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# The appearance of *Rosenella* (stromatoporoid sponge) in Baltica: new species from the Pirgu Stage (Katian, Upper Ordovician) of Estonia

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## ABSTRACT

The Katian Age, part of the Late Ordovician Epoch, was a period of significant stromatoporoid diversification. However, their fossil record is often less continuous, hindering our understanding of their diversity and diversification. Estonia, which was part of Baltica during the Ordovician, is one of the most intensively studied areas for stromatoporoids. In this study, we describe a new species of the stromatoporoid genus *Rosenella*, named *R. hosholmia* sp. nov., from the Upper Ordovician Pirgu Stage Adila Formation (late Katian in age) of Estonia. The specimens were collected from the Hosholm locality on Vormsi Island. *R. hosholmia* is characterised by high variability in cyst size and an alternation of sporadic layers of denser, either smaller or larger, cyst plates. The cyst plates display short, thin, sharp denticles, appearing as tightly clustered points in tangential sections. Ichnofossils *Planolites* and *Coprulus* occur with this new *Rosenella* species. This discovery marks the first record of *Rosenella* in the Ordovician of Baltica, extending the palaeogeographic range of this genus beyond its known occurrences in Gondwana, peri-Gondwanan terranes, and the Altai–Sayan Fold Belt of southwestern Siberia during the Middle to Late Ordovician interval. The finding highlights the potential for further discoveries in well-studied areas, and suggests that stromatoporoid diversity in Baltica may be higher than previously known. The lack of stromatoporoid faunal similarity between Baltica and any other continents, including Laurentia, during the Ordovician contrasts with other organisms such as cephalopods and brachiopods, indicating asynchronous dispersal patterns across different groups.

## Introduction

The Great Ordovician Biodiversification Event represents one of the most significant increases in marine biodiversity during the Phanerozoic (Sepkoski 1995; Webby et al. 2004). During this event, various reef-building organisms, including stromatoporoids, underwent substantial diversification (Webby 2002; Kröger et al. 2017a; Servais and Harper 2018). Stromatoporoids, a grade of hypercalcified sponges, first appeared in the Early Ordovician and became important reef-building organisms throughout the Palaeozoic Era, particularly from the Ordovician through the Devonian periods (Copper 2002; Webby 2002; Jeon et al. 2023a, 2025a). Their diversity increased significantly during the Middle and Late Ordovician as part of the broader radiation of reef-building organisms, including corals and bryozoans (Webby 2002; Lee and Riding 2018). The palaeogeographic distribution of Ordovician stromatoporoids has been used to discuss distinct palaeobiogeographic realms and provinces (Webby 1980; Lin and Webby 1989; Nestor and Webby 2013; Stock et al. 2015). Understanding the diversity and distribution of stromatoporoids is crucial for reconstructing the reef ecosystems of the Ordovician and interpreting the palaeobiogeographic patterns of the time. It is, therefore, essential to understand their entire diversity precisely.

Despite extensive studies of Ordovician stromatoporoids in Baltica (Riabinin 1951; Nestor 1960, 1964; Webby 1979), the recent discovery of a new stromatoporoid, *Aulacera vohilaidia* Jeon and Toom 2024, from the Upper Ordovician Adila Formation of Estonia marks the first known occurrence of an aulaceratid stromatoporoid in Baltica (Jeon and Toom 2024). The presence of previously unrecognised stromatoporoids in Estonia highlights the potential for discoveries in even well-studied areas. It suggests that the diversity of stromatoporoids in the Late Ordovician of Baltica may be higher than previously recognised.

The genus *Rosenella* Nicholson, 1886a, belonging to the labechiid family Rosenellidae, has been reported from Middle to Upper Ordovician strata of Gondwana and peri-Gondwanan terranes, such as northern China (Ozaki 1938; Jeon et al. 2023b), Malaysia (Webby et al. 1985), and eastern Australia (Webby 1969, 1991), the Altai–Sayan Fold Belt (Khalfina 1960), Siberia (Nestor 1976), and Laurentia (Galloway and Jean 1961). This genus is known to have first appeared in the Middle Ordovician of Gondwana and peri-Gondwanan terranes (Ozaki 1938; Webby et al. 1985), and subsequently spread to other continents, except Baltica (Nestor and Webby 2013; Stock et al. 2015).

In this study, we describe a new stromatoporoid species, *Rosenella hosholmia* sp. nov., from the Upper Ordovician strata of Estonia. This latest finding extends the palaeogeographic distribution of *Rosenella* to Baltica, a region where it had not previously been documented. This study aims to: 1) describe the features of the skeletal architecture of *Rosenella hosholmia* sp. nov.; 2) investigate the palaeogeographic distribution of *Rosenella* during the Late Ordovician and discuss the factors that may have influenced its dispersal to Estonia; and 3) assess the implications of the *Rosenella* discovery for our understanding of faunal connections between Baltica and other palaeocontinents during the Late Ordovician. We expect to further constrain the timing and tempo of the stromatoporoid radiation in Baltica during the Ordovician by integrating these new occurrence data with previously published data.

## Geological setting

During the Ordovician period, Estonia was situated in the shallow epicontinental sea of the Baltica palaeocontinent, which drifted from high latitudes to the equatorial region (Torsvik and Cocks 2017). This latitudinal shift led to an increase in carbonate sedimentation rates and the development of warm-water biotic communities (Nestor and Einasto 1997). The onset of a warmer climate, which facilitated the emergence of reefs and stromatoporoids, commenced in the Keila Regional Stage (equivalent to the early Katian Stage of the international timescale) and persisted throughout the remainder of the Ordovician (Nestor 1964, 1999; Kröger et al. 2017b).

The Katian Age witnessed a rapid diversification of rugose and tabulate corals (Sokolov 1951; Kaljo 2004; Kaljo et al. 2011), accompanied by an increase in bioproduction across Baltica (Delabroye et al. 2011; Hints et al. 2018; Truuver et al. 2021; Kröger 2025). The strata of the Pirgu age form a narrow west–east-oriented outcrop belt, which extends from Hiiumaa and Vormsi islands in the west to Lake Peipus in eastern Estonia (Fig. 1). The area was part of the Estonian Shelf of the Baltic Palaeobasin (Meidla et al. 2023). In northern Estonia's onshore part of the Ordovician shallow shelf, two distinct successive rock units of the Pirgu Regional Stage are exposed: the Moe and Adila formations (Hints et al. 2005). The Moe Formation is characterised by micritic and bioclastic nodules or bedded limestones with argillaceous intercalations, whereas the Adila Formation primarily consists of grey bioclastic limestone (Hints and Meidla 1997).

The Pirgu Regional Stage represents the thickest Ordovician unit in Estonia, although its thickness is reduced in the southern islands (Hints et al. 2005), with variations of up to 45 m (Hints and Meidla 1997). The boundary between the Moe and Adila formations approximately coincides with the boundary between the late Katian *Tanuchitina bergstroemi* and *Conochitina rugata* chitinozoan zones (Hints and Meidla 1997).

## Materials and method

The obtained specimens of stromatoporoids were collected from the Upper Ordovician Adila Formation (Pirgu Regional Stage; upper Katian) exposed along the Hosholm shore of Vormsi Island, Estonia (Fig. 1). Among the stromatoporoids, three specimens are identified as *Rosenella* and form the basis for describing the new species, *Rosenella hosholmia* sp. nov. (Fig. 3). These specimens are designated as type specimens; the holotype (GIT 840-381) was obtained from an outcrop located at 58° 57′ 46.9″ N, 23° 09′ 43.2″ E, whereas the paratypes (GIT 840-380 and GIT 840-329) were collected from the southern part of the outcrop near a tower at 58° 57′ 38.0″ N, 23° 09′ 56.8″ E (Fig. 1C–E). The stromatoporoids described herein were collected from localities of non-reef environments. The localities represent tropical, normal marine, relatively shallow sublittoral environments. Rugose and tabulate corals, bryozoans, cephalopods, gastropods, and stromatoporoids are common fossil components at the Hosholm localities (Vinn and Mõtus 2012). The gastropod *Maclurites neritoides*, the index taxon for the Adila Formation of the Pirgu Regional Stage (Isakar 1997), occurs with the new *Rosenella* species in the outcrops. The Hosholm localities represent a soft mud-bottom environment with a considerable influx of sediments (Vinn et al. 2022). The Adila Formation corresponds to the topmost part of the Katian and correlates with the late Boda warming event, immediately before the Hirnantian cooling (Young et al. 2023).

