Estonian Journal of Earth Sciences
2024, **73**, 2, 71–80

https://doi.org/10.3176/earth.2024.07

www.eap.ee/earthsciences
Estonian Academy Publishers

RESEARCH ARTICLE

Received 15 February 2024
Accepted 26 March 2024
Available online 6 August 2024

Keywords:
stromatoporoid, aulaceratid, Late Ordovician, Baltica, Estonia

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Citation:
Jeon, J. and Toom U. 2024. First report of an aulaceratid stromatoporoid from the Ordovician of Baltica. *Estonian Journal of Earth Sciences*, **73**(2), 71–80. https://doi.org/10.3176/earth.2024.07

First report of an aulaceratid stromatoporoid from the Ordovician of Baltica

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ABSTRACT

The aulaceratid stromatoporoids first appeared in the late Middle Ordovician and had achieved a worldwide distribution in tropical to subtropical shallow-marine environments by the Late Ordovician; however, their presence in Baltica has not been documented. Here, we report *Aulacera vohilaidia* Jeon and Toom sp. nov. from the Upper Ordovician Adila Formation (Pirgu Regional Stage; late Katian stage) of Estonia, which is the first record of an aulaceratid stromatoporoid in the Ordovician of Baltica. *Aulacera vohilaidia* Jeon and Toom sp. nov. is characterised by three distinct skeletal zones (axial, lateral, and outer), each of which consists of cyst plates with distinctive size and convexity. The axial zone is narrow, featuring large horseshoe-shaped cyst plates with a wavy, imbricated pattern in a line. The lateral zone consists of small cyst plates punctuated by sporadically developed pillars, and the outer zone comprises flat, parallel cyst plates. Ridged structures with cusps are formed by parallel cyst plates in the outer zone, and the growth surface displays a pustular reticulated structure with a polygonal morphology. The occurrence of *Aulacera vohilaidia* Jeon and Toom sp. nov. in Estonia extends the palaeogeographic distribution of aulaceratid stromatoporoids from peri-Gondwana, Laurentia, and Siberia to Baltica. The arrival of aulaceratid stromatoporoids in Baltica coincided with warming of the climate on the palaeocontinent and the expansion of the range of this group during the Late Ordovician.

Introduction

Aulaceratid stromatoporoids are readily distinguishable among stromatoporoids by their unique growth morphologies, which have tree-like shapes (Webby and Kershaw 2015). These shapes are characteristically erect to inclined and generally unbranching or seldom branching, which may be digitate or dendroid as a form of intraspecific variation, possibly in response to sedimentary interruption or as an inherent growth strategy (Webby and Kershaw 2015). These forms are not commonly seen among Palaeozoic stromatoporoids (Webby and Kershaw 2015). Limited taxonomic groupings of stromatoporoids adopted tree-like growth forms during the Palaeozoic; however, only aulaceratids show tree-like forms with sizes ranging from several centimetres to a few metres (Webby 2015a; Webby and Kershaw 2015). The skeleton size of aulaceratids varies considerably, from centimetre-scale to more than 2 m, forming aulaceratid 'forests' during the Late Ordovician (Cameron and Copper 1994; Copper et al. 2013; Nestor et al. 2010; Webby and Kershaw 2015).

The first appearance of this unique group of stromatoporoids in the fossil record is in middle to upper Darriwilian (Middle Ordovician) strata, and the most diverse taxa have been reported from North China (Dong 1982; Jeon et al. 2022a; Ozaki 1938; Yabe and Sugiyama 1930). Aulaceratids have not been observed in Upper Ordovician strata in North China (Jeon et al. 2023), but they were widely distributed in the remainder of peri-Gondwana at this time, including South China (Jeon et al. 2022b), Australian terranes (Webby 1971, 1991), Laurentia (Bolton 1988; Copper et al. 2013; Galloway 1957; Galloway and St. Jean 1961), and Siberia (Nestor 1976; Yavorsky 1955, 1957, 1963).

During the Katian (Late Ordovician), aulaceratids were absent from Baltica, in contrast to their common occurrences in both Laurentia and Siberia. There is little overlap in the stromatoporoid faunas of eastern Laurentia (Anticosti Island) and Baltica (Estonia), even though these continents were geographically close at the time (Kaljo et al. 1970; Nestor et al. 2010). The greatest faunal difference is the absence of aulaceratid stromatoporoids in Baltica, although they were common and moderately diverse in both Laurentia and Siberia during the Late Ordovician. Such differences in stromatoporoid fauna are thought to indicate that Baltica and Laurentia were palaeobiogeographically separate (Kaljo et al. 1970; Nestor et al. 2010).

In this study, we report a typical aulaceratid stromatoporoid, *Aulacera*, from Baltica for the first time. This report documents the presence of aulaceratid stromatoporoids and their late arrival to Baltica during the late Katian (Pirgu Regional Stage) of the Late Ordovician. This discovery provides important information on the dispersal of aulaceratids prior to their disappearance during the latest Ordovician.

Geological setting and material

During the Ordovician, Estonia was part of the shallow epicontinental sea in Baltica and drifted from high latitudes to the equatorial region (Torsvik and Cocks 2017). This shift resulted in increased rates of carbonate sedimentation and favoured the development of warm-water biotic communities (Fig. 1; Nestor and Einasto 1997). The onset of a warmer climate, which had enabled the appearance of reefs and stromatoporoids, began in the Keila Regional Stage (corresponding to the early Katian age of the international timescale) and continued thereafter (Kröger et al. 2017; Nestor 1964, 1999). During the Katian, tabulate and rugose corals diversified rapidly (Kaljo et al. 2011; Sokolov 1951), and bioproduction increased in Baltica (Delabroye et al. 2011; Hints et al. 2018; Truuver et al. 2021).

