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Noncalcified dasyclad algae from the Vasalemma Formation, late Sandbian (Late Ordovician) of Estonia

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ABSTRACT

The Vasalemma Formation, late Sandbian, Late Ordovician in Estonia contains a previously unknown flora of noncalcified dasyclad algae. The Vasalemma Formation is a locally restricted limestone unit, which is predominantly composed of an echinoderm grainstone. The formation, in its central areas, contains bryozoa- and echinoderm-rich reefs, and associated with these reefs, small patches of dolomitic lime-mudstone with an algal-Lagerstätte occur. The macroalgae are preserved as thin carbonaceous film associated with pyrite without any micro-structures evident. Three taxa could be distinguished: *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov., *Chaetocladus sp., Eocladus estoniense* Kröger, et Tinn spec. nov. All three taxa have simple monopodial morphologies and delicate laterals. Remarkable is the occurrence of branched laterals in *E. estoniense*, which to our knowledge, is among the earliest occurrences in North America, which show similarities in depositional environments and associated fauna but differ in morphological and taxonomical diversity.

1. Introduction

Macroalgae are important elements in modern marine ecosystems. They provide structure, habitat, and food for a wide range of organisms (Christie et al., 2009; Thomaz and Cunha, 2010). The documentation of the Palaeozoic fossil record of marine macroalgae traditionally focused on the relatively common skeletal forms (see, e.g., Nitecki et al., 2004; Toomey and Nitecki, 1985). Noncalcified macroalgae, in contrast, are only rarely, and under certain circumstances, preserved.

Recent reviews demonstrate that the reconstruction of the evolutionary and palaeoecological history of this important component of marine ecosystems becomes increasingly detailed (LoDuca et al., 2017; Bykova et al., 2020). The size, morphospace range, and morphological disparity of macroalgae continuously increased during the Early Palaeozoic with major change at the transition from the Cambrian toward the Ordovician (Bykova et al., 2020). This increase included an evolution from predominantly simple-tubiform, spherical or ribbon-like forms during the Cambrian, toward dominance of monopodially branched and dichotomously branched forms in the Ordovician, and increasingly more complex forms in the Silurian (LoDuca et al., 2017).

However, the database on which this history is drawn is relatively restricted. Only slightly more than 70 occurrences of noncalcified macroalgae are known from the Early Palaeozoic globally (this includes 16 from the Cambrian, 17 from the Ordovician, and 38 from the Silurian periods, and one record from Ordovician-Silurian boundary beds in India) (LoDuca et al., 2017; Shabbar et al., 2022). The temporal and spatial resolution of the fossil record, therefore, is relatively low. Hence every new occurrence is important and can provide additional detail on the evolution, palaeogeography, and palaeoecology of this group.

Noncalcified macroalgae commonly form occurrences of concentrations of many well-preserved specimens, probably representing environmentally restricted depositional environments. These occurrences

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Finland

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also have been called algal-Lagerstätten (e.g., LoDuca, 2019, and references therein).

The rich and well-preserved flora of the Estonian Kalana Lagerstätte (Raikküla Regional Stage, Aeronian, Llandovery) is one well known example of these exceptional algal occurrences (Tinn et al., 2009, 2015; Mastik and Tinn, 2015, 2017; Mastik, 2019). While the majority and best-preserved algal fossils come from the Kalana (Otisaare) quarry in Central Estonia, also a few other quarries nearby have yielded non-calcified thalli. Drill core sections from the region suggest that the Kalana Lagerstätte spreads on a much larger territory than solely the restricted area of the quarries (Mastik, 2019).

Undescribed occurrences of macroalgae in drill cores and quarries, preserved as black or dark brown carbonaceous compressions, reveal that their stratigraphical distribution in Estonia is greater than previously thought, ranging from the Juuru to Rootsiküla regional stages (Rhuddanian – Homerian, Silurian; Mastik, 2019).

Here we document a new Estonian occurrence, which qualifies as an algal-Lagerstätte from reef-associated facies within the Vasalemma Formation (Keila Regional Stage, Sandbian, Upper Ordovician). The occurrence represents a flora, which is nearly time-equivalent to that of the North American Platteville Formation (LoDuca, 2019), which gives the opportunity to compare an Ordovician algal flora in a snapshot of time in two different places of the Ordovician world.

