, which are common in Middle Ordovician phytoplankton assemblages from Baltica, are well represented, with several species, mainly in Assemblage A and sub-assemblage B1, up to the lower Sandbian. However, the presence of a majority of taxa with worldwide distribution supports the cosmopolitanism of the studied assemblages, already proposed to begin near the Darriwilian–Sandbian transition.

Notably, phytoplankton taxa with Silurian affinities, previously known from the Hirnantian, appear for the first time in the late Darriwilian part of the Borensult-1 drillcore (Dw3). Important taxa occurring are *Tylotopalla* and *Metaleiofusa*, which is definitively established from the beginning of the Sandbian (early Late Ordovician), together with the first appearance of the genus *Visbysphaera*. These occurrences question the relationship between the appearance of pioneering phytoplankton morphotypes and the Hirnantian glaciation.

Other taxa with no pre-Silurian records such as *Visbysphaera pirifera* subsp. *minor*, *Petaloferidium cazurum* and *Dorsennidium* cf. *D. estrellitae* are here present in the Sandbian, where bentonite beds are intercalated.

The genus *Frankea* is recorded for the first time from the Ordovician of Sweden, suggesting a high to middle latitudinal distribution instead of a peri-Gondwanan distribution.

The highest diversity corresponds to the Darriwilian and partly to the Sandbian assemblages, followed by a significant decline in the Katian. The main changes are observed in the Sandbian, with a significant drop in diversity, which is probably related to intense volcanic activity represented by the bentonite beds. Diversity as well as origination and turnover rates are the lowest in the interval bearing the suite of K-bentonites, particularly near the thickest of them. The marked drop in diversity in the Katian part of the succession, visible in both low originations and abundance, is possibly related to a regression at the onset of the GICE (Guttenberg isotope carbon excursion), with less favorable environmental and climatic conditions.

Changes in phytoplankton assemblages together with the onset of innovative morphologies of acritarchs were previously interpreted as a consequence of environmental and climatic perturbations related to the Ordovician glaciation. Here we show that the first appearances of these advanced taxa already occurred ca 15 Ma earlier, suggesting that a possible combination of factors such as sea level changes and volcanism triggered these changes, instead of a major event such as the Hirnantian glaciation. Additionally, these new findings challenge previous models of evolution and radiation of the Ordovician phytoplankton and set up Baltica as a new key area for paleogeographical research.





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# The detailed Middle to early Late Ordovician faunal succession and $\delta^{13}\text{C}_{\text{carbon}}$ chemistry of the Kårehamn drill core, offshore eastern Öland, Sweden: implications for stratigraphy and correlation

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The Middle to lower Upper Ordovician stratigraphy of the Kårehamn core, drilled ca 7 km offshore to the east of the Kårehamn village, northeastern Öland, is presented. The investigated core is one of four drill cores obtained during the preparation of the Kårehamn offshore wind farm. It is ca 41 m long and has a diameter of 10 cm. The lithostratigraphy, faunal (conodonts and chitinozoans) succession and  $\delta^{13}\text{C}_{\text{carbon}}$  isotope chemistry pattern are built upon this complete core. The drilling stopped at 64.5 m b.s.l. in the Swedish Orthoceratite limestone, within the upper *Lenodus variabilis* Conodont Zone. The horizon is largely equivalent to the strata that in Sweden were previously named “limestone with *Asaphus 'raniceps'”*, which is within the Orthoceratite limestone. It is characterized by and composed of mainly light-grey, highly fossiliferous and stylonitic limestone with little clay material. The next unit includes the *Yangtzeplacognathus crassus* and lower *Lenodus pseudoplanus* conodont zones. The upper *Lenodus pseudoplanus* (with *Microzarkodina ozarkodella* late form *sensu* Lindström), *Eoplacognathus suecicus* and *E. foliaceus* conodont zones are recorded from the overlying succession of the upper Orthoceratite limestone. This interval corresponds to the Segerstad, Skärlov and Seby topoformations of Jaanusson, all of which are included in the upper part of the Swedish Orthoceratite limestone. The prominent  $\delta^{13}\text{C}_{\text{carbon}}$  isotope MDICE peak recorded from the Kårehamn drill core is biostratigraphically precisely assigned to the upper part of the newly redefined *Eoplacognathus suecicus* Conodont Zone. The conformably overlying Folkeslunda Limestone is the top unit of the Orthoceratite limestone; it is composed of lime mudstone and grey bedded wackestone. Biostratigraphically, it is referred to the *Eoplacognathus reclinatus* Subzone of the *Pygodus serra* Conodont Zone corresponding to the lower part of the *Laufeldochitina striata* Chitinozoan Zone.