In northern Estonia, in the onshore part of the Ordovician shallow shelf, two distinct successive rock units of the Pirgu Regional Stage are exposed: the lower Moe Formation and the upper Adila Formation (Hints et al. 2005). The Moe Formation consists of micritic and bioclastic nodular or bedded limestones with argillaceous intercalations, and the Adila Formation comprises mainly grey bioclastic limestone (Hints and Meidla 1997). The Pirgu Regional Stage is the thickest of the Ordovician stages in Estonia but is thinner in the southern islands (Hints et al. 2004, 2005), with its thickness varying by up to 45 m (Hints and Meidla 1997). The boundary between the Moe and Adila formations coincides with the boundary between the late Katian *Tanuchitina bergstroemi* and *Conochitina rugata* chitinozoan zones (Hints and Meidla 1997).

The Adila Formation is exposed along the eastern coastline of Vohilaid Island, Estonia (Fig. 1). The outcrops are rich in shelly fossils. Stromatoporoids are rare, whereas tabulates and rugose corals are abundant and are commonly overturned. Of note is the presence of large corals, such as heliolitid tabulate corals that are several deci-centimetres in diameter, and metre-scale colonial rugose corals. The calcareous skeletons of bryozoans, corals and stromatoporoids are commonly bioeroded. Abundant fossils were collected from Vohilaid outcrop 2 (58°55′29.0″ N, 23°01′42.2″ E; Fig. 1), but only four specimens were preliminarily identified as stromatoporoids. Among this small stromatoporoid collection, only one specimen (GIT 748-27) shows a columnar growth morphology, which is a diagnostic feature of aulaceratid-type stromatoporoids (Fig. 2). The specimen was photographed by Gennadi Baranov at the Department of Geology, Tallinn University of Technology, Estonia, and seven thin sections were prepared by Juwan Jeon, Korea University, for taxonomic description.

Repository and institutional abbreviation**:** All remaining material and thin sections of the specimen (GIT 748-27) are deposited at the Department of Geology, Tallinn University of Technology, Tallinn, Estonia.

Systematic palaeontology

Order LABECHIIDA Kühn, 1927
Family AULACERATIDAE Kühn, 1927
Genus *Aulacera* Plummer, 1843

Type species. *Aulacera plummeri* Galloway and St. Jean in Galloway, 1957.

Other species. *A. bacula* (Yavorsky, 1955), *A. conica* (Yavorsky, 1955), *A. cylindrica* (Foerste, 1909), *A. denensis* Webby, 1991, *A. gunnensis* Webby, 1991, *A. inaequalis* (Yavorsky, 1963), *A. intermedia* (Foerste, 1909), *A. mediupustulis* (Yavorsky, 1963), *A. nodulifera* (Foerste, 1909), *A. nodulosa* (Billings, 1857), *A. peichuangensis* Ozaki, 1938, *A. radiata* Galloway and St. Jean, 1961, *A. sibirica* (Yavorsky, 1955), *A. tenuipunctata* (Yavorsky, 1955), *A. tenuipustulis* (Yavorsky, 1963), *A. undulata* (Billings, 1857), *A. undulatadirecta* (Yavorsky, 1955), *A. vulgaris* (Yavorsky, 1957).

Diagnosis. Emended from Webby (2015a). Variable in size from centimetres to metres, unbranched columnar skeleton differentiated into an axial column and a lateral zone; the axial column consists of a single row of large, stacked cyst plates; the lateral zone possesses several rows of smaller, imbricated cyst plates and sporadic development of short, rounded pillars; outer zone present in some taxa, consisting of relatively parallel cyst plates, with or without ridged structures. Outer growth surface varies from fluted to smooth.

Remarks. Aulaceratid stromatoporoids characteristically possess differentiated skeletal zones (axial and lateral) with an overall dendroid to columnar shape and may be unbranched or branched (Webby 2015a). The presence of a third skeletal zone in the outermost layer is variable among aulaceratid taxa. The middle–late Darriwilian aulaceratids *Sinodictyon* Yabe and Sugiyama, 1930 and *Ludictyon* Ozaki, 1938 lack the outer skeletal zone (Jeon et al. 2022a; Ozaki 1938; Yabe and Sugiyama 1930). *Aulacera peichuangensis* Ozaki, 1938 is the only Darriwilian *Aulacera* species, and it possesses axial and lateral zones (Ozaki 1938). In contrast, the Katian *A. denensis* Webby, 1991 from Tasmania has an outer zone, characterised by a recrystallised fabric (Webby 1991). *Aulacera* species from Laurentia also possess outermost layers with