1.1. Geological setting

The Vasalemma Formation of northern Estonia occurs in a relatively central area of the East European Craton, which during the time of the Early Palaeozoic formed the Baltic Palaeobasin of the Baltica Palaeocontinent. During the Middle and Late Ordovician time, the region was part of the northern, shallow shelf of the Baltic Palaeobasin, with a coastline probably situated further north toward the Finnish mainland and the centre of the basin directed toward the south in the direction of Latvia and Lithuania (e.g., Poprawa et al., 1999) (Fig. 1). Because of their relatively central position on the East European Craton, the Ordovician sediments of Estonia were little affected by diagenetic processes and its fossil content, and the sedimentary record is pristinely preserved (e.g., Ainsaar et al., 2010). Results from combined litho-, bio-, and chemostratigraphy allow for a high-resolution stratigraphic correlation of the strata of the Vasalemma Formation across Baltoscandia (Meidla et al., 2023; see also Kröger et al., 2014b; Kröger et al., 2014a). The strata can be age constrained as the latest Sandbian, belonging to

the uppermost Keila Regional Stage by bio-, and chemostratigraphy (Hints and Nolvak, 2023; Meidla et al., 2023; Fig. 1, 3).

The Vasalemma Formation forms a relatively narrow belt of a pelmatozoan grainstone spanning c. 20 km in the E-W direction, an N-S extension of c. 5 km, and with a thickness of up to 15 m. In its central parts, concentrations of patch reefs occur. In the Vasalemma quarry, the reefs can reach a thickness of up to 10 m. The median diameter of the reefs at Vasalemma quarry is 6 m, and their median nearest distance between them is 23 m (Kröger et al., 2023). The reefs consist of matrixrich (up to 75%) limestone core areas with bryozoans, echinoderms, receptaculitans and solenoporans as main reef builders (Kröger et al., 2014a; Kröger et al., 2023). On the reef flanks pockets and patches of argillaceous limestone to shale are common, which in places contain accumulations of cephalopods and illaenid trilobites (e.g., Kröger and Aubrechtová, 2017). The shaly and marly parts of these patches have a gray-greenish color, are finely parallel bedded and are rich in silt-size dolomite crystals. The patches generally have a thickness of less than one meter and a lateral expansion of several meters. The organic-walled microfossil assemblage is characteristic of the Keila Regional Stage.

2. Material and methods

2.1. Material

The material comprises c. 30 slabs with clusters of algae, which were collected in 2007 from the southeastern quarry wall of the Vasalemma quarry, northern Estonia (Fig. 1). The quarry exposes the Vasalemma and Kahula formations, late Sandbian, Late Ordovician (e.g., Kröger et al., 2014a; Kröger et al., 2023).

In the southeastern area of the quarry, the main lithology of the Vasalemma Formation is a massive echinoderm grainstone, which contains densely spaced patch reefs (e.g., Kröger et al., 2014a, Kröger et al., 2023). The material was collected from patches of argillaceous limestone at reef interspaces in the direct vicinity of a reef, comparable to the situation illustrated in Fig. 2. The material occurs in a finely parallel bedded argillaceous mudstone, which has a gray-greenish color and is rich in silt-size, floating (phorphyrotopic) euhedral dolomite rhombohedrons (Fig. 3). All figured and analyzed specimens are in the repository of the geological collections of the Department of Geology, Tallinn University of Technology (GIT).



Fig. 1. The fossil locality Vasalemma quarry, northern Estonia. 1. Overview on Baltoscandian area with geopolitical borders. 2. Palaeogeographic reconstruction of depositional environment (see text). 3. Stratigraphical context of the Vasalemma Formation (star).



Fig. 2. Typical outcrop at Vasalemma quarry with limestone of the reef core matrix, the surrounding crinoidal grainstone, pockets with abundant cephalopods and intraclasts, and patches with fossiliferous, argillaceous, dolomitic limestone – shale. Note: this is not a photo and reconstruction of the actual sampling location but illustrates the general facies pattern in which the macroalgae occur. Abbreviations: gst., grainstone; lst., limestone; mdst., mudstone.