The collected specimens were prepared into thin sections and polished slabs for a detailed microscopic examination of the skeletal elements and structural arrangement in longitudinal and tangential sections. Photographs of the specimens were taken in the Department of Geology, Tallinn University of Technology, Estonia, by Gennadi Baranov using a Canon EOS 5Dsr digital camera, and in the Department of Earth and Environmental Sciences of Chungnam National University, South Korea, by Juwan Jeon using a Nikon D750 digital camera with microlenses. Thin section preparation was carried out in the palaeoecology laboratory at Chungnam National University, South Korea. The suprageneric classification of stromatoporoids used in this study follows Webby (2015).

**Repository and institutional abbreviation.** The specimens' remaining material and thin sections are deposited at the Department of Geology, Tallinn University of Technology, Tallinn, Estonia (abbreviated GIT).

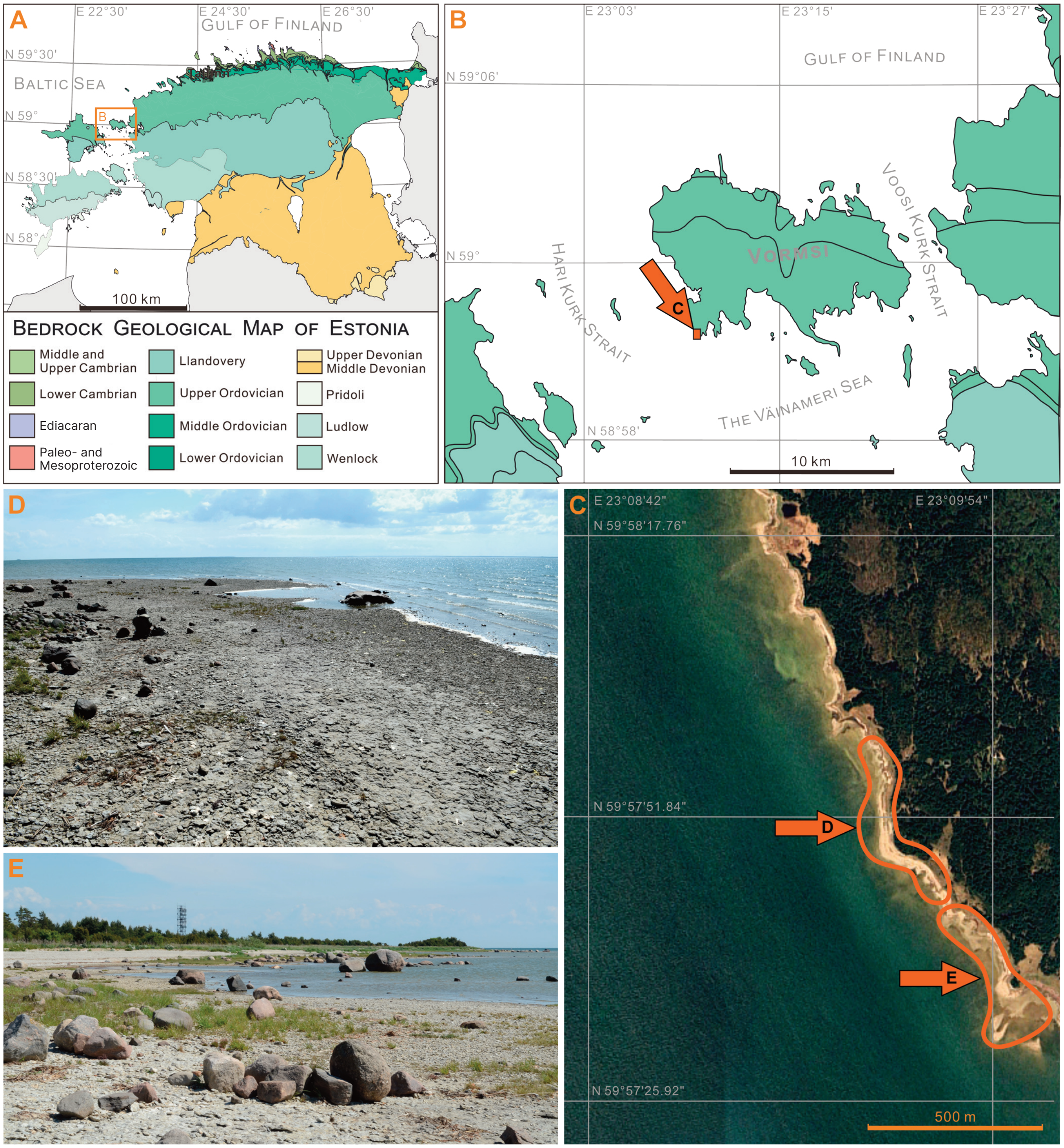

**Fig. 1.** Geographic and geological map of the study location in Estonia. **A** – location map of Estonia and the study locality (orange-outlined rectangle, expanded in B). **B** – detailed view of the study locality (orange arrow with C) on the western coast (Hosholm shore) of Vormsi Island. Maps in A and B adapted from Hints and Toom (2023). **C** – satellite image of the study area along the Hosholm shore of Vormsi Island (source: Google Earth). The upper outlined area (arrow D) indicates the outcrop where the holotype specimen GIT 840-381 was collected (58° 57′ 46.9″ N, 23° 09′ 43.2″ E). The lower outlined area (arrow E) indicates the outcrop near a tower on the Hosholm shore where paratype specimens GIT 840-380 and GIT 840-329 were collected (58° 57′ 38.0″ N, 23° 09′ 56.8″ E). **D** – view of the outcrop along the northern Hosholm shore, marked in C. **E** – view of the outcrop near a tower along the southern Hosholm shore, marked in C. Photos by Gennadi Baranov.

## Systematic palaeontology

Order LABECHIIDA Kühn, 1927
Family ROSENELLIDAE Yavorsky in Khalfina and Yavorsky, 1973
Genus *Rosenella* Nicholson, 1886a

*Type species. Rosenella macrocystis* Nicholson, 1886a, from Wenlock-age limestone, Visby, Gotland (type locality and the exact stratigraphic level are unknown; see Webby 2015, p. 712).

*Diagnosis.* Skeleton commonly composed of large-sized, overlapping, gently convex-upward cyst plates; in a few places alternating with flatter, thickened bands; with or without denticles (after Webby, 2015, p. 712).

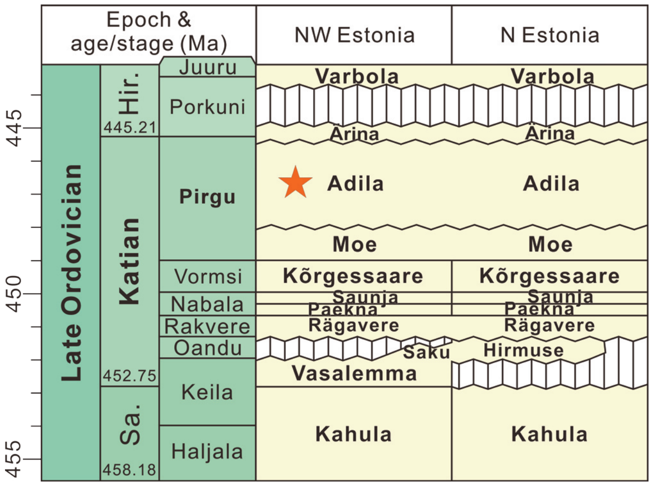

**Fig. 2.** Upper Ordovician stratigraphic column for northern and northwestern Estonia. The star indicates the Adila Formation, source of the *Rosenella* specimens. Stratigraphy and correlations modified from Hints and Toom (2023). Abbreviations: Sa. – Sandbian, Hir. – Hirnantian.

*Other known species. Rosenella amzassensis* Khalfina, 1960, *Rosenella cumingsi* Galloway and St. Jean, 1961, *Rosenella melkyiensis* Khromykh, 2001, *Rosenella woyuensis* Ozaki, 1938.

*Rosenella hosholmia* Jeon and Toom sp. nov.
Figs 3–6

*Etymology.* The species name refers to the Hosholm locality of Vormsi Island, Estonia, where the specimens of *Rosenella* were found.

*Holotype.* GIT 840-381 from the Upper Ordovician Adila Formation (Pirgu Regional Stage; upper Katian Stage) on the Hosholm shore of Vormsi Island, Estonia (58° 57′ 46.9″ N, 23° 09′ 43.2″ E) (Fig. 1C, D).