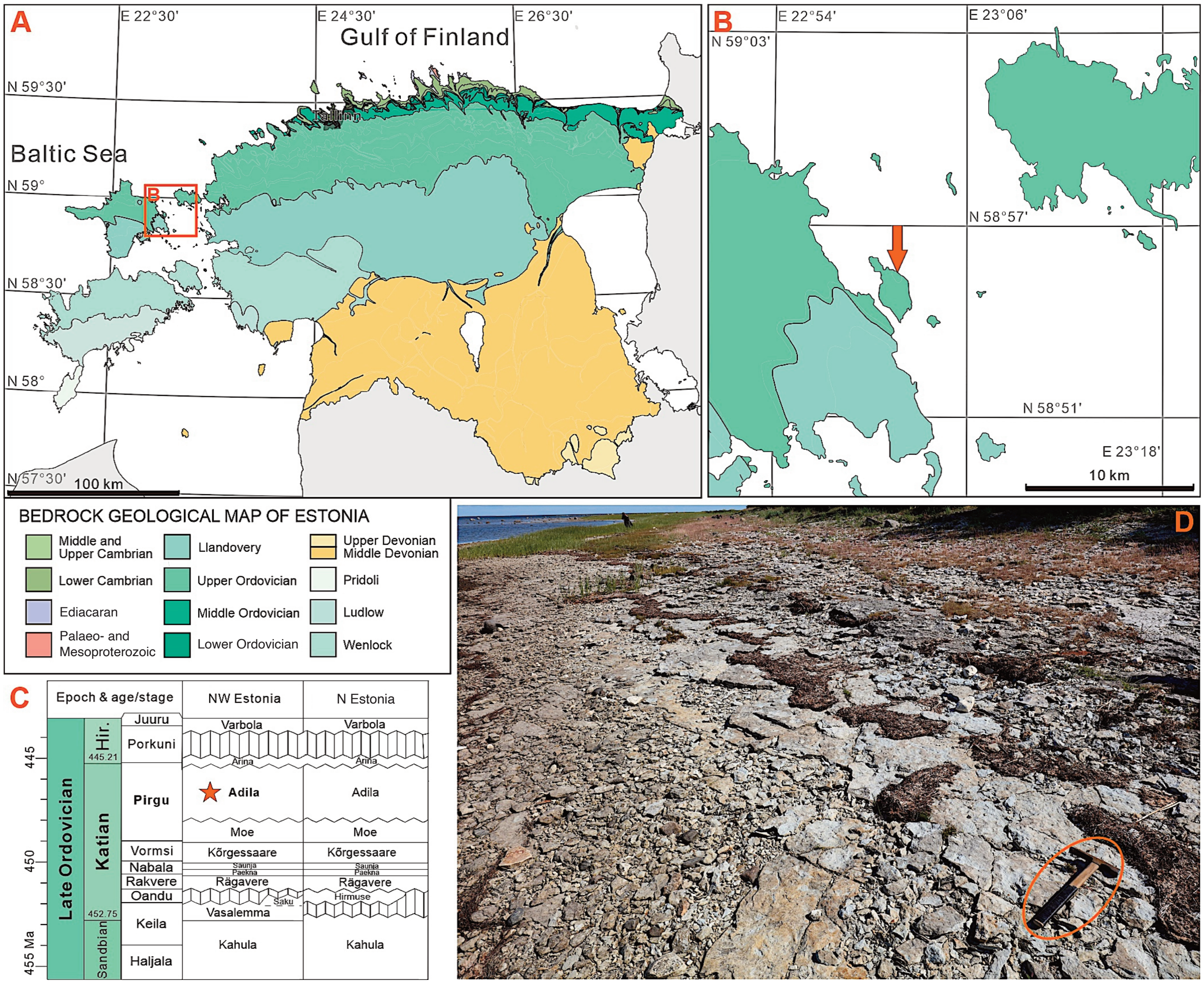

Fig. 1. Geological map of Estonia illustrating the geographical location and stratigraphic position of the study locality. **A** – location map of Estonia and the study locality (orange-outlined rectangle with B). **B** – enlargement of the area enclosed by the orange rectangle in A, showing the study locality (orange arrow; 58°55′29.0″ N, 23°01′42.2″ E) on the eastern coastline of Vohilaid Island, Estonia. Geological maps in A and B are modified after Hints and Toom (2023). **C** – stratigraphic chart of Upper Ordovician successions in northern to central Estonia. The stratigraphic position of the Adila Formation, where the *Aulacera* specimen was collected, is marked with a star. The stratigraphy and correlations are modified after Hints and Toom (2023). Abbreviation: Hir. – Hirnantian. **D** – photograph of the Vohilaid outcrop 2, geological hammer (orange ellipse) for scale.

flatter cyst plates than those of the lateral zone, and the growth surfaces of the Laurentian *Aulacera* taxa are characterised by an undulating appearance (Copper et al. 2013; Galloway 1957; Galloway and St. Jean 1961). The middle–late Darriwilian *Thamnobeatricea* Raymond, 1931 reported from North China has only two skeletal zones (axial and lateral), without denticles and pillars (Dong 1982; Jeon et al. 2022a). In contrast, Katian *Thamnobeatricea* taxa reported from the Tasmanian terrane and South China feature outer zones with a recrystallised fabric (Webby 1991; Jeon et al. 2022b). The South Chinese endemic aulaceratid genus *Sinabeatricea* Jeon, described by Jeon et al. (2022b), shows skeletal division into axial and lateral zones, with the axial zone characterised by a unique open radiating reticulate structure that has not been recognised in other aulaceratid stromatoporoids (Jeon et al. 2022b). The Australian genus *Alleynodictyon* Webby, 1971 exhibits a thin outer zone, mostly silicified, making it difficult to determine the internal structures (Webby 1971). The youngest Ordovician aulaceratid, *Quasiaulacera* Copper, Stock and Jin, 2013 has a well-developed outer zone with long pillars (Copper et al. 2013). Further investigations are required to ascertain whether the presence of the outer zone within aulaceratid genera reflects variations between each genus or is an interspecific feature.

Aulacera vohilaidia Jeon and Toom sp. nov.
Figs 2–4

Etymology. Named after the Estonian island of Vohilaid, where the specimen was collected.

Type specimen. Holotype, GIT 748-27.

Type locality. Vohilaid outcrop 2 (58°55′29.0″ N, 23°01′42.2″ E), the Adila Formation of late Pirgu age (late Katian, Late Ordovician).

Diagnosis. Aulacera with a columnar skeleton of a relatively small footprint, consisting of three differentiated skeletal zones (axial, lateral, and outer) with imbricated cyst plates of

Fig. 2. Overall view of *Aulacera vohilaidia* Jeon and Toom sp. nov., GIT 748-27, from the Upper Ordovician Adila Formation at the Vohilaid outcrop 2 in Estonia. **A** – field photograph of GIT 748-27, showing the recumbent position of *A. vohilaidia*, parallel to the bedding plane. Arrows indicate two small-sized borings, enlarged in B, and an encrusting bryozoan, enlarged in C. **B** – enlarged area, marked with arrow B in A, showing the growth surface with a pustular reticulated structure and polygonal texture, and two small-sized borings (orange arrows). **C** – enlarged area, marked with arrow C in A, showing a bryozoan encrusting on *A. vohilaidia*. **D** – bottom view of *A. vohilaidia*, and associated bioerosion. **E** – enlarged area, marked with a rectangle in D, showing detailed view of *Trypanites sozialis* Eisenack, 1934 infilled by micrite (orange arrows).

variable size and convexity; axial zone, relatively narrow, consisting of imbricated large horseshoe-shaped cyst plates, forming a wavy pattern without any vertical elements; surrounding lateral zone, composed of small cyst plates punctuated by short pillars but not protruding into the thin outer zone; cyst plates in the outer zone are flat and parallel, with lateral boundaries unclear; ridged structures with cusps, formed by parallel cyst plates that are held apart but not protruding into the surrounding sediment; growth surface characterised by a pustular reticulated structure with a polygonal morphology without any papillae and an undulating growth surface.

