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macroscopic algal fossils
from the Kalana *Lagerstätte,* Estonia

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43

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following published papers, which are referred to in the text by their Roman numerals. The papers are reprinted by kind permission of the publishers.

I **Mastik, V.**, Tinn, O. 2015. New dasycladalean algal species from the Kalana Lagerstätte (Silurian, Estonia). *Journal of Paleontology*, 89(2), 262–268.

II Tinn, O., **Mastik, V.**, Ainsaar, L., Meidla, T. 2015. *Kalania pusilla*, an exceptionally preserved non-calcified alga from the lower Silurian (Aeronian, Llandovery) of Estonia. *Palaeoworld*, 24(1–2), 207–214.

III **Mastik, V.**, Tinn, O. 2017. *Leveilleites hartnageli* Foerste, 1923 (Rhodophyta?) from the Ordovician of Laurentia and Silurian of Baltica: Redescription and designation of a neotype. *Palaeoworld*, 26(4), 602–611.

Author's contribution:

Paper I: The author took part in fieldwork, collection of material/specimens, studied the palaeontological collections of *Palaeocymopolia* specimens and was responsible for sample measurements, photography and preparation for scanning electron microscopy (SEM) studies, data interpretation and the writing of the manuscript.

Paper II: The author took part in fieldwork, collection of material/specimens, studied the palaeontological collections of *Kalania* specimens and was responsible for sample measurements, photography, SEM studies, and in part for writing the manuscript.

Paper III: The author took part in fieldwork, collection of material/specimens, studied the palaeontological collections of *Leveilleites* specimens and was responsible for sample measurements, photography and preparation for scanning electron microscopy (SEM; BSE; EDS) studies, data interpretation and the writing of the manuscript.

1. INTRODUCTION

Algae have been fundamentally important components in the biosphere and Earth system dynamics during the geological past and continue to play a substantial role in the aquatic ecosystems of the modern Earth (Graham et al., 2009). The estimated number of extant algal species ranges from 36 000 (John and Maggs, 1997) to more than 10 million (Norton et al., 1996). The global algae database, AlgaeBase, currently (16.10.2018) records more than 153 000 species (algaebase.org). Algae can inhabit a wide range of environments. They commonly live in aquatic conditions, from oceans to continental freshwater bodies, and can tolerate broad ranges of pH, temperature, turbidity, O_2 and CO_2 concentrations (Andersen, 1992; Barsanti and Gualtieri, 2014). In most places, they function as the primary producers in the food chain, producing organic material from sunlight, carbon dioxide and water (Lee, 2008). It has been estimated that in total, 40% of global photosynthesis is contributed by algae (Andersen, 1992). Algae can be planktonic and float in the water column, as do most microscopic unicellular species, or benthic – growing on rocks, sand, mud or even on other organisms. The body types of algae vary from microscopic (0.2–2.0 µm in diameter) to macroscopic (up to 60 m in length), from unicellular to multicellular (Barsanti and Gualtieri, 2014; Graham et al., 2009).

Algae are extremely diverse, representing a large polyphyletic group of various photosynthetic organisms. Researchers categorize algae into different phyla that are phylogenetically rather distinct from each other: Cyanobacteria (blue–green algae), Glaucophyta, Rhodophyta (red algae), Chlorophyta (green algae), Charophyta, Haptophyta (coccolithophorids), Cryptophyta (crypto-monads), Ochrophyta (golden algae, diatoms, brown algae), Cercozoa, Myxozoa (dinoflagellates) and Euglenozoa (euglenoids) (Andersen, 1992; Barsanti and Gualtieri, 2014; Graham et al., 2009).

Only a minuscule fraction of organisms is preserved as fossils after death, making the fossil record very incomplete. The biological remains are typically destroyed before they are buried under sediments. However, a small proportion of organic remains do become buried and eventually are fossilized. Of these, the preservation potential is higher with hard, mineralized shells, skeletons or cuticles (Bottjer et al., 2001; Briggs, 2001). The preservation potential of most of the algae composed of only organic tissue is typically low and, therefore, the evolution and diversity of algae through geological time are poorly known.