*Paratypes.* GIT 840-380 and GIT 840-329 from the Upper Ordovician Adila Formation (Pirgu Regional Stage; upper Katian), collected near a tower on the Hosholm shore of Vormsi Island, Estonia (58° 57′ 38.0″ N, 23° 09′ 56.8″ E) (Fig. 1C, E).

*Locality and stratigraphic horizon.* Exposure of the Upper Ordovician Adila Formation (Pirgu Regional Stage; upper Katian) along the Hosholm shore of Vormsi Island, Estonia (Figs 1 and 2).

*Materials.* GIT 840-329, GIT 840-380, and GIT 840-381.

*Diagnosis.* A species of *Rosenella* with highly variable and large cyst sizes and morphologies; smaller cysts commonly between larger cysts, forming an alternating arrangement; smaller cyst plates typically clustered together in groups, with intermittent larger cyst plates scattered among them. Denticles relatively consistent in size and shape, typically short, thin, and small, developed on the surfaces of cyst plates; denticles in tangential sections as small, tightly clustered points or dots, resembling a star cluster in appearance.

*Description.* Skeletons are laminar to low domical, with a maximum height of 130 mm and a maximum width of 60 mm (Fig. 3). Cysts exhibit a high degree of size variability, with smaller cysts commonly occurring between larger ones, forming an alternating arrangement (Figs 3–5). Smaller cyst plates are typically clustered in groups, with intermittent larger cyst plates scattered among them (Fig. 5). Cyst plates range from 0.66 to 7.74 mm in height (n = 72, average 2.53 mm) and from 1.79 to 19.25 mm in width (n = 72, average 6.81 mm). The width/height ratios of cysts vary from 1.14 to 5.86, with an average of 2.85 (n = 72). Cysts are preserved in two ways: filled with either micritic sediment or sparry calcite (Figs 4 and 5). Cysts filled with micritic sediments commonly display geopetal structures that align with the overall growth direction of the stromatoporoid skeleton (Figs 4B and 6D). Denticles are typically short, thin, and small, relatively consistent in size and shape, and develop on the surfaces of cyst plates (Figs 3F, 4D, 5D, 6B and 6E). In the tangential section – a cross-section perpendicular to the growth direction – the denticles appear as small, tightly clustered points or dots, resembling a star cluster in appearance (Fig. 4E–G).

*Remarks.* The skeletal architecture of *Rosenella hosholmia* sp. nov. is larger than that of any other Ordovician stromatoporoids reported in Estonia. Several fossil groups from the upper Katian of Estonia, including tabulate corals, rugosans, gastropods, cephalopods, and brachiopods, are notable for their large size of overall bodies or skeletal structures (Kaljo 1996; Toom et al. 2021; Hints and Rong 2024). For example, the tabulate coral *Paleofavosites abstrusus* Klaamann, 1961, which is common in the Adila Formation, represents this trend. The largest corallites of this species can measure up to 4.3 mm in diameter (Klaamann 1961).

*Rosenella hosholmia* sp. nov. bears a certain resemblance to *R. woyuensis* Ozaki, 1938, among other known Ordovician *Rosenella* species. These two Baltic and peri-Gondwanan species share similarities in the general morphology of their cyst plates but differ in the size range of the cyst plates, the arrangement of smaller and larger cysts, and the size of the denticles. *R. hosholmia* displays larger cyst sizes compared to those of *R. woyuensis* as described in Ozaki (1938), Webby et al. (1985), and Jeon et al. (2023b). Although Jeon et al. (2023b) report some abnormally large cysts in *R. woyuensis*, similar to those observed in *R. hosholmia*, the latter exhibits even larger dimensions.

A distinctive feature of *R. hosholmia* is the alternating arrangement of smaller and larger cysts at different growth stages, which is not explicitly mentioned in the descriptions of *R. woyuensis*, *R. amzassensis* Khalfina, 1960, or other known *Rosenella* species. The reason behind this alternating pattern in *R. hosholmia* is challenging to interpret, but it is more likely an unintentional development rather than an indication of seasonal banding or cyclicity (see discussions in Young and Kershaw (2005) on banding in stromatoporoids).

Both *R. hosholmia* and *R. woyuensis* possess denticles, but those of *R. hosholmia* are relatively consistent, short, thin,

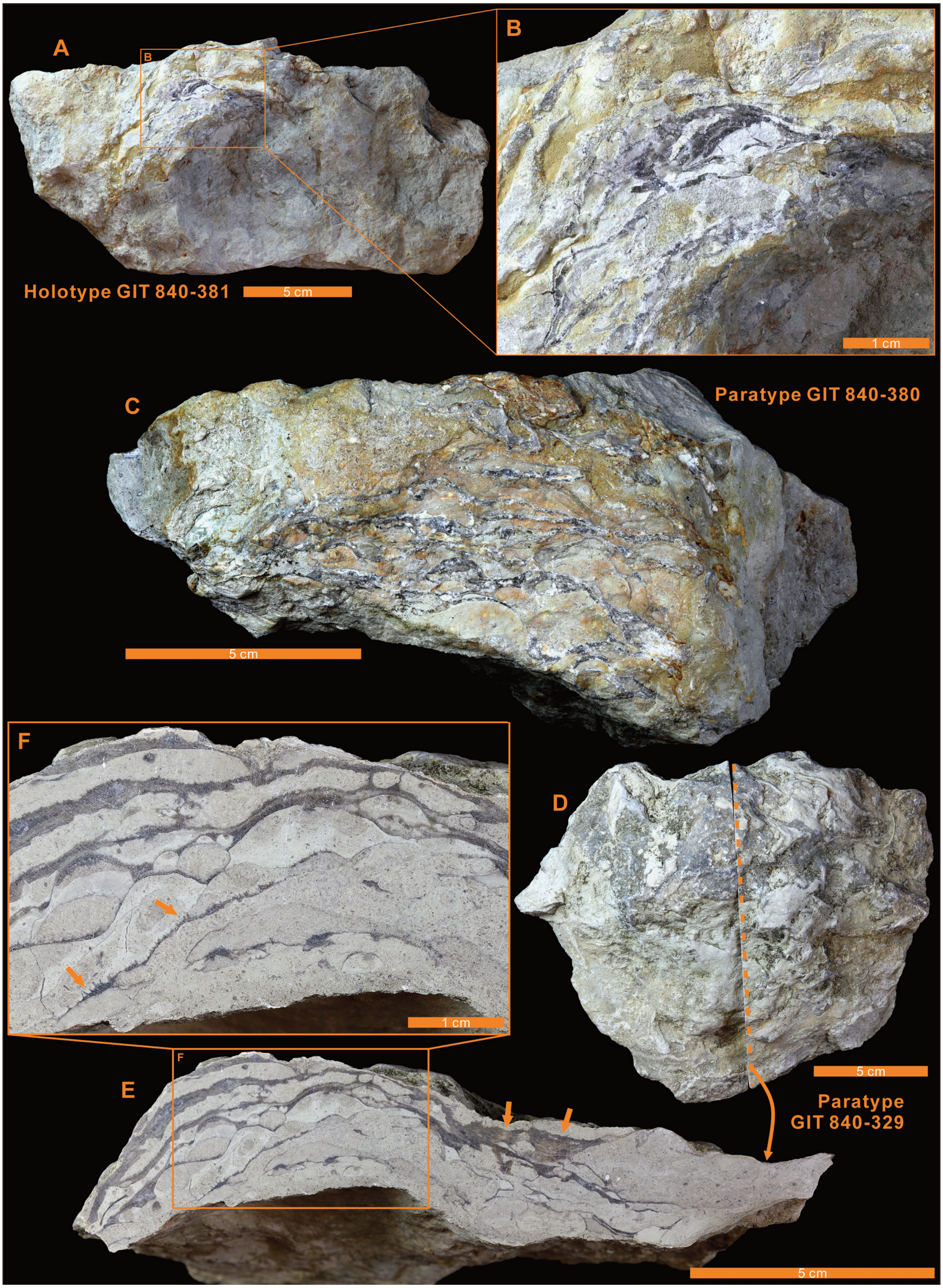

**Fig. 3.** Overall view of *Rosenella hosholmia* Jeon and Toom sp. nov. from the Upper Ordovician Adila Formation along the Hosholm shore. **A** – basal view of *R. hosholmia*, holotype GIT 840-381. **B** – enlarged area of A (rectangle), showing cyst plates with geopetal structures. **C** – *R. hosholmia*, paratype GIT 840-380, exhibiting variable cyst plate sizes. **D** – *R. hosholmia*, paratype GIT 840-329, viewed from above, showing its low-profile growth form. **E** – cross-sectional view of D (dashed line) of paratype GIT 840-329, showing variable cyst plate sizes in *R. hosholmia*; locally developed smaller and thinner cyst plates are indicated by orange arrows. **F** – enlarged area of E (rectangle). Note the development of short, sharp denticles on the cyst plate (arrows) and occurrences of *Planolites* within the cysts.