Description. The skeleton has an unbranched columnar shape, is fragmentary and measures approximately 335 mm long with a diameter of 48 mm (Fig. 2A, D). The preserved thickness of the skeleton is generally consistent, although it is unclear whether there was any growth variation in the early growth stage due to the absence of the basal skeleton and the fragmentary preservation. Therefore, the nature of initial growth in this form remains unknown. The toppled skeleton is preserved in a recumbent position (Fig. 2A). The growth surface displays a pustular reticulated structure with a polygonal morphology (Fig. 2B). The recumbent specimen was encrusted by bryozoans (Fig. 2C), and small borings less than

1 mm in diameter occur on the upper surface (Fig. 2B). The bottom surface of the stromatoporoid contains borings of *Trypanites sozialis* Eisenack, 1934, which are approximately 5 mm in diameter, infilled by micritic sediments (Fig. 2D, E).

The skeleton is composed of three skeletal zones (axial, lateral, and outer), each composed of cyst plates of variable size and convexity (Fig. 3A, B). The axial zone is narrow, occupying less than 12% of the diameter of the columnar skeleton (Fig. 3A–C, G). Large horseshoe-shaped cyst plates are aligned in slightly wavy imbricated lines (Fig. 3C). Each cyst is 1.34–3.98 mm high (n = 7; average = 2.62 mm) and 2.02–3.11 mm wide (n = 7; average = 2.41 mm). The height/width ratios of the cyst plates range from 0.51 to 1.68 (n = 7; average = 1.09). The axis of the columnar skeleton is surrounded by small, imbricated cyst plates, and the axis of the small cyst plates is inclined outwards from the centre of the horseshoe-shaped and large cyst plates (Fig. 3A, B, E, H, I). The lateral zone occupies the largest part of the skeleton but is thicker on one side of the stromatoporoid, with a maximum difference in thickness of 25.42 mm (Fig. 3A, B). Cyst plates in the lateral zone, which are imbricated, are 0.26–0.70 mm high (n = 80; average = 0.40 mm) and 0.31–0.66 mm wide (n = 80; average = 0.45 mm), and their height/width ratios range from 0.54 to 1.52 (n = 80; average = 0.90; Fig. 3E, H, I). Pillars without walls are sporadically distributed and penetrate two to three cysts with a cone-in-cone structure, but the height is uncertain due to poor preservation (Fig. 3E, H–J). Pillar thickness is between 0.19 and 0.54 mm (n = 16; average = 0.31 mm) and appears dot-like in tangential section. The outer phase, which is less than 2 mm thick, consists of up to eight distinct cyst plates. The convexity of cyst plates decreases to a moderate to low level, and they eventually become parallel to each other, thereby making it difficult to distinguish the exact boundaries of each cyst plate (Fig. 3D–F). The thicknesses of the parallel cyst plates are 0.21–0.42 mm (n = 30; mean = 20 mm). Each parallel cyst plate forms a ridged structure with a cusp, though they do not merge (Fig. 3F). The cusps of these ridges do not protrude into the surrounding sediment, and no undulating growth surface is observed (Fig. 3A, B, F).

Remarks. Aulacera vohilaidia Jeon and Toom sp. nov. shares skeletal similarities with *Aulacera* species from Laurentia, particularly in the presence of an outer zone composed of parallel cyst plates with ridged structures (Fig. 3F). However, the outer layer of *A. vohilaidia* is more distinctly differentiated than that of other *Aulacera* species. The external growth surface of *A. vohilaidia* appears relatively smooth compared with the undulating outer appearance of the giant aulaceratids from Laurentia (Figs 2A, B and 3A, B, F; Copper et al. 2013; Galloway 1957; Galloway and St. Jean 1961). The development of the outer zone may represent interspecific variation within *Aulacera*, but the exact timing of secretion of this skeletal zone during growth remains uncertain owing to the absence of the basal skeleton. Furthermore, the thickness of the outer zone among *Aulacera* species needs further careful investigation based on in situ skeletons, as it cannot be ruled out that recumbent skeletons had been eroded, potentially resulting in a thinner outer zone than when originally secreted (Fig. 4A, yellow arrow, indicating the eroded surface of the stromatoporoid skeleton, as evidenced by truncated cyst plates in the lateral to outer zones).

Two different sizes of *Trypanites sozialis* Eisenack, 1934 borings can be identified on the surface of *A. vohilaidia*, each indicating a different timing of formation. The smaller borings, with diameters less than 1 mm, are confined to the outer zone of *A. vohilaidia* and generally do not penetrate deep into the lateral zone (Fig. 3D). These smaller borings exhibit a distinct boundary line, indicating that they were formed after the cementation of the outer zone. In contrast, the larger borings penetrate through the outer zone and extend into the lateral zones of the stromatoporoid approximately perpendicular to the substrate (Figs 2D, E and 4). At the interface boundary between the large *T. sozialis* and the stromatoporoid, the cyst plates are truncated, and the cysts are filled with sediments similar to those filling the *Trypanites* borings (Fig. 4). This finding indicates that the trace-makers of the large *Trypanites* penetrated the skeleton of *A. vohilaidia* after the stromatoporoid had fallen to the seafloor. These trace-makers tend to cluster on relief heights and prefer substrates with a homogeneous and dense texture (Knaust et al. 2023; Toom et al. 2023). After the initial colonisation, the large stromatoporoid fragment was tumbled during episodic events, becoming encrusted by bryozoans and providing living space for smaller borers. As indicated by the eroded areas with sharp boundaries on the stromatoporoid's lower surface (yellow arrow in Fig. 4A), the stromatoporoid fragment was most likely overturned several times before its final burial.