Fig. 3. Macroalgae bearing sediment of the Vasalemma Formation, Sandbian, Ordovician of Estonia. 1. Polished cross-section (sample GIT 204127 taken from GIT 611-26) with a layer with macroalgae (arrow a) and layers rich in skeletal elements, such as bryozoans (arrow b) (photo G. Baranov, Tallinn). 2. SEM photograph of sample GIT 204127, bedding parallel with scolecodont in the center (dark area) and numerous dolomite rhombohedrons.

2.2. Methods

The specimens were photographed under light macroscopy and submersed in water for better contrasts. Micro-chemical images and analyses of the samples were obtained with a scanning micro X-ray fluorescence (micro-XRF) M4 Tornado with AMICS instrument, supplied by Bruker at the Geological Survey of Finland (GTK). The system uses a 30-W rhodium anode X-ray tube and two 30 mm² silicon drift detectors (SDDs) with a resolution of <145 eV (MnK α) at 275 kcps (kilocounts per second). The Rh X-ray source was operated under maximum energy settings (50 kV, 600 μ A). The beam was focused by a polycapillary lens on a fixed spot size of 20 μ m under 2 mbar vacuum. The samples were mapped in two separate runs using a step size of 50 μ m and a pixel dwell time of 10 ms for a complete scan of the sample and a step size of 35 μ m

and a pixel dwell time of 10 ms for a detailed map. The qualitative elemental maps were generated using the Bruker M4 software.

For microfossil extraction, a 150 g sample with algal remains was dissolved in 10% acetic acid. Organic-walled microfossils, such as chitinozoans and scolecodonts, were picked from the residue after sieving through a 45-µm screen, stored in glycerine and identified under a stereomicroscope.

3. Systematic palaeobotany

Order: DASYCLADALES (Pascher, 1931)

Family: TRIPLOPORELLACEAE (Pia, 1920) Granier and Bucur in Granier et al., 2013

Tribe: SALPINGOPORELLEAE (Bassoulet, 1979), emend (LoDuca,

1997)

Subtribe: CHAETOCLADINAE (LoDuca, 1997)

Genus: Chaetocladus (Whitfield and Hall, 1894), emend (LoDuca, 1997)

Chaetocladus vasalemmense Kröger, et Tinn spec. nov.

Fig. 4, 2, Fig. 5, Fig. 6; Plate I, 1–7, 9; Plate II, 1–6.

Etymology: The epithet vasalemmense refers to the type locality. *Locality*: Vasalemma quarry, Estonia

Holotype: GIT 611-2-1 and counterpart 611-1-1 (two opposite sides of a slab)

Additional material: Specimens at slabs GIT 611-1, -10 to -15, -20, -23 to-25, -27 to-29.

Stratigraphic horizon: Vasalemma Formation, Keila Regional Stage, Sandbian, Ordovician.

Diagnosis: Thallus non-calcified, slender, thallus <12 mm wide; central axis c. 0.9 mm wide, with euspondyl, acrophorous ramifications; unbranched laterals; verticils nearly equally spaced at c. 0.9 mm.

Description The holotype is a 15 mm long fragment of an apical part of a 7–8 mm wide thallus with a 0.9–1 mm wide, cylindrical axis with euspondyl, acrophorous ramifications, with a vertical spacing of 0.9–1 mm at its base and 0.3 mm at the tip of the axis (Plate I, 4). The laterals are c. 0.1 mm in diameter, 7–8 mm long. The preservation does not allow for an estimation of then number of laterals per verticil. The structure of the laterals appears to be homogenous (without internal structures evident under light microscopy). The tip of the thallus is rounded with densely spaced laterals. The axial interspaces between the verticils have a concave outline with narrowest diameter just apically of the verticil (Plate I, 7). The structure of the axis is homogenous and nondivided. The number of laterals per verticil is difficult to determine because of the poor preservation of the axial areas but appears to be between eight to ten.

Slab GIT 611-29 contains more than ten fragments assigned herein to *C. dubius.* Two of them are thalli with a length of c. 70 mm, preserving rhizoidal holdfast structures but not the tip (Fig. 5). At its basal c. 7 mm, the axis of these specimens is slightly thickened (diameter c. 1.3 mm) compared to the more distal axis parts (with diameters of c. 0.9–0.8 mm). At the base of the axis, simple rootlets with diameters of c. 0.4 mm appear and numerous 0.1 mm thick irregularly spaced filaments. No reproductive organ structures have been observed.