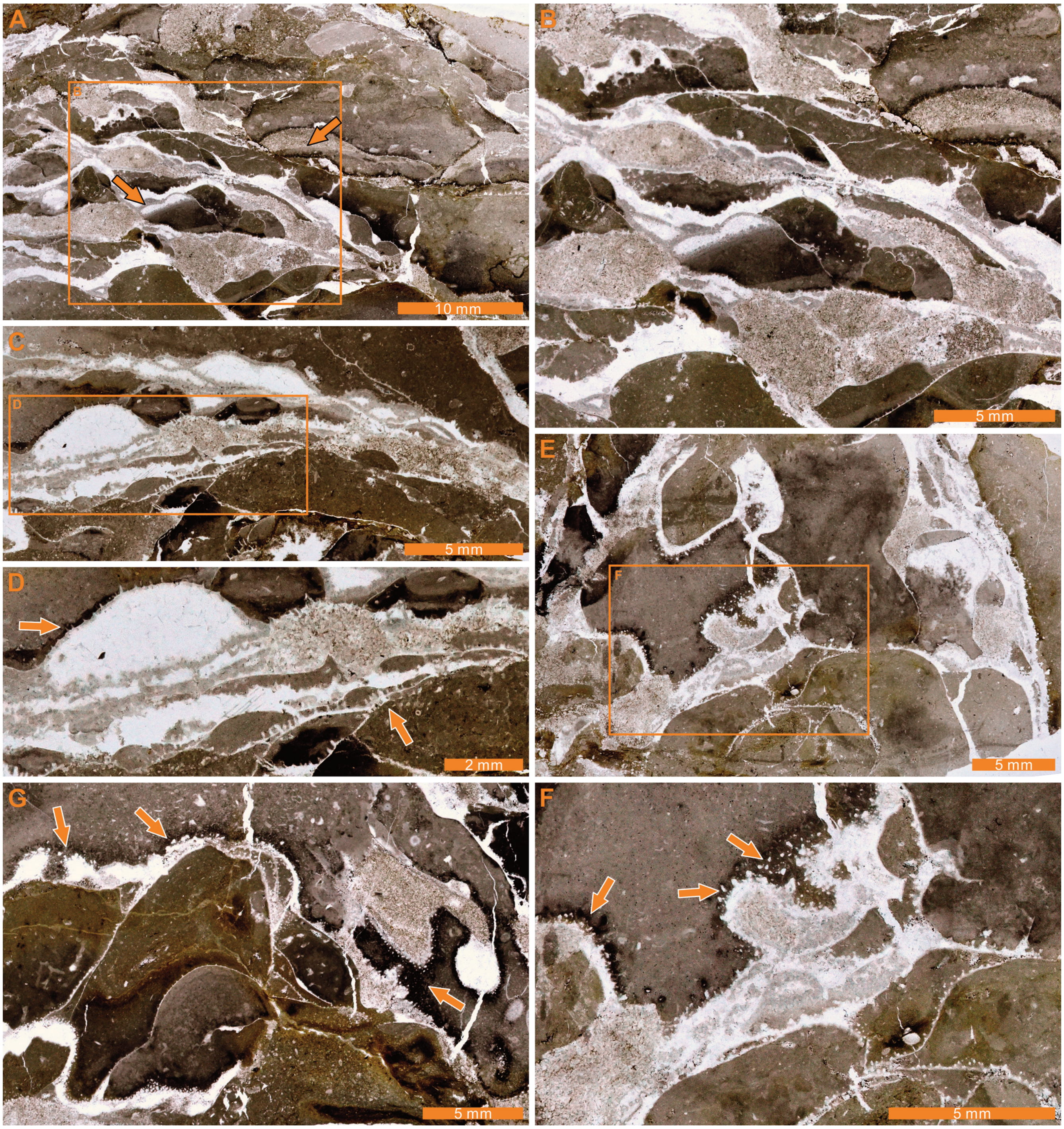

**Fig. 4.** *Rosenella hosholmia* Jeon and Toom sp. nov., holotype GIT 840-381. A–D – longitudinal sections of *R. hosholmia*. **A** – variably sized cyst plates with geopetal structures (arrows). **B** – enlarged area of A (rectangle). **C** – variably sized cyst plates filled with either micritic sediments or calcite spar. **D** – enlarged area of C (rectangle), showing denticles developed on cyst plates (arrows). E–G – tangential sections of *R. hosholmia*. **E** – tangential view, showing irregular patterns of cyst plates and denticle development around them. **F** – enlarged area of E (rectangle). **G** – tangential view highlighting denticles developed around cyst plates.

and small, appearing as tightly clustered points or dots in tangential sections. In contrast, the denticles of *R. woyuensis* are larger (Webby et al. 1985), while *R. amzassensis* lacks denticles altogether (Khalfina 1960). *R. amzassensis* is suspected to be a junior synonym of *R. woyuensis*, but this requires confirmation through the study of a sufficient number of specimens.

*Rosenella cumingsi* Galloway and St. Jean, 1961, a Laurentian species, also possesses cysts with considerable variation in morphology and dimensions, but they are smaller than those of *R. hosholmia*, *R. woyuensis*, and *R. amzassensis*. The cysts in *R. cumingsi* are characterised by a broad, irregularly undulating, and low-profile appearance, with approximately eight cysts occurring within 2 mm vertically and two cysts within 2 mm horizontally (Galloway and St. Jean 1961, p. 46). This species also exhibits irregularly developed denticles (Galloway and St. Jean 1961).

Larger cyst plates with high convexity are commonly filled with micritic sediments, whereas smaller cyst plates are dominantly filled with calcite spar (Figs 4–6). This tendency