Discussion

The palaeobiogeographic and biostratigraphic distributions of aulaceratid stromatoporoids during the Ordovician have been compiled, including the discovery of *Aulacera vohilaidia* Jeon and Toom sp. nov. in Baltica (Fig. 5). Aulaceratid stromatoporoids have been documented in Middle to Upper Ordovician rocks on nearly all major continents and terranes, except until now in Baltica (Nestor and Webby 2013; Stock et al. 2015). The earliest-known appearance of aulaceratid-type stromatoporoids is from the middle–late Darriwilian of the Middle Ordovician (Webby et al. 2015; Jeon et al. 2022a). Four genera of aulaceratids (*Aulacera*, *Ludictyon*, *Sinodictyon*, and *Thamnobeatricea*) have been identified only in North China, with no occurrences reported in other contemporary terranes of middle–late Darriwilian age (Dong 1982; Jeon et al. 2022a; Ozaki 1938; Stock et al. 2015; Yabe and Sugiyama 1930). Aulaceratids made their appearance at around the same time as other groups of labechiid stromatoporoids, such as *Labechia* and *Labechiella* (Jeon et al. 2022a; Stock et al. 2015; Webby 2015b; Webby et al. 2015). However, unlike the widespread distribution of other labechiid stromatoporoids globally and regionally during the same period, aulaceratid stromatoporoids were localised to North China (Nestor and Webby 2013; Stock et al. 2015; Webby 2015b).