The Furudal Limestone – on Öland known as the Källa Limestone and Persnäs Limestone – overlies the Orthoceratite limestone and represents an important change of the depositional environment in the Baltic Basin. The Källa Limestone contains the *Eoplacognathus robustus* Conodont Subzone of the *Pygodus serra* Conodont Zone and the *Laufeldochitina striata* Chitinozoan Zone. *Pygodus protoanserinus* Zhang is the transitional taxon from *P. serra* to *P. anserinus* and is securely and precisely recorded for the first time in the region.

The important conodont species *Pygodus anserinus* Lamont and Lindström is recorded from the Persnäs Limestone (= upper Furudal Formation) from which also the *Laufeldochitina striata* Chitinozoan Zone is documented. *Pygodus anserinus* extends into the overlying Dalby Formation, in which it is succeeded by the lower *Amorphognathus tvaerensis* Conodont Zone. The diagnostic chitinozoans *Eisenackitina rhenana*, *Laufeldochitina stentor*, *Conochitina savalaensis*, *Belonechitina intonsa* and *Conochitina viruana* are well documented from the same formation. The top of the core is within the *Baltoniodus variabilis* Conodont Subzone of the *Amorphognathus tvaerensis* Conodont Zone of the Bergström conodont zonation.

The precise integrated biostratigraphy of the conodonts and chitinozoans along with the carbon isotope curve are results of this study, which largely agree with those of previous research of the Baltic Basin and thus provide data for precise correlation across the Baltic Basin. The fossil assemblages are clearly related to the east Baltic chronostratigraphic scheme and to the new chronostratigraphic scheme of Scandinavia, and the succession is referred to the established stages of the two systems.



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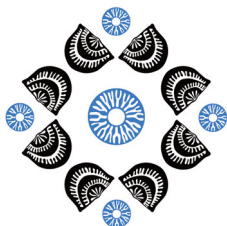
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# Late Ordovician jawed polychaete fauna from the Spiti Valley, northern India

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The final part of the Ordovician Period was characterised by major perturbations in climate, environments and ecosystems, as proved by numerous studies. These changes resulted in one of the biggest extinctions in Earth's history. Most research in early Palaeozoic biogeography is based on data derived from extensively studied localities in North America and Europe, and much less information is available from other parts of the world. Here, we present the first results of our study on Katian/Hirnantian scolecodonts from the Spiti region, India. This area was part of the Tethyan Himalaya of the Gondwana palaeocontinent, located at low palaeolatitudes. Various representatives of algae, bryozoans, corals, cephalopods, conodonts, ostracods and other groups have already been described from this region. Palaeontological data and facies analysis indicate shallow-water conditions within the subtropical–tropical realm. In addition, the specific carbon isotope ( $\delta^{13}\text{C}_{\text{carb}}$ ) trend suggests that late Ordovician carbonate deposits in the region occurred during the pre-Hirnantian global warming interval, the so-called Boda Event. The migration pathways of bryozoan communities have shown that those from Spiti were very similar to the faunas of Laurentia, Baltica, Siberia and southern China during the early Late Ordovician. It is assumed that taxa originating in Laurentia, crossed the Tornquist Sea from Baltica to Avalonia, then to southern Europe, and subsequently extended along the shelf of northern Gondwana, including India and Australia.

The organic-walled microfossils of the Spiti region have previously received much less attention than the shelly faunas and conodonts. In the present study, we have focused on scolecodonts – the jaws of polychaete worms, a group that has been abundant since the Cambrian, playing an important role in various marine ecosystems. Polychaetes are a vital part of the food chain and play an essential role in organic matter decomposition and nutrient cycling processes within sediments. The jawed polychaetes are also known for their high resistance to ecological stress. In Spiti, scolecodonts are mainly found in silty limestones containing 60–70% of carbonate minerals. The majority of scolecodonts were recovered from the lithological units 8 and 13 of the studied section, representing well-stabilised shallow-shelf carbonate environments close to the top of a transgressive system tract in otherwise relatively nearshore to shoreline settings.

Our results show that at least seven jawed polychaete genera are present in the assemblage. A new endemic ramphoprioid species belonging to the genus *Megaramphoprion* has been recorded. Other taxa include representatives of *Oeononites*, *Mochtyella*, *Vistulella*, *Atraktoprion*, *Xanioprion* and paulinitids, which occur in both scolecodont-rich units. The same genera occur in coeval strata in Baltica and Laurentia. On the other hand, some genera such as *Pistoprion* and *Kalloprion* are missing in the Spiti samples and also in other Gondwanan collections. In Laurentia, the family Hadoprionidae is already present in the Late Ordovician, but in Gondwana it appears in the late Silurian. Paulinitids are common in late Katian and Hirnantian strata (*Amorphognathus ordovicicus* conodont Zone) in Laurentia and Gondwana, as well as in Baltica. Similarly to coeval Laurentian polychaete faunas, labidognath and prionognath taxa outnumber the species with a placognath-type jaw apparatus. The distinct and abundant genus *Pteropelta* in Baltica and Laurentia has so far not been recorded in the latest Ordovician of Gondwana.