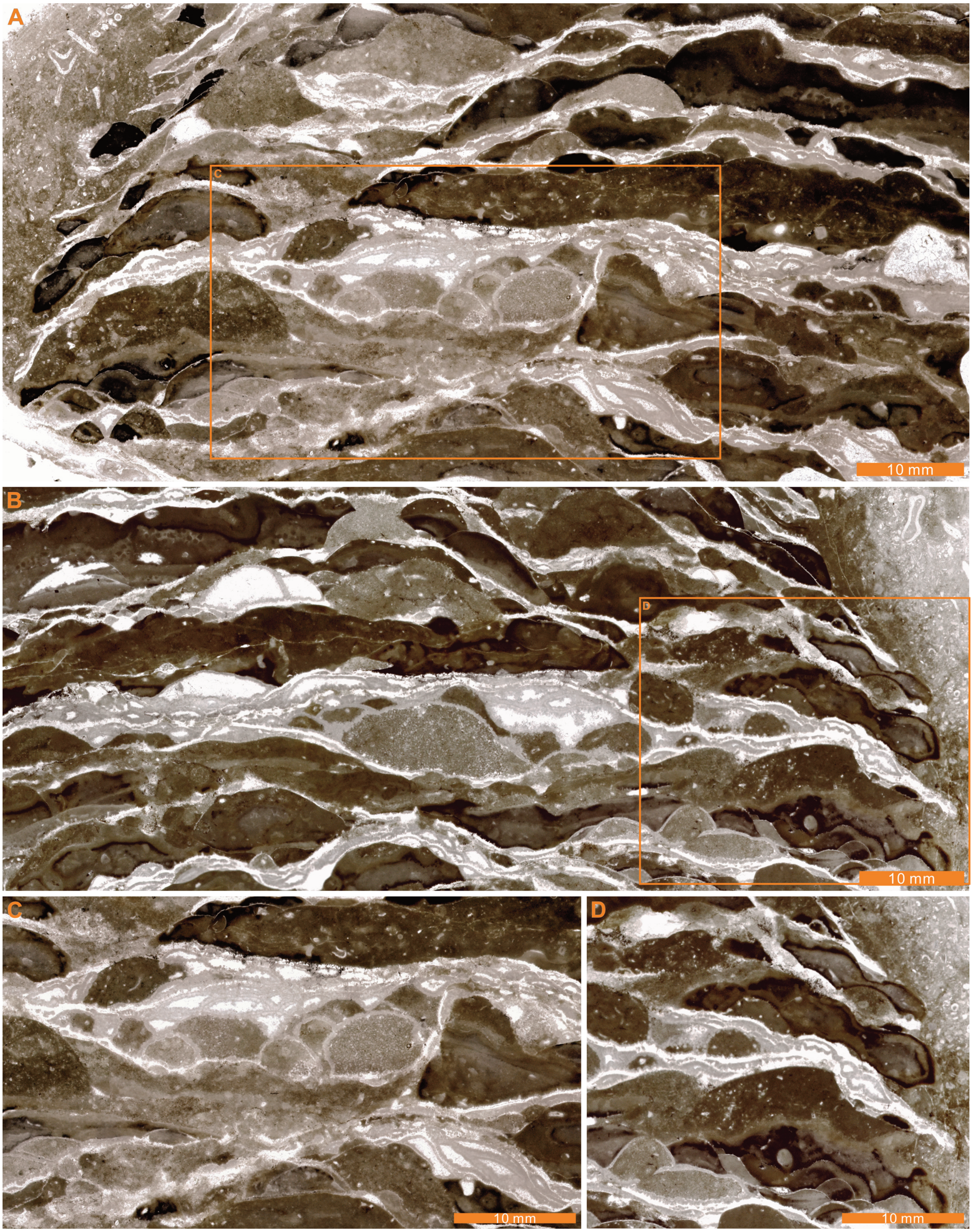

**Fig. 5.** *Rosenella hosholmia* Jeon and Toom sp. nov., paratype GIT 840-380, showing variation in cyst plate size. **A, B** – overall view of variably sized cyst plates. Note that larger cysts are mostly filled with micritic sediments, whereas smaller ones are filled with calcite spar. **C, D** – enlarged areas of A and B (rectangles). **C** – imbricated patterns of variably sized cyst plates. **D** – marginal area of *R. hosholmia* with ragged edges, due to sedimentation.

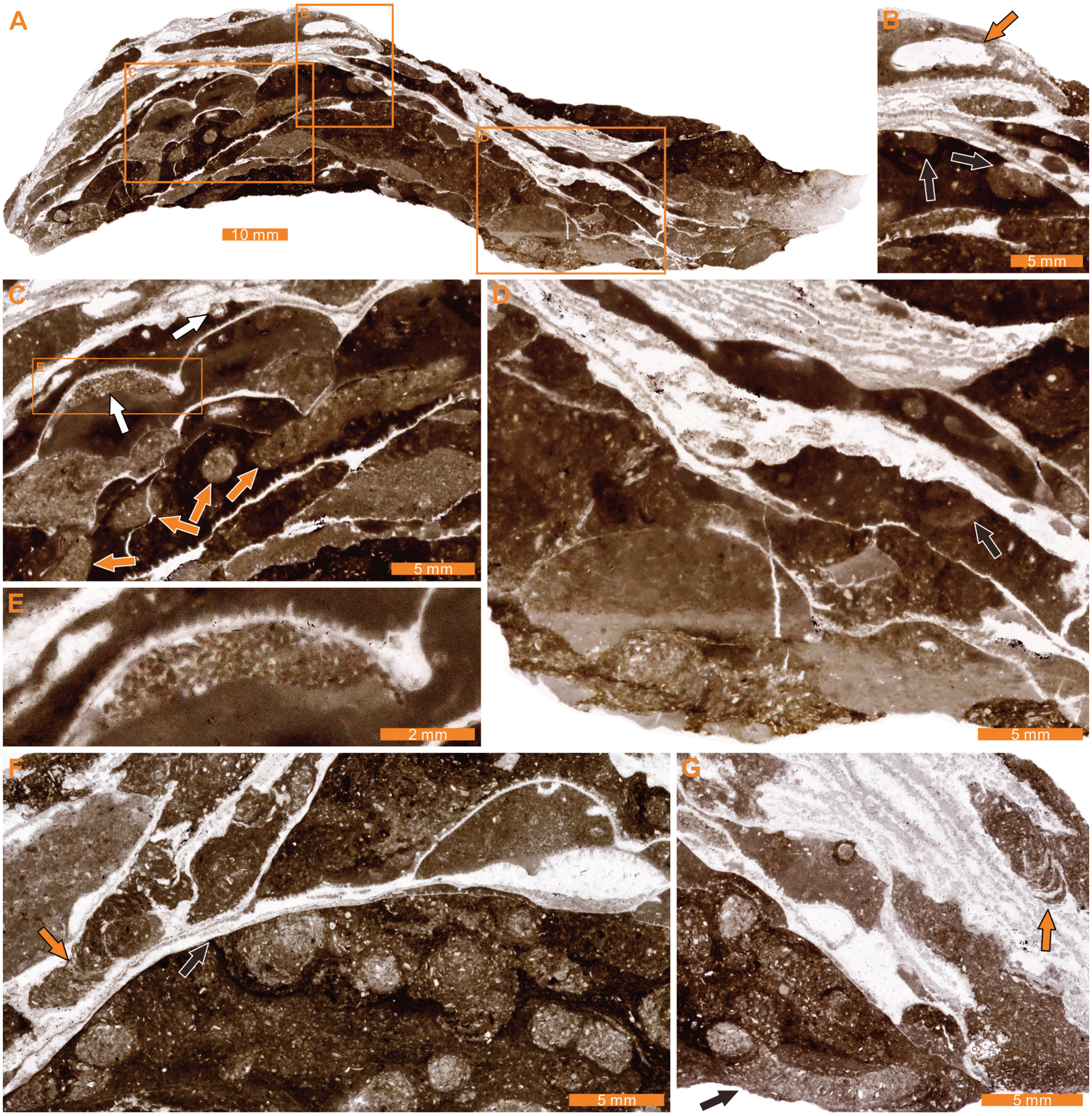

**Fig. 6.** *Rosenella hosholmia* Jeon and Toom sp. nov., paratype GIT 840-329, showing association with the ichnofossils *Planolites* (burrows with circular or elongated shapes, depending on cross-sections) and *Coprulus* (faecal pellets). **A** – overall thin-section view of paratype GIT 840-329, corresponding to its slab view in Fig. 3E. B–D – enlarged areas of A (rectangles). **B** – *Planolites* filled with either micritic sediment (black arrows) or sparry calcite (orange arrow). Note the semi-circular *Planolites* underneath *R. hosholmia*, with their tops cut off. **C** – micrite-filled cysts containing *Planolites* (orange arrows) and *Coprulus* (white arrows). **D** – geopetal structures in micrite-filled cysts, aligned with the stromatoporoid growth direction. **E** – enlarged area of C (rectangle and white arrow), showing details of *Coprulus* in cyst. **F** – *Planolites*, associated with *R. hosholmia*, showing active backfilling (orange arrow). Note the relatively large circular *Planolites* with a flat contact against the cyst plate of *R. hosholmia* (black arrow). **G** – elongated and curved *Planolites* (black arrow) and its active backfilling (orange arrow), associated with the stromatoporoid.

has not been investigated in other species of *Rosenella* or other labechiid stromatoporoids possessing large cyst plates. However, this pattern does not appear to be universal across all *Rosenella* species. In *Rosenella woyuense* Ozaki, 1938, for instance, cysts – regardless of plate size – show geopetal structures formed by micritic sediments and calcite spar above (Jeon et al. 2023b, fig. 4), suggesting that partial destruction of the cyst plates limited sediment influx. Thus, the larger cyst plates in *R. hosholmia* sp. nov. were possibly influenced by the underlying substrate on which they were secreted.

Horizontal burrows identified as *Planolites* isp. occur underneath the skeleton of *R. hosholmia* and within its cyst plates (i.e. cysts) (Fig. 6). These burrows are smooth, unlined, and clearly distinguishable from the host micritic matrix by their slightly coarser filling and lighter colour. The shape of burrows is circular to elongated in vertical sections (Fig. 6B, C, F, G), and sinuous cylindrical in tangential sections. Burrowing spaces are rarely filled by calcite spar, thus clearly showing their overall curved shape (Fig. 6B), but sediment-filled burrows show evidence of active backfilling (orange arrows in Fig. 6F, G and black arrow in Fig. 6G). *Planolites* is facies-crossing ichnogenus produced by deposit-feeding vermiform organisms (e.g. Pemberton and Frey 1982; Fillion and Pickerill 1990). Faecal pellets, identified as *Coprulus oblongus* Mayer, 1952 occur intermittently in *Planolites* isp. and the cysts of *R. hosholmia* (white arrows in Fig. 6C and details in Fig. 6E). The pellets are homogeneous, isolated, and ellipsoidal in shape, with an irregular distribution and a sharp boundary against the underlying micritic substrate (Fig. 6E). These small faecal pellets are common within different shelly fossils in the Upper Ordovician sediments. Pellets are composed of the same material as the host sediment, which suggests that deposit or suspension feeders were the trace makers (Toom et al. 2020). These trace makers likely fed within the sediment, while also seeking shelter within the stromatoporoid skeleton. Mángano et al. (2019) suggested that shells shielded pellets and burrows from compaction, thereby facilitating early cementation.