Measurements from 16 specimens assigned to *C. vasalemmense* show a mean axis diameter of 0.92 mm. The largest axis diameter is 1.3 mm and smallest is 0.8.

Remarks: The specimens described above are similar in general morphology to specimens assigned to C. dubius (Spencer, 1884).

Specifically, the axis width, lateral width, and verticil spacing are within the range of the species description given by LoDuca (1997) (see also LoDuca, 1997, table 1). However, the thalli of the Vasalemma specimens are larger than the Silurian type-material with a total thallus length of c. 70 mm (versus c. 50 mm given in LoDuca, 1997), and lateral length of 8 mm (versus 5 mm in LoDuca, 1997). Moreover, uncertainty exists in C. dubius about the number of laterals per verticil and about the spacing of verticils (i.e., the existence of repetitive bands of narrowly spaced verticils) (see LoDuca, 1997). A specimen from the Big Hill Formation (Katian), Michigan, USA, has bands of two or three closely spaced verticils at a lateral distance of c. 1 mm (LoDuca, 2019, p. 211). Such a condition is also assumed for the type-material of C. dubius (see argumentation in LoDuca, 2019). The Vasalemma specimens, described herein, differ from the type-material of C. dubius and from the specimen from the Big Hill Formation in having distinct, evenly spaced verticils and no repetitive elements or bands of differently spaced verticils (see Plate I, 7, Fig. 4, 2). The number of laterals per verticil is difficult to evaluate in the specimens from the Vasalemma Formation because the axial regions are to poorly preserved to reveal the precise location of the attachment points of the laterals.

Chaetocladus sp.

Plate I, 10-11

Locality: Vasalemma quarry, Estonia.

Studied material: GIT 611-2-6.

Stratigraphic horizon: Vasalemma Formation, Keila Regional Stage, Sandbian, Ordovician.

Description: Specimen GIT 611-2-6 (Plate I, 10, 1.11) consists of fragments of at least six thalli which converge toward their base. The longest thallus has a length of 45 mm, a width of 1.4 mm at its base and 4.5 at is apical end. All thalli are fragmentarily preserved without tip and basal holdfast structures. The thalli have ramifications at a vertical distance of 1.6–1.8 mm. The laterals are homogenous and unbranched with a diameter of c. 0.1 mm, c. 30 occur across the diameter. The diameter and shape of the main axis cannot be determined.

Remarks: The specimen can be assigned to *Chaetocladus* because it consists of a cylindrical thallus with densely spaced unbranched laterals, which is longitudinally divided by ramifications. It differs from other species of *Chaetocladus* in its combination of relatively long ramifications with a narrow thallus. However, a species-level determination is impossible because of its fragmentary character. The possibility also exists, that the narrow thallus is result of taphonomic processes, such as current alignment and / or minor transport during and immediately prior to burial.

Genus: Eocladus (LoDuca et al., 2011)



Fig. 4. Details of 1. Eocladus estoniense Kröger, et Tinn spec. nov. (GIT 611-2-2) with well-preserved bifurcating laterals, and 2. Chaetocladus vasalemmense Kröger, et Tinn spec. nov. (GIT 611-2-4) from the Vasalemma Formation, Sandbian, Ordovician of Estonia with well-axial region. Arrows denote positions of verticils. 1, 2, same scale.



(caption on next page)

Plate I. Non-mineralized macroalgae from the Vasalemma Formation, Sandbian, Ordovician of Estonia. 1, 2, 4–7. *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov. 3. *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov. two vertically positioned specimens, *Eocladus estoniense* Kröger, et Tinn spec. nov. horizontally positioned specimen at lower half of figure, note lingulate brachiopod (arrow) associated with *E. estoniense*. 1., Specimen GIT 611-25-3, photo G. Baranov (Tallinn). 2., Slab GIT 611-25-4 (photo G. Baranov, Tallinn). 3., specimen GIT 611-2-1 (holotype), arrow indicates lingulate brachiopod. 4., specimen GIT 611-2-2 (holotype). 5., specimen GIT 611-12-1. 6., specimen GIT 611-12-2. 7., specimen GIT 611-2-3. 8. *Eocladus estoniense* Kröger, et Tinn spec. nov., specimen GIT 611-2-4, note lingulate brachiopod (arrow). 9. *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov. and fragment of possible bryopsidalan chlorophyte (arrow), specimen 611-15. 10, 11. *Chaetocladus* sp. specimen GIT 611-2-6.