In addition to scolecodonts, the studied organic-walled microfossil assemblage contains chitinozoans belonging to the genera *Acanthochitina*, *Conochitina*, *Spinachitina*, and possibly *Tanuchitina*. The diversity is lower than presented by previous authors and reported from other regions.



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# Phylogeny and evolutionary modularity of a trilobite family over the Ordovician Radiation

Ernesto E. Vargas-Parra and Melanie J. Hopkins

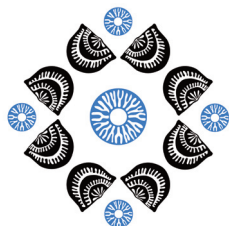
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Trilobites are organized in packages; the adult trilobite body plan is composed of a cephalon (head), thorax (midsection), and pygidium (tail). These packages, or modules, are composed of traits that evolve semi-independently such that change in one module does not necessarily beget change in another module. At the macroevolutionary level, this decoupling and relaxation of evolutionary constraints is thought to promote evolvability. Thus, it is thought that modularity facilitates rapid diversification in diverse evolutionary directions, the hallmark of an adaptive radiation, as evolutionary rates among modules can vary along phylogenetic branches. Trilobites provide an unmatched fossil record, due to their biomineralized exoskeleton, to examine the long-term relationship between macroevolutionary diversification and modularity.

However, the lack of a phylogenetic framework for major trilobite groups hampers the study of macroevolutionary questions. For instance, the trilobite family Pterygomtopidae diversified during the Middle and Late Ordovician in Baltica, Avalonia, Laurentia, and Siberia. This group traditionally comprises four subfamilies with strong biogeographic signal including Pterygomtopinae, Chasmopinae, Eomonorachinae, and Monokainae. However, relationships between and within subfamilies remain unresolved. Further, relationships with other families in the sub-order Phacopina, especially with Phacopidae, remain unclear.

To even begin tackling the relationship between macroevolution and modularity, phylogenetic relationships must be resolved in this trilobite group. To do so, we constructed a comprehensive character matrix comprising >240 characters including discrete, meristic, and continuous characters. Analyses include taxa from all 36 genera assigned to Pterygomtopidae and include Ordovician exemplars from the trilobite families Diaphanometopidae, Phacopidae, Dalmanitidae, and Acastidae. We ran Bayesian phylogenetic analyses to produce trees that would co-estimate topology and evolutionary rates using the birth-death model.

Further, we quantified the 3D morphology of the trilobite head using high-density geometric morphometrics for exemplar taxa within Pterygomtopidae to identify the structure and degree of modularity of the trilobite head in this group. Future work will assess evolutionary rates for the trilobite head and, importantly, evolutionary rates of individual modules over the Ordovician Radiation to determine an increase or decrease in modularity over this diversification event.



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# Developing a phylogenetic framework for tiny Ordovician brachiopods (Atrypida: Anazyginae and Catazyginae) from the eastern United States

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Elucidating how environmental change can facilitate the differentiation of evolutionary lineages and the establishment of new species is a critical issue for understanding both the history of life and modern biota. Notably, speciation events are known to be the main drivers of biodiversity; thus, generating well-constrained phylogenetic hypotheses to investigate speciation processes and facilitators can provide key data on links between biogeography, speciation, and diversification. During the Great Ordovician Biodiversification Event (GOBE), articulate brachiopods were a key group on the rise. By the Middle to Late Ordovician, the brachiopod order Atrypida was no exception. The atrypids diversified greatly and established evolutionary novelties such as helical and calcite-supported lophophores. The Ordovician epicontinental seas in eastern Laurentia provided an excellent environment for reproductive isolation and speciation, with sea-level fluctuations, ideal climate conditions, and active tectonic settings. However, speciation patterns and drivers within two widely-distributed atrypid subfamilies, Anazyginae (*Anazyga* spp. and *Zygospira* spp.) and Catazyginae (*Catazyga* spp.), remain poorly known. In this project, we seek to develop a robust phylogenetic framework for these clades and use that framework to evaluate speciation processes and facilitators during the Late Ordovician.

Morphological data will be collected from published literature and museum collections for a target group of 18 species, five recently reviewed species of *Zygospira*, seven species of *Anazyga*, and five species assigned to *Catazyga*. *Protozyga exigua* will be included for outgroup comparison. Specimens will be assessed at the Smithsonian National Museum of Natural History, which houses the comprehensive Cooper Collection, and specimens loaned from other museums. A morphological matrix will be created using more than 40 characters, including both external and internal characters. The resulting character matrix will be analyzed via Bayesian phylogenetic inference using the MrBayes software package. The Bayesian framework assesses the posterior probability in a generated tree by incorporating likelihood models and uncertainties, such as data insufficiency. Hence, given the incompleteness of the nature of morphological data for these clades, Bayesian inference is an ideal and efficient method to reconstruct phylogenetic relationships. Speciation mode and biogeographic patterns will then be analyzed using the BioGeoBears software package. Through this process, we aim to understand the speciation relationships within a monophyletic clade (Anazyginae and Catazyginae) and ancestor forms.