## Discussion: distribution of Ordovician stromatoporoids in Estonia

Ordovician stromatoporoids are patchily distributed both in reef and non-reef environments in Estonia (Nestor 1964, 1999) (Fig. 7; Table 1). Not only Estonia but also other regions show similarly patchy distribution patterns, with occurrences scattered across different palaeocontinents and

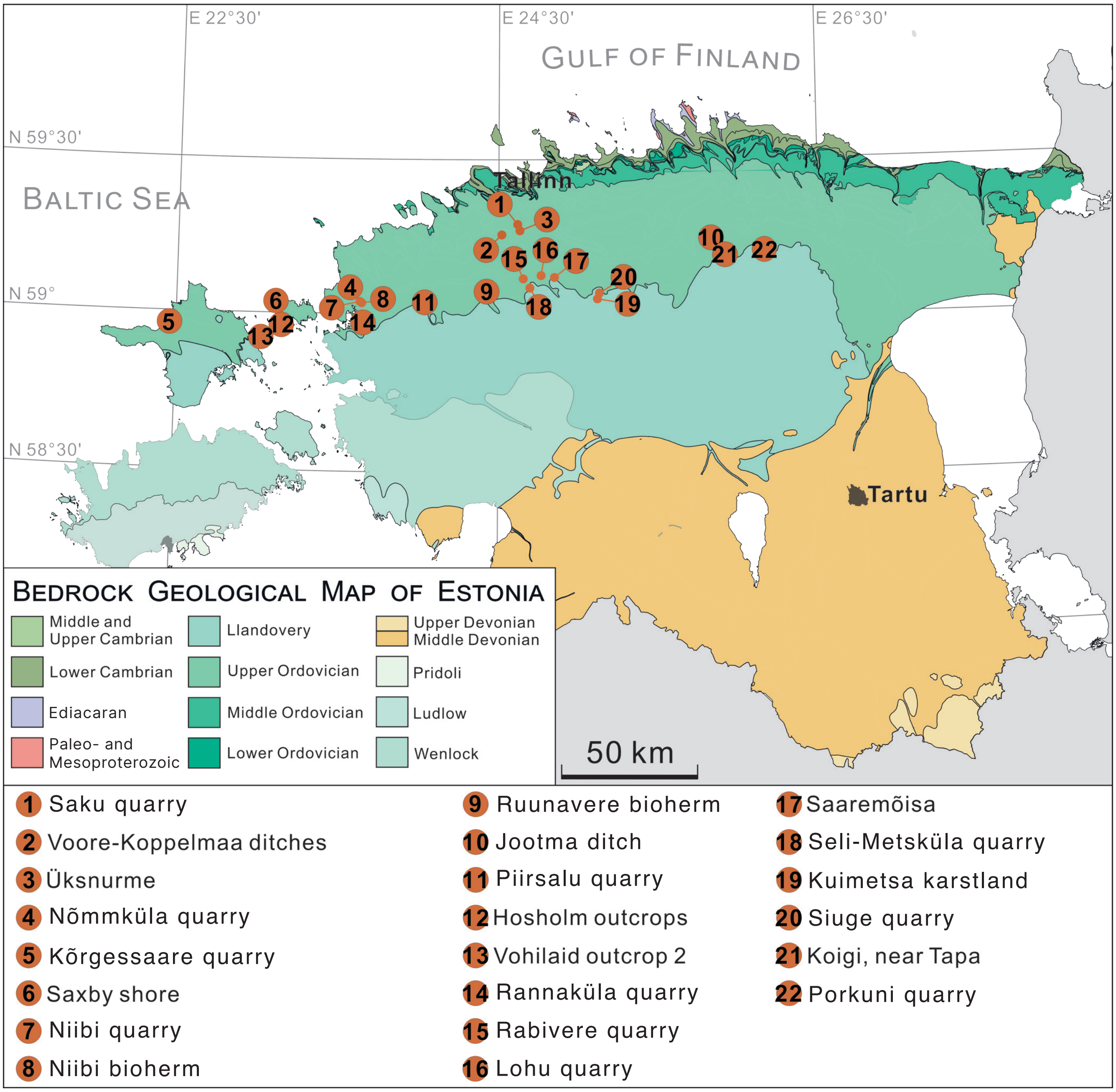

**Fig. 7.** Geographic distribution of Ordovician stromatoporoid occurrences in Estonia. See Table 1 for a list of reported stromatoporoids from each locality.

**Table 1.** List of Ordovician stromatoporoids reported in Estonia

| Locality | GPS coordinates | No. in Fig. 7 | Reported stromatoporoids | Stratigraphy | Lithostratigraphy | References |
|---|---|---|---|---|---|---|
| Saku quarry | 59° 17′ 59.8″ N, 24° 38′ 47.2″ E | 1 | *Cystistroma sakuense* (Nestor, 1964) | Oandu Stage | Saku Member | Nestor 1964 |
| Voore-Koppelmaa ditches | 59° 15′ 59.6″ N, 24° 32′ 33.1″ E | 2 | *Cystistroma canadense* (Nicholson & Murie, 1878) | Oandu Stage | Saku Member | Nestor 1964 |
| Üksnurme | 59° 16′ 47.9″ N, 24° 39′ 15.2″ E | 3 | *Cystistroma canadense* (Nicholson & Murie, 1878) | Oandu Stage | Saku Member | Rõõmusoks 1970 |
| Nõmmküla quarry | 59° 04′ 32.7″ N, 23° 36′ 46.3″ E | 4 | *Clathrodictyon microundulatum* Nestor, 1964 | Vormsi Stage | Kõrgessaare Formation | Nestor 1964 |
|  |  |  |  | Pirgu Stage | Moe Formation | Rõõmusoks 1966 |
| Kõrgessaare quarry | 58° 58′ 25.0″ N, 22° 27′ 34.0″ E | 5 | *Clathrodictyon vormsiense* Riabinin, 1951 | Vormsi Stage | Kõrgessaare Formation | Nestor 1964 |
| Saxby shore | 59° 01′ 40.0″ N, 23° 07′ 2.00″ E | 6 | *Clathrodictyon vormsiense* Riabinin, 1951 | Vormsi Stage | Kõrgessaare Formation | Riabinin 1951 |
| Niibi quarry | 59° 02′ 32.9″ N, 23° 39′ 06.6″ E | 7 | *Cystistroma canadense* (Nicholson & Murie, 1878) | Pirgu Stage | Moe Formation | Nestor 1964 |
|  |  |  | *Plumatalinia ferax* Nestor, 1960 |  |  | Nestor 1960, 1964 |
|  |  |  | *Clathrodictyon microundulatum* Nestor, 1964 |  |  | Nestor 1964 |
| Niibi bioherm | 59° 02′ 27.0″ N, 23° 39′ 23.0″ E | 8 | *Plumatalinia ferax* Nestor, 1960 | Pirgu Stage | Moe Formation | Nestor 1960, 1964 |
| Ruunavere bioherm | 59° 04′ 47.9″ N, 24° 27′ 04.1″ E | 9 | *Plumatalinia ferax* Nestor, 1960 | Pirgu Stage | Moe Formation | Rõõmusoks 1966 |
| Jootma ditch | 59° 13′ 38.6″ N, 25° 52′ 58.3″ E | 10 | *Cystostroma estoniense* Nestor, 1964 | Pirgu Stage | Adila Formation | Nestor 1964 |
| Piirsalu quarry | 59° 02′ 37.6″ N, 24° 02′ 57.7″ E | 11 | *Cystostroma estoniense* Nestor, 1964 | Pirgu Stage | Adila Formation | Rõõmusoks 1966 |
| Hosholm outcrops | 58° 57′ 38.0″ N, 23° 09′ 56.8″ E | 12 | *Rosenella hosholmia* Jeon & Toom 2025 | Pirgu Stage | Adila Formation | This study |
| Vohilaid outcrop 2 | 58° 55′ 29.0″ N, 23° 01′ 42.2″ E | 13 | *Aulacera vohilaidia* Jeon & Toom 2024 | Pirgu Stage | Adila Formation | Jeon and Toom 2024 |
| Rannaküla quarry | 58° 57′ 50.3″ N, 23° 40′ 18.0″ E | 14 | *Cystistroma canadense* (Nicholson & Murie, 1878) | Pirgu Stage | Adila Formation | Nestor 1964 |
|  |  |  | *Plumatalinia ferax* Nestor, 1960 |  |  | Rõõmusoks 1966 |
| Rabivere quarry | 59° 07′ 23.6″ N, 24° 40′ 33.1″ E | 15 | *Clathrodictyon microundulatum* Nestor, 1964 | Pirgu Stage | Adila Formation | Rõõmusoks 1966 |
| Lohu quarry | 59° 07′ 42.5″ N, 24° 47′ 16.0″ E | 16 | *Cystistroma canadense* (Nicholson & Murie, 1878) | Pirgu Stage | Adila Formation | Rõõmusoks 1966 |
| Saaremõisa | 59° 07′ 17.6″ N, 24° 51′ 58.8″ E | 17 | *Clathrodictyon microundulatum* Nestor, 1964 | Pirgu Stage | Adila Formation | Rõõmusoks 1966 |
| Seli-Metsküla quarry | 59° 05′ 25.4″ N, 24° 42′ 51.3″ E | 18 | *Pachystylostroma fragosum* Nestor, 1964 | Porkuni Stage | Ärina Formation | Nestor 1964 |
| Kuimetsa karstland | 59° 03′ 25.6″ N, 25° 08′ 33.6″ E | 19 | *Ecclimadictyon porkuni* (Riabinin, 1951) | Porkuni Stage | Ärina Formation | Nestor 1964 |
| Siuge quarry | 59° 04′ 48.1″ N, 25° 09′ 16.1″ E | 20 | *Ecclimadictyon porkuni* (Riabinin, 1951) | Porkuni Stage | Ärina Formation | Nestor 1964 |
| Koigi, near Tapa | 59° 10′ 53.0″ N, 25° 57′ 07.2″ E | 21 | *Clathrodictyon gregale* Nestor, 1964 | Porkuni Stage | Ärina Formation | Nestor 1964 |
|  |  |  | *Ecclimadictyon koigiense* Nestor, 1964 |  |  | Nestor 1964 |
| Porkuni quarry | 59° 11′ 14.5″ N, 26° 11′ 14.8″ E | 22 | *Ecclimadictyon koigiense* Nestor, 1964 | Porkuni Stage | Ärina Formation | Rõõmusoks 1966 |
|  |  |  | *Clathrodictyon mammillatum* (Schmidt, 1858) |  |  | Nestor 1964 |
|  |  |  | *Clathrodictyon gregale* Nestor, 1964 |  |  | Nestor 1964 |
|  |  |  | *Clathrodictyon zonatum* Nestor, 1964 |  |  | Nestor 1964 |