The oldest generally acknowledged algal fossil is the iconic rhodophyte *Bangiomorpha pubescens* that has been documented in sediments from two localities in northeastern Canada (Butterfield, 2000; Knoll et al., 2013) and dated between 1.222 and 1.174 Ga (Yang et al., 2016). Molecular clock analyses have inferred the divergence of red–green algal lineages at around 1.5 Ga (Yoon et al., 2004), 1.1 Ga to 790 Ma (Berney and Pawlowski, 2006) or 1.166 Ga (Gibson et al., 2018). However, a few significantly older putative algal fossils have also been described (Bengtson et al., 2017; Han and Runnegar, 1992;

Moczydlowska et al., 2011) with age estimates at 1.8 to 1.6 Ga. Their age, which is hundreds of millions of years older than most phylogenetic estimates for red–green algal divergence, have raised questions about their correct assignment (Gibson et al., 2018). The earliest fossils attributed to green algae date from the Precambrian (ca. 1.2 Ga) (Knoll, 2003; Tappan, 1980), but molecular clock analyses have estimated the origin of the green algal lineage (Viridiplantae) between 700 and 1500 million years ago (Berney and Pawlowski, 2006; Douzery et al., 2004; Hedges et al., 2004; Leliaert et al., 2012). Brown algae (phaeophytes) have soft tissues only, and mostly for that reason a consistent fossil record is lacking (Draisma et al., 2003). As molecular clock studies indicate a post-Palaeozoic origin for phaeophytes (Brown and Sorhannus, 2010; Silberfeld et al., 2010), it has been argued that Proterozoic and Palaeozoic taxa described as brown algae could resemble brown algae only superficially. The Phanerozoic fossil record of algae has greatly benefited from the ability of several algal groups to precipitate or deposit $CaCO_3$ (Brownlee and Taylor, 2002). However, as the vast majority of algae do not calcify (Taylor et al., 2009), all fossils of noncalcifying macroalgae are of special value.

Sedimentary deposits that preserve the remains of organisms without hard parts are collectively known as *Lagerstätten*. Algal-*Lagerstätten*, especially from the early Palaeozoic, are rather rare. Altogether 22 deposits are known up to date (LoDuca et al., 2017), the most important ones being in the Czech Republic (Steiner and Fatka, 1996), Canada (Fry, 1983; LoDuca et al., 2011, 2013), Ukraine (Ishchenko, 1985) and the USA (LoDuca and Brett, 1997). Typical algal-*Lagerstätten* are thallophytic-alga-dominated biotas, where abundant thallophytic marine algae dominate the biota and shelly taxa are rare or lacking.

The Kalana *Lagerstätte* is a typical *Konservat-Lagerstätte*, where the individual preservation is exceptional and soft tissues of animals and plants are often preserved in high detail (Tinn et al., 2009). The first specimens of fossilized algae in the Kalana quarry were discovered by Tõnu Pani in 2006. By 2018 we knew (Tinn et al., 2009; PAPERS I–III) that this carbonate succession contained not only rich and diverse algal flora, but also numerous exceptionally preserved faunal fossils.

The succession that opened in Kalana has drawn the attention not only of palaeontologists, but the quarry has also become a site of different sedimentological, geophysical and mineralogical-geochemical studies, all aiming at understanding the processes during and after the deposition of these early Silurian carbonate rocks (Eensaar et al., 2017a, 2017b; Gaškov et al., 2017; Männik et al., 2016; Preeden et al., 2008).

The main aims of this thesis are as follows:

- to study and describe the most widespread algal taxa in Kalana, their anatomy, reproductive structures and growth stages, and to evaluate the relationships between their extant/extinct relatives;
- to study the distribution of the closest extant relatives of the algae found in Kalana together with the sedimentary features of the strata containing the exceptionally preserved biota in order to reveal the palaeoenvironmental settings of the locality;
- to study the spatial and stratigraphic distribution of the taxa described in the Kalana *Lagerstätte* in Lower Palaeozoic strata of the northern Baltic Palaeobasin.

2. *LAGERSTÄTTEN*

Under normal marine conditions, where oxygen is present in the water column and shallow sea-bottom sediments, scavenging and microbial decay rapidly remove soft tissues from mineralized skeletal elements. Only in rare cases the organic remains become buried and preserved in sediments (Bottjer et al., 2001; Briggs, 2001).