Eocladus estoniense Kröger, et Tinn spec. nov.

Fig. 4, 1-; Plate I, 3, 8.

Etymology: The epithet estoniense refers to the fossil source in Estonia.

Locality: Vasalemma quarry, Estonia.

Holotype: GIT 611-2-2 and counterpart 611-1-2 (two opposite sides of a slab)

Additional material: Specimens at slabs GIT 611-1, 611-2, 611-10 to 611-15, and 611-23 to 611-26.

Stratigraphic horizon: Vasalemma Formation, Keila Regional Stage, Sandbian, Ordovician.

Diagnosis: Thallus non-calcified, slender, unbranched, thallus <10 mm wide; central axis c. 1 mm wide, with euspondyl, acrophorous ramifications; branched laterals; branching with angles of more than c. 30° at least to the fourth order, verticils nearly equally spaced at distance of c. 1 mm.

Description: The holotype (Plate I, 3) is a c. 25 mm long fragment of a thallus, which is c. 10 mm wide at its widest position and has a 0.9-1 mm wide central axis. The central axis is homogenous, non-divided, and with verticils with a vertical spacing of c. 1 mm, and with eight primary laterals per verticil. The interspaces between the axis verticils are symmetrically concave along and perpendicular to the growth axis (Plate I, 8). The laterals are homogenous (without internal structures evident under light microscopy), c. 0.1 mm in diameter and form a bristled nearly tubular thallus (Plate I, 3). The total length of the laterals amounts to c. 3 mm with a first branching at c. 1 mm from the axis, and subsequent branching at distances of 0.5 mm from previous branching, respectively. The laterals bifurcate with an angle of typically between 45 and 90°. No reproductive organs or holdfast structures occur.

Remarks: E. xiaoi LoDuca et al., 2011, the type species and previously only known species of *Eocladus*, differs from the new species in having a more delicate central axis (0.3 mm versus 1.0 mm), a narrower spacing of the verticils (0.6 mm versus 1 mm), and with shorter laterals (c. 10 mm versus 3 mm), which bifurcate in a low angle ($<30^{\circ}$ versus $45-90^{\circ}$) toward at least to the fourth order. Additionally, and although the precise number of laterals is difficult to ascertain in the specimens studied herein and in *E. xiaoi* (see, LoDuca et al., 2011) it appears, that the number of primary laterals per verticil is higher in the former (eight versus four). Results from student's t-test (p = 0.014) of measurements of *E. estoniense* (n = 6) and *C. vasalemmense* (n = 16) show that the mean axis diameter of the latter (0.92 mm) is significantly smaller than that of *E. estoniense* (1.03 mm). This can be interpreted as evidence for a specifically thinner axis in *C. vasalemmense* compared to *E. estoniense*.

Callithamnopsis Whitfield, 1894 from the Platteville Formation (late Sandbian, Ordovician), Wisconsin, differs from *E. estoniense* Kröger, et Tinn spec. nov. in having a more delicate axis (0.2 mm v. 1 mm) with less laterals per verticil (4–6 versus 8). This results in a bushier, and more robust appearance of the latter (see LoDuca, 2019).

Archaeobatophora typa Nitecki, 1976 from the Big Hill Formation (Katian) is similar to *E. estoniense* Kröger, et Tinn spec. nov. in general appearance and with respect to the dimensions of the central axis and laterals but differs in having laterals with stout and thick primaries and hairlike thin subsequent branchlets. In *E. estoniense* the diameter of the laterals is c. 0.1 mm throughout.

4. Results

4.1. Fossil assemblage

A count of specimens on slabs GIT 611-1, and 611-2, 611-10 to 611-15, and 611-23 to 611-27 resulted in 99 identifiable dasyclad fragments; 78 (79%) of them are *C. vasalemmense* Kröger, et Tinn spec. nov., 15 (15%) are *E. estoniense* Kröger, et Tinn spec. nov., and 6 (6%) are *C.* sp. Additionally, a poorly preserved fragment of a possible bryopsidalan chlorophyte, possibly related to *Inocladus* LoDuca et al., 2021) is present.

The dasyclads are accompanied by abundant spheres of the prasinophycean *Leiosphaeridia baltica* (Plate I, 3, 4, 8), which sometimes occur within the meshwork of laterals of the dasyclad thalli but are also abundant in the surrounding sediment.