basins. This distribution is likely the result of a combination of factors (Webby 2002; Jeon et al. 2022a). Environmental conditions, such as water depth, temperature, and nutrient availability, differed among locations, potentially influencing the distribution and abundance of stromatoporoids (Webby 2002; Jeon et al. 2022a). The preservation and exposure of suitable facies for stromatoporoid growth and fossilisation were inconsistent across all locations, resulting in gaps in the fossil record (Jeon et al. 2022a). Sampling biases and gaps, particularly in less accessible or less explored regions, may also have contributed to the apparent patchy distribution (Jeon et al. 2022a). Collectively, these factors hindered the recognition of the true diversity and diversification of early stromatoporoid assemblages during the seminal Great Ordovician Biodiversification Event interval. Such gaps can obscure the progressive nature of biodiversification events in reef evolution (Jeon et al. 2025b), and the sporadic finds of these stromatoporoid assemblages – even in well-studied areas such as Baltica – may have initially led to an underestimation of their diversity and importance as major reef-builders.

The Estonian record is one of the most complete and well-studied, with representatives of several key genera such as *Clathrodictyon*, *Ecclimadictyon*, *Cystistroma*, and *Cystostroma* known from multiple localities and stratigraphic levels (Nestor 1964, 1999; Rõõmusoks 1966, 1970) (Fig. 7; Table 1). However, the discovery of *Rosenella hosholmia* sp. nov. in a previously less frequently visited locality on Vormsi Island highlights that this patchiness extends to the regional scale as well. During the previous century, stromatoporoid studies in Estonia mainly focused on the mainland, while the western islands, including Hiiumaa, Vormsi, and Vohilaid, were less studied, likely due to sampling bias and limited access during the Soviet period. Similarly, a recent report of *Aulacera vohilaidia* Jeon and Toom, 2024 from Vohilaid Island in western Estonia, which has not been found on the mainland, implies that the stromatoporoid faunal composition in the western areas may differ from that of the mainland and warrants further investigation (Jeon and Toom 2024). The mainland stromatoporoid fauna, in particular labechiid, is generally characterised by the genus *Cystistroma* (Nestor 1999), which has not been reported from the western islands, highlighting the need for further study. This difference in faunal composition emphasises the significance of continued investigation and extensive taxonomic research across the entire country to fully comprehend the diversity and distribution of stromatoporoids in Estonia during the Late Ordovician.

The discovery of *Rosenella hosholmia* sp. nov. in Estonia extends the palaeogeographic distribution of this genus to Baltica (Fig. 8). Previously, this genus was known to have a global distribution during the Middle to Late Ordovician, with occurrences reported from several palaeocontinents, including Laurentia, Siberia, and Gondwana (Nestor and Webby 2013; Stock et al. 2015) (Fig. 8). However, it had not been identified in Baltica prior to the present study – a finding that aligns with the recent discovery of *Aulacera vohilaidia* Jeon and Toom, 2024. The presence of these genera in Baltica implies that some degree of faunal exchange or connectivity between Baltica and other palaeocontinents occurred during the Late Ordovician, although it did not affect the overall faunal assemblage. This exchange could have been facilitated by the warming climate on the palaeocontinent and the global expansion of stromatoporoids during this time (Jeon and Toom 2024). However, it is important to note that the majority of Ordovician stromatoporoids in Baltica still differ from those in Laurentia, indicating that Laurentia likely exerted only negligible faunal influence on Baltica, despite their palaeogeographic proximity (Nestor et al. 2010; Jeon and Toom 2024). This pattern of provincialism contrasts sharply with cephalopods, which exhibit strong Laurentian affinities (Kröger 2025), and brachiopods, which show

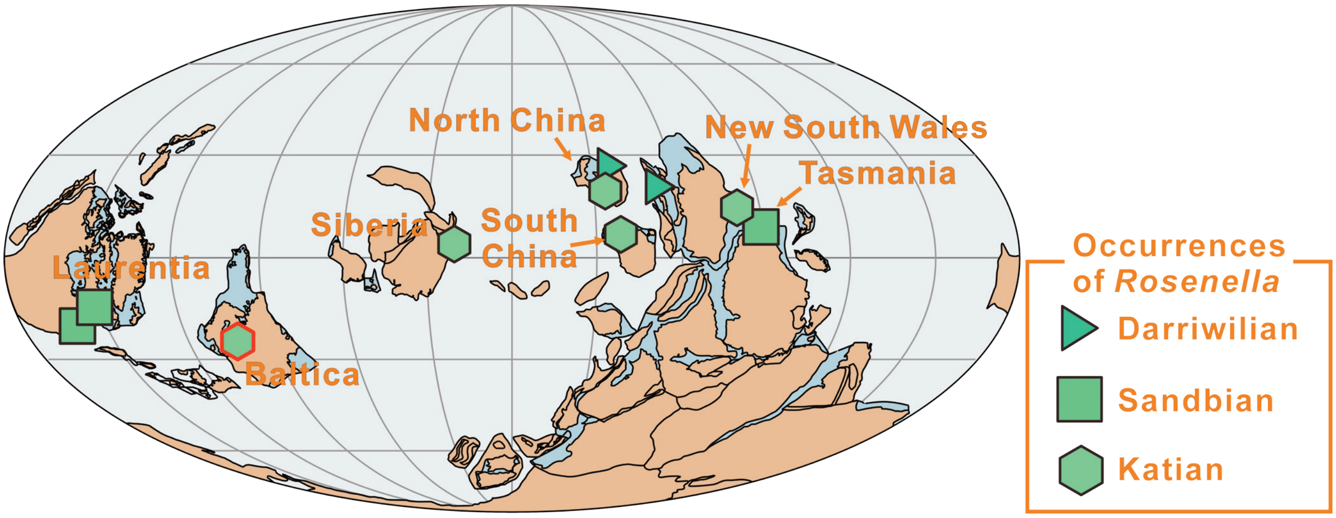

**Fig. 8.** Palaeobiogeographic distribution of the stromatoporoid *Rosenella* during the Ordovician. The compilation includes occurrences from various continents and terranes, based on data from Ozaki (1938), Khalfina (1960), Galloway and St. Jean (1961), Webby (1969, 1991), Webby et al. (1985), Jeon et al. (2022b), Jeon et al. (2023a), and this study (red outline). Palaeogeographic reconstruction modified from Torsvik and Cocks (2017).