Systematic revision results in more precise species identities, through which it is possible to track character evolution within the genera. The results include (1) consistency in morphological traits within genera, such as shell ribs and the number of lophophore whorls, and (2) articulated differences among the three genera, evidencing derived states from a common ancestor. Combining phylogenetic and biogeographic analyses within the Atrypida provides essential information for understanding the impacts of geological and biotic changes on marine species across the Middle and Upper Ordovician. Thus, incorporating unique characters such as the number of whorls, shell ribs, and size in phylogenetic frameworks can elucidate evolutionary trends and phylogenetic relationships within the clade and provide evidence of how those factors impacted atrypids' distribution and abundance throughout the Paleozoic.



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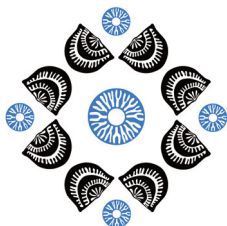
Ordovician graptolitic shale, Ordos Block,  
shale gas, diachroneity, graptolite zonation

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# Distribution pattern of the Ordovician black shale constrained by graptolite zonation in the western margin of the Ordos Block, North-West China

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The graptolitic shale from the late Middle to early Late Ordovician along the western margin of the Ordos Block is a good target bed for shale gas exploration. The horizontal well Zhongping-1 drilled by the Changqing Oilfield Company in 2019 produces a daily gas output of  $6.42 \times 10^4$  m<sup>3</sup> and has proved the tremendous potential for shale gas exploration on the west margin of the Ordos Block. However, strong heterogeneity of total organic carbon (TOC), thickness, porosity and other parameters of the black shale have been revealed at different levels and localities. Therefore, a study of graptolite zonation, aiming to illustrate and predict the temporal and spatial distribution of the black shale in high resolution, is essential for shale gas exploration.

A total of four wells were investigated carefully during the summer of 2022 and 102 samples were collected for the identification of graptolites. The well Qitan-9, the northernmost of the studied wells, is located in the Ordos Etok Banner, Inner Mongolia Autonomous Region. The graptolite faunas can be assigned into two biozones, the *Pterograptus elegans* Biozone and the *Jiangxigraptus vagus* Biozone. The latter is correlated with the *Didymograptus murchisoni* Biozone. The base of the *J. vagus* Biozone is defined at the first appearance datum (FAD) of *J. vagus* at the depth of 4741.42 m.

The well Ren-16 is located in the Etok Front Banner, Inner Mongolia Autonomous Region. The *Nemagraptus gracilis* was found at the depth of 2880.06 m. Additionally, graptolites *Pseudazygograptus incurvus*, *Cryptograptus tricornis* and *Reteograptus geinitzianus* were collected from the level of 2881.93 m, showing also the characteristics of the *N. gracilis* Biozone. The boundary between the *N. gracilis* Biozone and *J. vagus* Biozone is tentatively placed at the depth of 2881.93 m.

The well Li-105 is located in the Yanchi County, Wuzhong City, Ningxia Hui Autonomous Region. Graptolites are well preserved in this drill core. Some of them are preserved in 3D or half relief. *N. gracilis* was found at the depth of 4262.60 m while *Climacograptus bicornis* appears first 5.19 m above this depth. Accordingly, the base of *C. bicornis* Biozone is placed at the FAD of *C. bicornis* at the depth of 4257.41 m.

The well Yintan-2, the southernmost of the studied wells, is located in the Huanxian County, Gansu Province. According to the graptolite fauna, two biozones can be distinguished, the *Climacograptus bicornis* Biozone and the *Nemagraptus gracilis* Biozone. The boundary between these biozones is placed at the FAD of *C. bicornis*, i.e. at the depth of 3866.82 m.

The spatial and temporal distribution of the black shale, as constrained from the graptolite zonation, shows that the black shale is strongly diachronous, getting younger southwards along the western margin of the Ordos Block. The base of black shale is diachronous from the *P. elegans* Biozone in well Qitan-9 to the *J. vagus* Biozone in well Ren-16 and the *N. gracilis* Biozone in wells Li-105 and Yintan-2. The top of the black shale is also diachronous from the *J. vagus* Biozone in the well Qitan-9 to the *N. gracilis* Biozone in the well Ren-16 and *C. bicornis* Biozone in the wells Li-105 and Yintan-2.