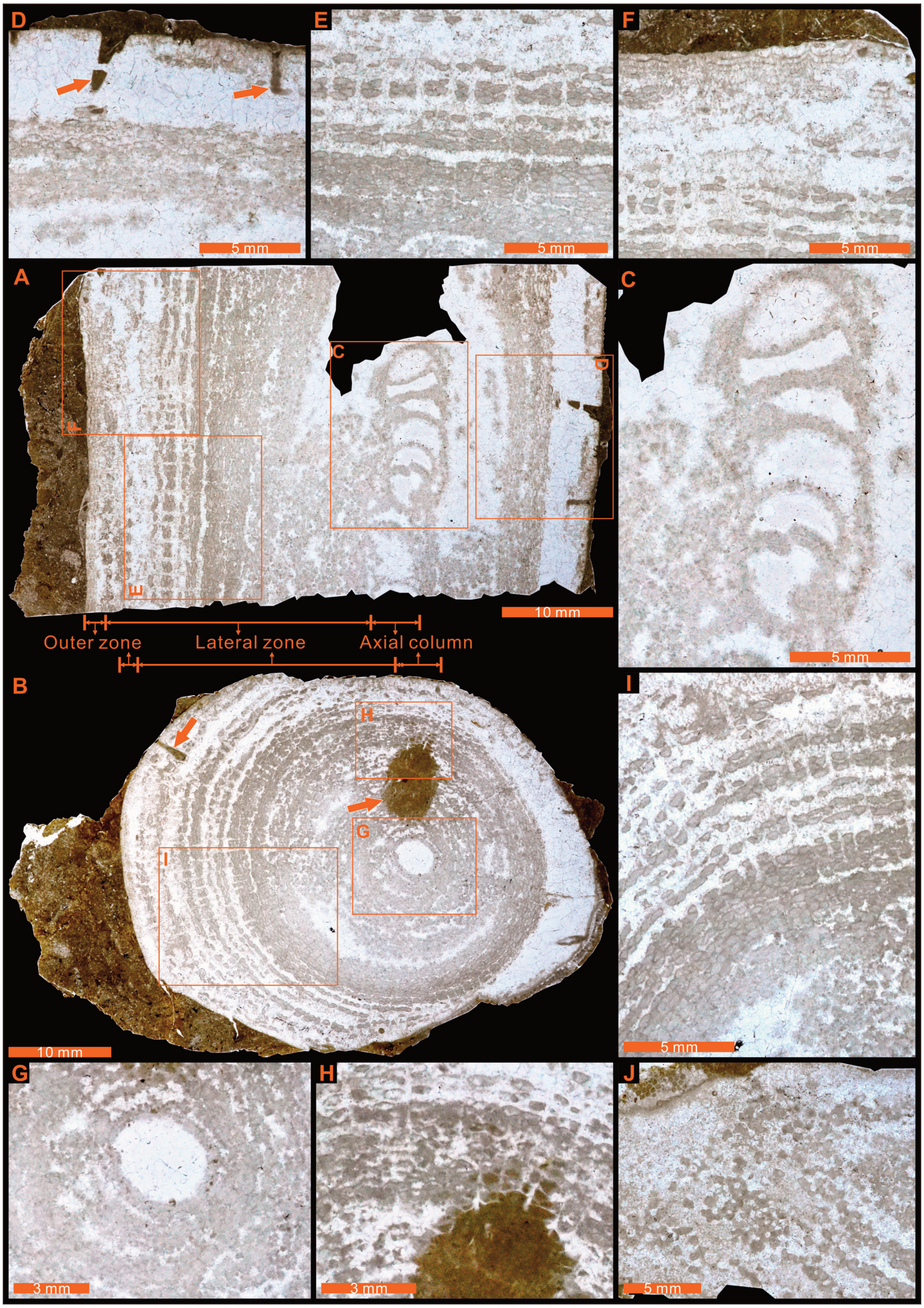

Fig. 3. *Aulacera vohilaidia* Jeon and Toom sp. nov., GIT 748-27, from the Upper Ordovician Adila Formation at the Vohilaid outcrop 2 in Estonia. **A** – longitudinal section of the columnar skeleton of *A. vohilaidia*. **B** – tangential section of the columnar skeleton of *A. vohilaidia*. **C** – enlarged view of the narrow axial zone of the columnar skeleton, showing the large horseshoe-shaped cyst plates with a wavy imbricated pattern. **D** – lateral zone, showing small, imbricated cyst plates without pillars. Note that the small-sized *Trypanites sozialis* Eisenack, 1934 borings (orange arrows) are confined to the outer zone and do not reach the deeper lateral zone. **E** – lateral zone, showing small, imbricated cyst plates punctuated by wall-less pillars. **F** – lateral to outer zones, showing the change of the convexity of cyst plates from moderate to low levels, which eventually align parallel, forming ridged structures. **G** – enlarged tangential section of the axial large horseshoe-shaped cyst plates. **H** – enlarged view of small, imbricated cyst plates with thin pillars, truncated by a large unidentified boring. Note the truncated cyst plates and cyst infilled with sediments similar to the filling of the boring at the boundary between the boring and the stromatoporoid structure. **I** – longitudinal section of the lateral zone, showing varying preservation of pillars. **J** – tangential section of the lateral zone, showing dot-like appearance of pillars. Note that there is an encrusting bryozoan on the stromatoporoid (top left).

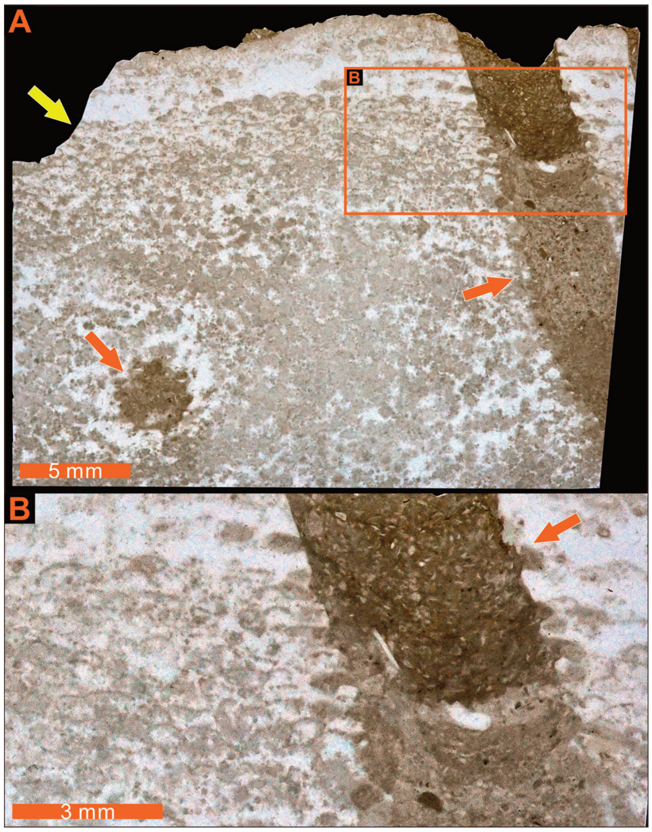

Fig. 4. *Aulacera vohilaidia* Jeon and Toom sp. nov., GIT 748-27 and associated *Trypanites sozialis* Eisenack, 1934, GIT 748-27-2, from the Upper Ordovician Adila Formation at the Vohilaid outcrop 2 in Estonia. **A** – two borings with different orientations in the lateral zone of *A. vohilaidia*: *T. sozialis*, approximately perpendicular to the surface, and an unidentified small boring (orange arrows). The yellow arrow points to the eroded surface of *A. vohilaidia*, indicating that the groove is not a natural feature of the stromatoporoid, which was eroded after toppling. **B** – enlarged view of cyst plates in the lateral zone truncated by *T. sozialis* and filled by micritic sediments (orange arrow). Different colours of micritic sediment layers probably indicate early lithification of the underlying sediment.

In the Late Ordovician, aulaceratid stromatoporoids expanded to other peri-Gondwanan terranes near North China, eventually reaching Laurentia and Siberia (Nestor and Webby 2013; Stock et al. 2015). This wide dispersal of aulaceratids was likely facilitated by their diversification (Jeon et al. 2022b). The Katian age marked a peak in the diversity of aulaceratids, as well as other labechiid stromatoporoids, coinciding with the first appearance of clathrodictyids and actinostromatids (Webby 2004). Few endemic taxa, such as *Sinabeatricea* in South China (Jeon et al. 2022b) and *Alleynodictyon* in Australia (Webby 1971), were present in specific terranes. Laurentia and Siberia boasted a relatively high diversity of aulaceratids, particularly within the genus *Aulacera* (Galloway 1957; Galloway and St. Jean 1961; Yavorsky 1955, 1957, 1963). This diversity may be attributable to taxonomic over-splitting, although verification of all type materials is needed.

Conversely, diverse aulaceratid stromatoporoids in Laurentia are also assumed, necessitating further investigation (personal communication with Jisuo Jin and David Harper in June 2021, and Paul Copper in November 2020). Notably, the gigantic aulaceratids found in Upper Ordovician successions on Anticosti Island presumably reached heights of more than 2 m, boasting tree-trunk-like columnar skeletons (Cameron and Copper 1994; Copper et al. 2013). Similar to the Laurentian examples, aulaceratids were diverse and widespread on the Siberian Platform (Dronov et al. 2016; Yavorsky 1955, 1957, 1963). These gigantic organisms thrived in the soft, muddy sediments of carbonate ramps or deeper platforms under low to moderate energy conditions (Cameron and Copper 1994; Nestor et al. 2010). Smaller-sized aulaceratids likely inhabited shallower environments, such as more restricted, onshore, lagoonal-type platform and island shelf settings (Jeon et al. 2022a; Webby, 1971, 1991, 2004). Middle–Late Ordovician aulaceratids, such as branching columnar genera like *Alleynodictyon* and *Thamnobeatricea*, are found in bedded, muddy carbonate successions characteristic of restricted, onshore, lagoonal-type environments under low to moderate energy conditions (Webby 1971, 1991, 2004). These environments were prevalent in a number of regions, including North America, Russia, North China, New South Wales, and Tasmania (Webby 2004). Aulaceratids with distinctive morphologies appear to have inhabited different environments. Therefore, the environmental tolerance of aulaceratid species may have been narrower than that of more widely distributed labechiid stromatoporoids that lived at the same time.