Avalonian connections (Harper et al. 2013; Candela 2015), implying that different groups followed distinct dispersal trajectories and timelines.

The distinct nature of the Baltic stromatoporoid fauna may be attributed to a combination of palaeobiogeographic isolation, environmental differences, and structural divergence, which require further testing. Alternatively, a shift in the palaeogeographic location and a warming climate may have promoted a wider range of skeletal architectures in stromatoporoids (see Kershaw and Jeon 2024 for a review of stromatoporoid faunal development history, including the latest perspectives informed by living representatives and their calcification ability throughout geological history). The spread of stromatoporoids to Baltica – or the secretion of new skeletal architectures there – during the late Katian Age was likely influenced by warmer climatic conditions and a palaeogeographic shift of Baltica towards the equatorial region (Jeon and Toom 2024; Kershaw and Jeon 2024). This movement provided a favourable environment, contributing to their wider distribution and increased diversity. These factors highlight the ongoing need for further research to uncover new insights into stromatoporoid diversity and palaeobiogeography.

Previous studies have shown that stromatoporoid diversity increased throughout the Ordovician, with a significant radiation event in the late Middle Ordovician (late Darriwilian), followed by a second, smaller diversification pulse in the Sandbian of the early Late Ordovician (Webby 2004). The Late Ordovician, notably the Katian Stage, is marked by a high global diversity of stromatoporoids (Webby 2004). The presence of a new species in the Pirgu Regional Stage, which roughly corresponds to the late Katian, implies that the diversity of stromatoporoids in the Late Ordovician of Baltica is higher than previously recognised. This finding, together with the first report of aulaceratid stromatoporoids in Baltica by Jeon and Toom (2024), highlights the importance of continued research and exploration, even in well-studied areas, regardless of whether they represent reef or non-reef environments.

The discovery of new taxa and the extension of known genera to new palaeogeographic regions underscore that our understanding of stromatoporoid diversity and diversification history remains incomplete. As more data are gathered and analysed, we can expect to gain a clearer picture of the patterns and processes that shaped the diversification and palaeobiogeography of these important reef-building organisms during the Ordovician and beyond. The discovery of new stromatoporoid species in the well-studied Ordovician rocks of Estonia underscores the importance of sustained palaeontological research, even in regions with a long history of investigation (e.g. Rosen 1867; Nicholson 1886b; Riabinin 1951; Nestor 1960, 1964, 1999; Kaljo et al. 1963). Continued exploration of both new and existing localities, combined with detailed taxonomic and palaeoecological analyses, will be essential for fully documenting the richness of the stromatoporoid fossil record in Estonia and beyond, and for better understanding their role in the Great Ordovician Biodiversification Event and the development of metazoan-dominated reef ecosystems.

## Conclusions

- *Rosenella hosholmia* sp. nov. is distinguished by a wide range of cyst sizes, which alternate between sporadic layers of denser, either smaller or larger cyst plates. Short, thin, and pointed denticles occur on the surface of cyst plates, the surfaces appearing as tightly grouped points or dots in tangential sections. The *Rosenella* species occurs with ichnofossils *Planolites* and *Coprulus*.
- The finding of *Rosenella hosholmia* sp. nov. marks the first known occurrence of the genus *Rosenella* in Baltica during the Ordovician, expanding its palaeobiogeographic distribution beyond Laurentia, peri-Gondwana, Australia, and the Altai–Sayan Fold Belt.
- The spread of stromatoporoids (or the secretion of new skeletal architectures in Baltica), including *Rosenella hosholmia*, to Baltica during the late Katian Age was driven by warmer climatic conditions and a shift in Baltica's palaeogeography towards the equatorial region. This transition most likely provided a favourable environment that facilitated their broader distribution and enhanced diversity in the area.
- Alongside recent discoveries of new taxa, Ordovician stromatoporoid assemblages in Baltica remained markedly distinct from those in other palaeocontinents, including Laurentia, despite their closer geographical proximity. This contrasts with other groups, such as cephalopods and brachiopods, which showed greater faunal similarities to Laurentia and Avalonia, respectively. The discrepancy in palaeobiogeographic patterns implies that different marine taxa experienced varying dispersal opportunities and constraints, shaped by their ecological requirements and evolutionary histories.
- Estonia has an outstanding record of stromatoporoid fossils, with a long and intensive history of study across various localities and stratigraphic levels. The discovery of new species reveals that our understanding of stromatoporoid variety and distribution in the Baltica is still incomplete, highlighting the patchy distribution of stromatoporoid occurrences both globally and within specific regions.
- Ongoing exploration and detailed taxonomic analysis of stromatoporoids are essential for fully understanding the diversification and palaeoecological significance of these important reef-building organisms. Discoveries such as *Rosenella hosholmia* emphasize the need for further research to uncover new insights into stromatoporoid diversity and palaeobiogeography.

### Data availability statement

The data supporting the findings of this study are included in this article, and the materials have been deposited at the

Department of Geology, Tallinn University of Technology, Tallinn, Estonia.

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## *Rosenella* (stromatopoorne käsn) ilmumine Baltika paleokontinendile: uus liik Pirgu lademest (Katy lade, Ülem-Ordoviitsium)

**Juwan Jeon ja Ursula Toom**

Katy eal, mis on osa Hilis-Ordoviitsiumi ajastust, toimus stromatopooride oluline mitmekesistumine. Stromatopooride levikuandmed on aga sageli katkendlikud, mis takistab arusaamist nende mitmekesisusest ja mitmekesistumisest. Eesti, mis kuulus Ordoviitsiumi ajal Baltika paleokontinendi koosseisu, on stromatopooride osas üks intensiivsemalt uuritud alasid. Töös kirjeldatakse Eestist, Ülem-Ordoviitsiumi Pirgu lademe Adila kihistust (hilis-Katy-ealistest kihtidest) leitud stromatopooride perekonna *Rosenella* uut liiki *R. hosholmia* sp. nov. Kirjeldatud eksemplarid on kogutud Vormsi saarelt, Hosholmi poolsaare paljanditest. *R. hosholmia*'t iseloomustab tsüstide suuruse suur varieeruvus ning väiksemate ja suuremate tsüstplaadikihtide ebakorrapärane vaheldumine. Tsüstplaatide pindadel on lühikesed, õhukesed, teravad dentiiklid, mis tangentsiaalsetes lõigetes paistavad tihedalt koondunud punktidena. Stromatopooride kolooniatega on seotud jäljekivistised *Planolites* ja *Coprulus*. Töös kirjeldatakse perekond *Rosenella* esmaleidu Baltika Ordoviitsiumis, laiendades selle perekonna paleogeograafilist leviala kaugemale selle teadaolevatest esinemistest Gondwanas, peri-Gondwanas ja Altai–Sajaani kurrutusvööndis Edela-Siberis Kesk- ja Hilis-Ordoviitsiumi ajastul. Kirjeldatud liigi esinemine toob välja edasiste uuringute potentsiaali ka hästi uuritud piirkondades ning viitab sellele, et stromatopooride mitmekesisust Baltika paleokontinendil võidakse alahinnata. Lisaks annab *Rosenella* esinemine Eestis ülevaate paleogeograafilistest seostest ja faunavahetusest Baltika ning teiste paleokontinentide vahel Hilis-Ordoviitsiumi ajastul. See uuring aitab mõista kihtpoorsete käsnade mitmekesistumise mustreid Suure Ordoviitsiumi Bioloogilise Mitmekesistumise Sündmuse ajal, kuid jätkuvalt on väljakutseks stromatopooride katkendlike levikuandmete korreleerimine.