The temporal and spatial distribution pattern of the black shale in the Ordos Region of North China shows that the sedimentary facies change from north to south and the depocenter has migrated southwards. This pattern differs significantly from the results of some former studies showing facies belts were being distributed westwards from the platform to shallow shelf, and further on to deep shelf and slope-basin. The distribution pattern of the black shale supports the hypothesis that the Alxa oldland thrust southwards is the driving force for southward migration of the depocenter during the foreland basin evolution process. Neither the peripheral foreland basin associated with the Ordovician arc-land collision event in the North Qinling orogenic belt nor the rift basin hypothesis is consistent with this pattern. The black shale distribution pattern as constrained from the graptolite zonation calls for a reconsideration of the tectonographic and palaeogeographic properties of the western margin of the Ordos Block.



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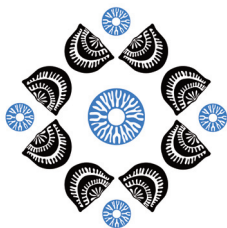
Soom Shale, Hirnantian, Gondwana,  
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# Early land plant remains from the uppermost Ordovician–?lowermost Silurian Cedarberg Formation of South Africa

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The Cape Supergroup forms a regionally extensive and extremely thick Ordovician to Carboniferous succession of sedimentary rocks in southwestern South Africa. It includes the Lower–Middle Ordovician–lowermost Devonian Table Mountain Group, which incorporates the uppermost Ordovician Soom Shale Lagerstätte (within the Cedarberg Formation). The Soom Shale Lagerstätte accumulated in an unusual cold-water setting, associated with the decaying South African ice sheet, towards the end of the Hirnantian glaciation. The deposits of this glacial marine environment, characterised by anoxic bottom waters, preserve a highly unusual marine biota. It includes specimens exhibiting exceptional preservation of their soft tissues in clay minerals. Overlying deposits of the Soom Shale are shales and thin sandstones ascribed to the Disa Member that accumulated in a shoreface-shelf setting. Associated with these deposits are relict Soom taxa, in addition to a handful of *Clarkeia*-type brachiopod faunas, suggesting a probable earliest Silurian age for the upper part of the Cedarberg Formation.

Previous palynological investigations of the Soom Shale have yielded typical marine elements, including chitinozoans, scolecodonts and rare acritarchs, but also common terrestrial elements in the form of dispersed spore tetrads. The latter are historically important as they represent an early report, by Jane Gray and colleagues, of dispersed cryptospore tetrads and were the first evidence for early land plants from Africa south of the Sahara (Ordovician eastern Gondwana at 30° S).

Herein we report on a palynological investigation of an exposure of the Cedarberg Formation from the northernmost outcrops of the Cape Supergroup at Matjiesgoedkloof, Western Cape Province. Recently the sedimentology and ichnology of the underlying ice-marginal shallow-marine deposits of the Pakhuis Formation were described. Although macrofossils have not been recovered from these strata, they yield a fascinating ichnofauna that is diverse and disparate, comprising trackways and burrows. These show colonisation of glacial deposits by makers of burrows and trackways that lived in brackish water conditions as ice sheets retreated.

Our palynological investigation yielded assemblages of abundant and well-preserved palynomorphs. Although of moderate–high thermal maturity, they are much less coalified than palynomorphs from the more southerly exposures. Surprisingly, the assemblages are dominated by land plant spores with extremely rare, if any, marine palynomorphs. This may be a consequence of high freshwater influx from the decaying ice sheet's glaciers excluding normal marine biota (although the ichnological evidence demonstrates the presence of at least some organisms). The dispersed spore assemblage is somewhat unusual in that it is dominated by tetrads to the exclusion of monads and dyads. Coeval assemblages from similar palaeolatitudes in Gondwana (e.g. from the Arabian Plate) are far more diverse. This possibly reflects the close proximity of the vegetation to the ice sheet.



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# High-resolution carbon isotope stratigraphy of the Lower and Middle Ordovician succession of the Yangtze Platform, China

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Variation in the relative abundance of the stable carbon isotopes has been widely used to correlate Ordovician marine successions over the past two decades. To date, only a few of studies of Ordovician carbon chemostratigraphy have been conducted in South China. Most of the previous studies in this field have focused on specific time intervals and/or events in the Middle and Upper Ordovician. The Lower and Middle Ordovician of the Yangtze Platform is typically represented by a sedimentary succession dominated by carbonate rocks, which is ideal for studying the carbon chemostratigraphy. Three sections spanning the Nantsinkuan/Lunshan, Fenhsiang, Hunghuayuan, and Dawan/Zitai formations, corresponding to the Tremadocian–Dapingian in age, have been sampled for high-resolution  $\delta^{13}\text{C}$  chemostratigraphy. Our new  $\delta^{13}\text{C}$  data reveal five tie-points with the potential for global correlation: (1) a positive  $\delta^{13}\text{C}$  excursion in the lower Nantsinkuan Formation within the Tremadocian *Rossodus manitouensis* Zone; (2) an excursion with two peaks roughly within the late Tremadocian *Paltodus 'deltifer'* Zone; (3) a positive  $\delta^{13}\text{C}$  shift in the lower Hunghuayuan Formation, within the early Floian *Serratognathus diversus* Zone; (4) a gradual positive  $\delta^{13}\text{C}$  shift in the late Floian, ranging from the uppermost *S. diversus* Zone to the basal *Oepikodus evae* Zone; (5) a minor negative shift in the lower Dawan/Zitai Formation, within the early Dapingian *Baltoniodus triangularis* Zone. These excursions are herein used for correlation of the Yangtze Platform strata with successions from South China, North China, the Argentine Precordillera, North America and Baltica. From a palaeogeographical perspective, the Gudongkou, Xiangshuidong and Daling sections represent depositional environments along an inner to outer ramp profile. The  $\delta^{13}\text{C}$  data from these sections show successively heavier (higher)  $\delta^{13}\text{C}$  values with increasing depositional depth, which can be interpreted as due to remineralization of organic carbon within the carbonate rocks formed in the shallow-water environment.