The occurrence of aulaceratid stromatoporoids in Baltica indicates that aulaceratids reached Baltica during their Late Ordovician dispersal. The movement of Baltica towards the equatorial regions might have occurred during the great expansion of aulaceratids in the Late Ordovician. The absence of aulaceratid stromatoporoids in Baltica has previously been interpreted to indicate an independent palaeobiogeographic unit separate from Laurentia (Kaljo et al. 1970; Nestor et al. 2010). However, a proposal to group Laurentia and Baltica in the same palaeobiogeographic unit was based on the occurrence of *Cystistroma canadense* (Nicholson and Murie 1878) in both continents (Jeon et al. 2022b). Nonetheless, it should be noted that the majority of Ordovician stromatoporoids in Baltica differ from those in Laurentia. In particular, although *Aulacera* is relatively diverse in both Laurentia and Siberia, *A. vohilaidia* is readily distinguishable from other taxa on each continent. Therefore, it may be more plausible to conclude that Laurentia had only minimal faunal influences on Baltica, which probably did not affect the overall stromatoporoid fauna and community in Baltica.

Although Ordovician stromatoporoids have been extensively studied in Estonia (Nestor 1964), aulaceratids had not previously been identified, most likely due to the sporadic distribution and random occurrence characteristic of stromatoporoids. Stromatoporoids are not common in the Vohilaid locality, where the specimen of *A. vohilaidia* was collected, while tabulate and rugose corals are abundant. Further investigations of stromatoporoids along the coastline of eastern Vohilaid Island should be conducted to minimise the sampling bias. The sampling bias is probably partially responsible

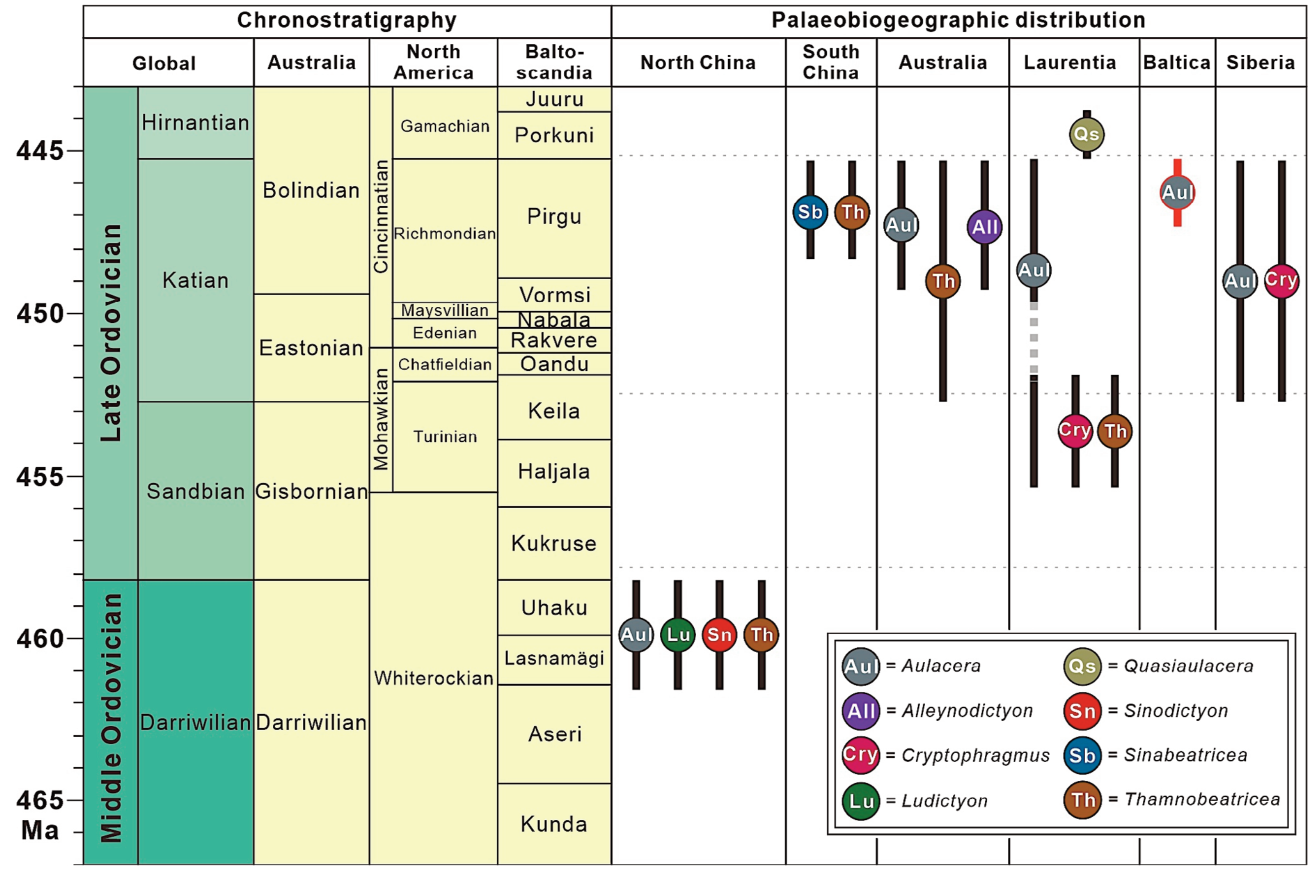

Fig. 5. Stratigraphic and palaeobiogeographical distributions of aulaceratid stromatoporoids during the Ordovician. The occurrences of aulaceratid stromatoporoids in each continent and terrane are compiled from Bolton (1988), Copper et al. (2013), Dong (1982), Galloway (1957), Galloway and St. Jean (1961), Jeon et al. (2022a, 2022b), Nestor (1976), Ozaki (1938), Webby (1971, 1991), Yavorsky (1955, 1957, 1963), Yabe and Sugiyama (1930) and this study.

for the lack of aulaceratids in Baltica; in addition, there was difficulty in accessing the western islands of Estonia during the Soviet period, which further hindered our understanding of the Late Ordovician stromatoporoid diversity of Estonia. Therefore, there is potential for further discoveries of aulaceratid stromatoporoids in Baltica, which could improve our knowledge of their dispersal prior to their mass extinction during the Late Ordovician glaciation.