Small lingulate brachiopods (diameters c. 0.7 mm) occur preferably in association with the thalli and are in several cases preserved directly attached to the axis (Plate I, 3, 4, 8, 2). Additionally, tube-fragments of the cnidarian *Sphenothallus* (Plate II, 1, 2), and scolecodonts are abundant (Fig. 3, 2) and bryozoan colonies occur. In one case several thalli are preserved attached to a bryozoan colony (Fig. 6).

The fauna of scolecodont-bearing polychaetes contains at least 17 species, including e.g., Oenonites gadomskae, O. tuberculatus, Incisiprion incisus, Pteropelta kielanae, Mochtyella cristata, Xanioprion sp. Leptoprion sp., Atraktoprion cf. cornutus, Protarabellites cf. staufferi etc. These are typical of the Kahula Formation (Keila Regional Stage) in several sections in northern Estonia (Hints, 1998, 2000). The recovered chitinozoan assemblage is of relatively low diversity, partly due to the small sample size, containing Cyathochitina kuckersiana, Belonechitina capitata, B. comma, Conochitina elegans, Euconochitina primitiva and Pistillachitina sp. Closely similar assemblage has been reported from the Keila Regional Stage in other Estonian sections (e.g., Hints and Nõlvak, 2023). Additionally, the microfossil examination revealed abundant prasinophycean algae (Leiosphaeridia and Tasmanites), enigmatic Parachitina curvata and rare melanoscleritoids. The occurrence of well-preserved dendroid graptolites and fragments of branched bryozoan colonies is also noteworthy.

4.2. Preservation

The thalli are preserved as flattened a thin black film and as dispersed darkened matter within the micritic matrix tracing the outline of the former body (Fig. 3, 1). In many places the axis appears as a firmly black area and the laterals as brownish areas within the micritic matrix. The axes are commonly fragmented and fractured by small irregular patches and cracks. Microscopic details at the surfaces of the axis or the laterals are not evident using light microscopy. Most specimen are flattened but 3-D preservation occurs. The results from micro-XRF scanning allow to indirectly identify the black material as carbon because other potential black minerals, such as iron- and manganeserich oxides or pyrite (FeS) can be excluded (Plate II, 2). The analysis also revealed that in association with the axis dispersed FeS is concentrated (Plate II, 2). The FeS concentration is not identical with the outline of the black material of the axis as preserved under light microscopy but instead forms irregularly spaced patches around the axis in the central parts of the thalli. Remarkable is the abundance of phosphatic (apatitic) shells from brachiopods and Sphenothallus in association with the algae (Plate II, 2, 4) because phosphatic shells are very rare in other parts of the Vasalemma Formation.



(caption on next page)

Plate II. Micro-XRF images of slab specimen 611-25-3 with multiple specimens of *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov. on the right, *Eocladus estoniense* Kröger, et Tinn spec. nov. with multiple specimens of associated lingulate brachiopods (arrow a), and a fragment of *Sphenothallus* in the center (arrow b). 1., photograph of a complete slab. 2., Scan of a complete slab, imaging of Iron (Fe), Sulfur (S), Phosphorus (P), Calcium (Ca), Titanium (Ti), and free energy range (F1). Note the phosphatic skeleton of *Sphenothallus* in the center, and several pyritic areas. 3., Detail of 2 with the selection of Sulfur and Iron showing the pyritic areas. 4., Detail of 2 with the selection of Phosphorus, highlighting lingulate shells and fragments of *Sphenothallus*. Note the association of brachiopods with algae thalli. 5., Detail of 2 with the selection of Titanium, highlighting areas with concentrations of Ti-Fe oxide minerals. 6., Detail of 2 with the full spectrum of elements selected for micro-XRF imaging.



Fig. 5. Chaetocladus vasalemmense Kröger, et Tinn spec. nov. (GIT 611-27-1) from the Vasalemma Formation, Sandbian, Ordovician of Estonia, nearly complete specimen with preserved rhizoid holdfast structures (photo G. Baranov, Tallinn).