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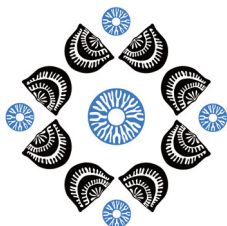
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# Oxygen isotope compositions of conodonts – analytical challenges of *in situ* SIMS studies

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Reliable deep-time environmental and climate reconstructions are needed to understand the drivers of Earth's system evolution over geological time. Palaeozoic temperature estimates, including reconstructions of the climate change through the Ordovician, are based mainly on oxygen isotope ( $^{18}\text{O}/^{16}\text{O}$ ;  $\delta^{18}\text{O}_{\text{VSMOW}}$ ) thermometry derived from carbonate rocks with fossils such as calcitic brachiopods and phosphatic conodonts that are often the best preserved repositories of environmental conditions.

Palaeoenvironmental reconstructions are reliable only if the geochemical data is obtained using well-calibrated analytical tools. Most previous research devoted to oxygen isotope composition of conodonts has been conducted using the bulk method (gas source isotope ratio mass spectrometry (GS-IRMS)) that typically requires pooling several dozens of conodont elements for a single isotope ratio measurement. As such, studies of conodont-poor intervals and assessments of taxon-specific  $\delta^{18}\text{O}$  variability require extensive sample preparation and are challenging using the bulk method. Such challenges can be addressed by *in situ* secondary ion mass spectrometry (SIMS) analyses using only picogram sampling masses. However, several studies have reported inconsistencies between SIMS and GS-IRMS  $\delta^{18}\text{O}$  data for the same research material. We aim to solve this controversy by establishing a robust analytical protocol for conodont isotope analysis by SIMS.

Here we present conodont data on *Pterospathodus* and *Amorphognathus* specimens extracted from Ordovician strata in Nurme and Mehikoorma-421 boreholes (Estonia). Oxygen isotope composition of conodonts was analysed by both SIMS and GS-IRMS, where we paid particular attention to four inorganic apatite reference materials in order to understand the offset between these two techniques that have been reported in the literature. While the results of GS-IRMS measurements conducted using high-temperature reduction of  $\text{Ag}_3\text{PO}_4$  represent exclusively  $\delta^{18}\text{O}$  of phosphate-bound oxygen, SIMS analyses do not discriminate between different oxygen components (e.g.,  $(\text{PO}_4)^{3-}$ ,  $(\text{SiO}_4)^{4-}$ ,  $(\text{CO}_3)^{2-}$ , and  $(\text{OH})^-$ ) in apatite, inherently providing information on pooled isotope compositions. We conducted quantitative chemical analyses of selected conodont elements by electron probe microanalysis to assess to what extent matrix effects cause the offsets between the two isotope techniques. We also used scanning electron microscopy and white light optical profilometry to evaluate sample topography and porosity, which have a major impact on SIMS data quality.

We collected oxygen isotope data using a CAMECA 1280-HR large geometry instrument at the Potsdam SIMS user facility over several months to determine reproducibility of the results and to optimise a routine measurement protocol. Our tests included a variety of instrumental settings, e.g., different raster parameters for both pre-sputtering and data collection, which yielded slightly differing results due to different instrumental mass fractionation. SIMS is a comparative method, and as such relies on reference materials that have been previously characterised by bulk methods, ideally provided by multiple laboratories. We noted that the inconsistent offsets between SIMS and GS-IRMS data obtained for a given conodont specimen (with SIMS  $\delta^{18}\text{O}$  values in most cases being higher) are linked to reference material measurements that are necessary for conodont data calibration and are often biased towards lighter  $\delta^{18}\text{O}$  values. Our tests show that such bias is even more significant when calibration is based on a single reference material characterised by a single GS-IRMS laboratory, which has been a common practice in past conodont studies.