For the Hirnantian age, marked by a significant decline in stromatoporoid diversity (Webby 2004), only one genus of aulaceratid stromatoporoid, *Quasiaulacera*, has been found in the Ellis Bay Formation of Anticosti Island (Copper et al. 2013). On Anticosti Island, the dominant aulaceratid changes from *Aulacera* to *Quasiaulacera* through the Katian to Hirnantian interval (Copper et al. 2013). An unusual occurrence of an aulaceratid stromatoporoid, *Ludictyon*, has been reported from lower Silurian rocks in southern China (Dong and Yang 1978). However, this early Silurian stromatoporoid exhibits skeletal similarities to rosenellid stromatoporoids, as confirmed by specimens housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China. Therefore, it is highly likely that typical Ordovician aulaceratids had disappeared by the end of the Hirnantian and probably did not continue into the Silurian (Fig. 5).

Aulaceratid-type architecture, represented by *Pararosenella* Vassiljuk and Bogoyavlenskaya in Bogoyavlenskaya et al. (1990), reappeared in the Upper Devonian (Famennian) succession of Ukraine and the northern Caucasus (Bogoyavlenskaya et al. 1990). The relationship between this Late Devonian taxon and Ordovician aulaceratids is uncertain, but the similarity is most likely the result of convergence of the growth morphology. Further detailed studies are needed to understand the relationship between Ordovician and Late Devonian aulaceratids, their environments, and their precise stratigraphic occurrences.

Conclusion

The discovery of *Aulacera vohilaidia* Jeon and Toom sp. nov. from the Upper Ordovician Adila Formation of Estonia marks the first known occurrence of aulaceratid stromatoporoids in Baltica. This finding extends the known palaeogeographic distribution of aulaceratid stromatoporoids to Baltica; the group was previously documented in North China, South China, Australian terranes, Laurentia and Siberia. *Aulacera vohilaidia* sp. nov. contributes to our understanding of the morphological diversity within the group. The new species exhibits distinctive features and possesses three skeletal zones with different cyst-plate morphologies: a narrow axial zone with large horseshoe-shaped cyst plates; a lateral zone composed of small cyst plates punctuated by sporadically developed columns; and an outer zone with flat, parallel cyst plates with ridged structures and cusps. The later arrival of aulaceratid stromatoporoids in Baltica, relative to other continents and terranes, is consistent with the establishment of warm-water environments from the early Katian onward, resulting from the movement of Baltica towards the equatorial zone and the global expansion of aulaceratids and other stromatoporoids during this period. In addition, given the specific distribution of aulaceratid stromatoporoids in environments characterised by low to moderate energy conditions, the finding of the columnar *Aulacera* in Estonia may provide insights into the environmental conditions in which this stromatoporoid lived, as well as the migration patterns of stromatoporoids during the Late Ordovician.

Acknowledgements

We sincerely thank Gennadi Baranov (Department of Geology, Tallinn University of Technology), who kindly helped us obtain detailed photographs of GIT 748-27. We also extend our gratitude to Paul Copper, David Harper and Jisuo Jin, who generously provided photographs of interesting aulaceratids from North America and Greenland. The manuscript benefited from the helpful comments and suggestions of reviewers Carl Stock and Stephen Kershaw. This study was supported by the Estonian Research Council (grant No. PUTJD1106), the National Research Foundation of Korea (grants Nos 2021R1A2C1009687 and RS-2023-00209495) and a grant from Korea University. This paper is a contribution to IGCP project 735 ‘Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification’. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

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Aulatseratiidse stromatopoori esmaleid Baltika paleokontinendilt Ordoviitsiumis

Juwan Jeon ja Ursula Toom

Aulatseratiidsed stromatopoorid saavutasid üleilmse leviku Hilis-Ordoviitsiumis, kuid selle rühma esinemine Baltika paleokontinendil oli siiani teadmata. Käesolevas töös kirjeldatakse Eesti Ülem-Ordoviitsiumi Pirgu lademe Adila kihistust (globaalne Katy lade) pärit uut kihtpoorsete käsnade liiki *Aulacera vohilaidia* Jeon ja Toom sp. nov. Kirjeldatud liik on esimene aulatseratiidne stromatopoor Baltika Ordoviitsiumist. *A. vohilaidia* sp. nov. skeletti iseloomustab kolm erinevat osa: telgmine, keskmine ja välimine. Iga osa koosneb erineva suuruse ja kujuga skeletiplaatidest. Skeleti telgmine tsoon on kitsas ja selle hobuserauakujulised suured laaminad kattuvad, kujundades lainelise mustri. Keskmine tsoon koosneb väikestest laaminatest, mida punkteerivad hajusalt arenenud sambad. Välimist tsooni iseloomustavad lamedad paralleelselt asetsevad laaminad, mis moodustavad soonilise mügaratega struktuuri. Kihtpoorse käsna kasvupinda iseloomustab hulknurkse morfoloogiaga pustuloosne võrkjas struktuur. Aulatseratiidseid stromatopoore teatakse peri-Gondwanast, Laurentiast ja Siberist. *A. vohilaidia* sp. nov. leid Eestist laiendab selle rühma paleogeograafilist levikut Baltika paleokontinendile. Aulatseratiidsete stromatopooride jõudmine Baltika paleokontinendile on kooskõlas sealse kliima soojenemisega ja selle rühma levila suure laienemisega Hilis-Ordoviitsiumis.