5. Discussion

5.1. Interpretation of the assemblage

The dasyclad assemblage of the Vasalemma Formation contains exclusively monopodial morphotypes (i.e., with unbranched thalli) of the genera *Chaetocladus* and *Eocladus*. Noteworthy is the occurrence of growth forms with bifurcate secondary elements (laterals) in the Vasalemma Formation. These specimens are herein assigned to *E. estoniense* Kröger, et Tinn spec. nov., and are, to our knowledge, together with *Callithamnopsis fruticosa* (Hall) from the Platteville Formation of Wisconsin (LoDuca, 2019) among the oldest dasyclads with complex secondary structures.

The preserved thalli are in many places fragmentary and without discernable holdfasts, which could be interpreted as evidence for an allochthonous or parautochthonous origin of the algae. However, some clusters of algae appear in near life position, forming groups of more than ten thalli (Plate I, 1, 2), a composition, which is unlikely to be preserved after transport by wave action or strong currents. Two



Fig. 6. Association of *Chaetocladus vasalemmense* Kröger, et Tinn spec. nov. (GIT 611-28-1) from the Vasalemma Formation, Sandbian, Ordovician of Estonia, which appears to be in life position, and attached to a domal bryozoan colony.

specimens of *C. vasalemmense* Kröger et Tinn spec. nov. preserved with holdfast structures (Fig. 5) could indicate that these specimens were deposited in place. Additionally, a domal bryozoan colony is preserved with associated thalli of *C. vasalemmense*, which appear to be in lifeposition, attached to the bryozoan-skeleton (Fig. 6).

The composition of the skeletal fauna preserved within these sediments, predominantly delicate erect forms (e.g., dendroidal bryozoans, Sphenothallus,) also supports the interpretation of the assemblage as parautochthonous and as originating from low energy, shallow water paleoenvironment. The abundance of small (sub-mm-sized) lingulates not only is evidence that the algae provided habitat for a fauna (a fact that is well known from extant marine environments, e.g., Christie et al., 2009), but it could also indicate a somewhat environmentally restricted (with respect to temperature and / or salinity) paleoenvironment. The early diagenetic dolomite present in the sediment and the absence of heavy bioturbation supports this interpretation (see e.g., Flügel, 2004, Chapter 7.8.2 on dolomitization models for the interpretation of porphyrotopic dolomite). The assemblage is therefore interpreted as deposited in place or nearly so. Most probably, it records locally restricted (tidal?) ponds, small-scale basins or lagoonal patches associated with the reefs.

The concentration of patches of finely dispersed pyrite within the central areas of the algal thalli can be interpreted as evidence of enhanced bacterial activity during algal decay (Plate II, 2). More generally, the pyrite concentration could indicate the presence of mucus, or protein-rich (=sulfur-rich) organic material associated with the algal thalli (see, e.g., Kurth et al., 2015).

5.2. Comparison with other non-calcified macro-algae occurrences

The macroalgae occurrence in the Vasalemma Formation is nearly contemporaneous with those known from the Platteville Formation (Sandbian), Wisconsin, USA, and slightly older than the occurrence of Chaetocladus dubius (Spencer, 1884) in the Big Hill Formation (late Katian) of Michigan, USA (LoDuca, 2019). With these occurrences, the Vasalemma algae flora shares the dominance of Chaetocladus, a taxon with monopodial thallus morphology and simple unbranched laterals. The specimens in the Vasalemma Formation assigned herein to Eocladus are, to our knowledge, the oldest dasycladalans with branched laterals (i.e., with complex monopodial morphologies sensu Bykova et al., 2020). Therefore, the Vasalemma macroalgae occurrence widens not only the palaeogeographic range of these oldest Ordovician dasycladalans, but also broadens their known morphological spectrum. The North American occurrences and the Vasalemma findings came from shallow warm water palaeonvironments of relatively low palaeolatitudes (see e. g., Cocks and Torsvik, 2011; Torsvik and Cocks, 2013). Although, based on reconstructions of Torsvik and Cocks (2013), the Vasalemma area, Estonia, was located at palaeolatitudes of $>30^\circ$ South and thus were non-tropical during the Sandbian.

A common attribute, which characterizes many of the algal lagerstätten, seems to be the shallow restricted marine environment within the photosynthetic zone (often indicated also by specific fauna, such as small lingulate brachiopods, e.g., in Vasalemma and Platteville, LoDuca, 2019), short distance transportation of algal thalli proved by the preservation of their delicate structures), and the absence or rarity of bioturbation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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