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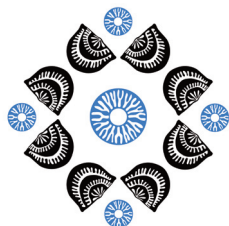
brachiopods, ostracods, trilobite,  
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# A summary of the Brazilian Paraná Basin Ordovician

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The study of the Ordovician of Paraná Basin culminated on the three-fold lithostratigraphic subdivision of the Rio Ivaí Group as follows: Alto Garças, Iapó and Vila Maria formations. The history of deposition of these rocks is linked to the transition from a marine fluvial environment into the glacial diamictites and shales with dropstones, overlain by post-glacial transgressive shales, siltstones and sandstones. The Ordovician–Silurian transition is marked by a glacial and an extinction event that impacted the marine diversity of life and the permanence of the first land plants. At least three sections, designated as the sections 1, 2 and 3 below, had their sedimentary facies, taphonomy, organic carbon content and thermal maturation analysed as well as their macro- and microfossil assemblages recognized.

All studied sections were productive for macro- and microfossils, although the section 1 has limited occurrence and lower preservation of palynomorphs. The greatest fossil diversity was recovered from the section 2. To date, the diversity recovered from the Ordovician–Silurian of the Paraná Basin comprises 12 fossil groups, namely ostracods, brachiopods, bivalves, gastropods, cryptospores, fungi, acritarchs, chitinozoans, prasinophyte algae, scolecodonts, a possible graptolite and, more recently, a trilobite of the order Dalmanitidae. 51 species of palynomorphs of terrestrial and marine origin were recognized. This is the highest diversity reported from the glacial–postglacial transition in the Ordovician–Silurian boundary interval of Brazil. 18 species of cryptospores, acritarchs and fungi occur in the basal diamictites (the Iapó Formation) as well as the discinoid *Kosoidea australis*. In the upper part of these diamictites, the palynomorph assemblage comprises 26 taxa, most of which persist also in the postglacial shales. Still, in the shales with dropstones of the Iapó Formation, brachiopods (*K. australis*, infau-nal lingulids, *?Palaeoglossa* and rhynchonelliformeans), endemic ostracods such as *Satiellina paranaensis* and pyritized specimens of a widely common Hirnantian index species *Harpabollia harparum* occur together with indeterminate ostracod species. At least two different species of bivalve mollusks were also found as well as a gastropod species (*Bucanella* sp.).

Observing the palynomorph assemblage, it was possible to record also chitinozoans restricted to the lowermost portion of the Vila Maria Formation. This part of the formation was observed in the outcrops 2 and 3 and contains postglacial chitinozoan assemblages that are not younger than the earliest Rhuddanian. Some centimeters above this interval but still in the lower part of the Vila Maria Formation, the occurrence of *Spinachitina debbajae* followed by *Spinachitina silurica* refer to the Silurian in the Paraná Basin. In the section 1, the recovery of a trilobite thorax configures the oldest record of this group in Brazil and shows that this ancient sea was also thriving with life even after the glaciation-related Hirnantian extinction event.



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# Ordovician geology and stratigraphy of China: A synthesis

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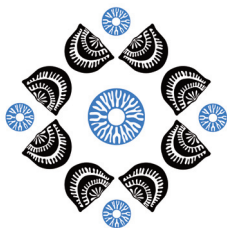
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China presently comprises several tectonic blocks and regions assembled over geological time and having independent histories. During the Ordovician, these blocks included South China, North China, Tarim, Qaidam, Junggar, Qiangtang-Qamdo, Lhasa and partially Himalaya, Sibumasu and Indochina, as well as the Altay-Xing'an and Songpan-Garze fold belts, which were discrete but adjacent. Twelve stratigraphic megaregions bounded by tectonic sutures or major fault zones are recognised for the Ordovician System. Some of them are further subdivided into regions according to specific lithological and biotic facies or distinct stratigraphic successions. The palaeontological features and biostratigraphic framework of these stratigraphic megaregions and regions are summarised. The unified biostratigraphic framework presented herein includes 33 graptolite and 27 conodont biozones through the Ordovician, together with supplementary biozones, communities or associations of brachiopods, trilobites, cephalopods, chitinozoans, acritarchs and radiolarians. With the constraints of integrative chronostratigraphy, biostratigraphy, chemostratigraphy, cyclostratigraphy and magnetostratigraphy, along with some geochronological data, our understanding of the temporal and spatial distribution of the Ordovician lithostratigraphic units on these major blocks has been significantly advanced. The refined integrative stratigraphic framework of the Ordovician provides a precise constraint on the major tectonic orogenies and biotic events evident in China.



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# Reconstruction of the first consumer-driven marine ecosystem on Earth, perspectives from early Cambrian small skeletal fossils from China

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Biological activity was the major triggering factor driving Earth's organic and inorganic cycles across the biosphere, lithosphere, and atmosphere. A key question in the evolution of Earth's ecosystem is when and how different animals emerged and flourished and how their appearance impacted the hydrosphere-atmosphere-lithosphere cycles. The Cambrian Explosion of metazoans in the Ediacaran–Cambrian boundary interval resulted in sudden appearance of most of the readily fossilizable modern animal groups as macro-consumers in the Earth's oceans. This explosive radiation event led for the first time to the emergence and diversification of animals on Earth, to the establishment of complex trophic webs with animals as consumers, and marks the onset of the Phanerozoic oceanic ecosystem. Our presentation aims to discuss the at least half-billion-year-old world of tubular and conical shelled organisms (sponges, conulariids, cancelloriids, hyoliths, mollusks, tomotiids, and other lophotrochozoans) that are unseen in the present-day oceans but were recovered by us from the siliciclastic and carbonate rocks in and outside of China. Additionally, to study the body fossils of exceptionally preserved biotas (Konversat-Lagerstätten) across China, efforts are underway to understand how the early animals, notably early bilaterians, created the over 500-million-year-old oceanic ecosystems without the influence of land plants, which appeared later.



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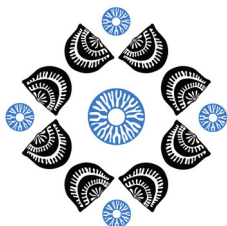
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# An integrative biostratigraphic, chemostratigraphic, and sequence stratigraphic perspective of the Ordovician–Silurian boundary on Anticosti Island (Canada)

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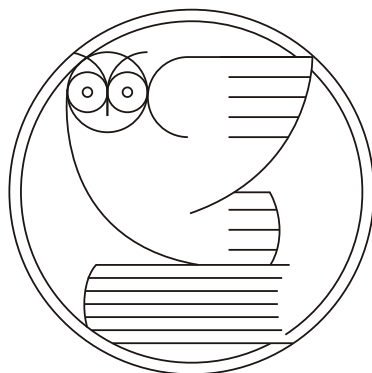
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Anticosti Island, Canada, has long been recognized as an exceptional Ordovician–Silurian boundary succession with the potential to serve as one of the best records of climatic, oceanographic, and biological events associated with the Late Ordovician mass extinction. However, differing interpretations as to the position of the Hirnantian Stage within the stratigraphic succession due to the paucity of diagnostic graptolites, the apparent absence of a typical *Hirnantia* fauna within the Upper Ordovician Ellis Bay Formation, and lateral facies variability among outcrops has hindered the study of the Ordovician–Silurian boundary on the island, particularly in the eastern half of the outcrop belt. Definitively identifying the stratigraphic position of the Hirnantian Stage within the succession is therefore critical for understanding this classic Ordovician–Silurian boundary section, as well as for the integration of data from Anticosti into our global understanding of the Late Ordovician mass extinction.

Here, we take an integrative approach to studying the Ellis Bay and lowermost Becscie formations, combining new paleobiological, geochemical, radiometric, and sequence stratigraphic constraints from ongoing fieldwork with existing biostratigraphic, geochemical, and palynological studies in the context of newly measured stratigraphic sections. These formations record six depositional sequences bounded by regionally traceable but subtle unconformities, often mantled by thin siliciclastic veneers reworked into transgressive lag facies. Many of these unconformities have gone unrecognized despite more than a century of work at certain localities. Furthermore, despite previous controversy, multiple lines of evidence favor a Hirnantian age for the entire Ellis Bay and lowermost Becscie formations, including newly recognized occurrences of *Hirnantia* and *Hindella* in the lower Ellis Bay Formation, a two-phased positive carbon isotope excursion, with the second phase reaching ~6‰ in the Laframboise Member of the Ellis Bay Formation, and a U–Pb TIMS age of  $443.61 \pm 0.52$  Ma from zircons in a bentonite from the mid-Ellis Bay Formation. While graptolite and conodont biostratigraphy support this age model, determination based on chitinozoan biozonation is more equivocal but may be controlled by facies preferences. Conodont, brachiopod, and chemostratigraphic data additionally suggest that the Hirnantian Stage may extend slightly into the lower Becscie Formation on the western end of Anticosti and well into the lower Becscie Formation in the eastern part of Anticosti.

Our reappraisal of a classic Ordovician–Silurian boundary section has important implications for understanding the sequence of climatic, environmental, and biological events throughout the Late Ordovician mass extinction. Given that the Ellis Bay and lowermost Becscie formations are indeed Hirnantian in age (encompassing ~2 My), these formations record six fourth-order depositional sequences of approximately ~333 ky. Furthermore, comparison of the Hirnantian of Anticosti to coeval exposures suggests that other regions may be incomplete at the level of the fourth-order cycles that occur in the Ellis Bay Formation. Resulting uncertainties in correlations based on unconformities and interpretations of stratigraphic architecture may therefore greatly complicate global correlation of Hirnantian records. Further study of this issue is critical, as stratigraphic architecture is expected to be an overarching control on the expression of oceanographic, climatic, and biotic events at a regional scale, complicating the interpretation of the pattern and drivers of the Late Ordovician mass extinction.



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