The German word '*Lagerstätten*' was originally used to describe mineral and ore deposits of economic worth. Adolf Seilacher, in 1970, first coined the term 'Fossil-*Lagerstätten*' to describe the deposit containing fossils that are so exceptionally preserved or abundant that it warrants special exploitation and scientific attention. Seilacher et al. (1985) distinguished two types of fossil *Lagerstätten*: *Konzentrat-Lagerstätten* and *Konservat-Lagerstätten. Konzentrat-Lagerstätten* are deposits where a large number of fossils are preserved but the quality of individual preservation may not be exceptional. Such *Lagerstätten* could demonstrate some mechanisms of concentration, for instance, evidence of mass mortality (Bottjer et al., 2001; Seilacher, 1990). The other type is *Konservat-Lagerstätte*, where the individual preservation is exceptional and soft tissues of animals and plants are preserved in detail. Conservation deposits usually result from catastrophic burial-preservation events, where the exceptional preservation is favoured by anoxic bottom conditions and large episodic influxes of sediment. *Konservat-Lagerstätten* are unevenly distributed through geologic time or space, suggesting that some global phenomena may play a key role in exceptional fossil preservation (Allison and Briggs, 1993; Muscente et al., 2017). *Konservat-Lagerstätten* assemblages are most common in the Ediacaran, Cambrian, lower-middle Cretaceous, Palaeogene and Neogene, and relatively rare in the Devonian, upper Triassic and uppermost Cretaceous (Muscente et al., 2017).

The deposit where noncalcified macroalgae dominate the non-biomineralized component of the biota is also called an algal-*Lagerstätte* (Bottjer et al., 2001; Seilacher, 1990) or the thallophytic-alga-dominated biota (LoDuca, 1995). Algal or algal-bearing *Lagerstätten* worldwide are described in a number of papers, including Fry (1983), Lamsdell et al. (2016), Lin (1984), LoDuca and Brett (1997), LoDuca et al. (2017), Ruedemann (1909), Walcott (1919), Whitfield (1894), Xiao et al. (2014) and Yang et al. (1999b).

3. PREVIOUS STUDIES

3.1. Precambrian and early Palaeozoic record of noncalcified algal fossils

The record of fossil algae goes back to the Mesoproterozoic (Bengtson et al., 2017). Algal diversity remains conspicuously low through that time – 11 genera and 13 species have been discovered and documented from the 1600–1000 Ma old rocks. All Mesoproterozoic algal fossils are minuscule, only up to few millimetres in size, filamentous or spherical morphologically simple forms. To date, the most ancient algae have been reported from the early Mesoproterozoic (~1600 Ma), from central India (Bengtson et al., 2017). The fossils were found in the middle of cyanobacterial mats and the biota show features characteristic of modern eukaryotic red algae. The specimens of *Bangiomorpha pubescens* represent the oldest example of eukaryotic sex and complex multicellularity. These red algal fossils were found from the shallow-water carbonates of the 1200 Ma Old Hunting Formation, Somerset Island, Arctic Canada (Butterfield, 2000). Kumar (2001) has described eight different macroscopic algal species from the black shales of the 1000 Ma Old Vindhyan Supergroup, central India.

Twenty-seven macroscopic algal fossil genera and more than 35 species have been reported from the middle-late Neoproterozoic. Several algae-bearing biotas have been described from the Doushantuo Formation, South China – Miaohe biota (Xiao et al., 2002), Wenghui biota (Wang et al., 2014a) and Lantian biota (Yuan et al., 2011). All carbonaceous macroalgae of that age were found from black shale sediments. They are morphologically simple, delicately dichotomously branched or cylindrical in form, and at least a few centimetres high. One genus, *Chuaria*, spherical in shape, has been described from the Mesoproterozoic, Neoproterozoic and also from the Cambrian (Fu et al., 2011; Kumar, 2001; Xiao et al., 2002).

The fossil record does not show any signs of 'Cambrian explosion' of macroalgae. Cambrian noncalcified algal fossils are similar to the Neoproterozoic algal fossils. Most of the Cambrian algal fossils are delicately dichotomously branched or cylindrical in form, but a few are leaf-like in shape. From the Cambrian, 32 genera and 42 species have been documented and described (LoDuca et al., 2017). In China, fossils have been reported from several formations: Kaili (Fu et al., 2011; Wu et al., 2011, 2016; Yang, 2006; Yang et al., 1999b, 2001), Niutitang (Wu et al., 2013; Yang et al., 1999a), Yuanshan (Hu, 2005; Xu, 2002, 2004), Yanjiahe (Guo et al., 2010) and Huaqiao (Babcock et al., 2011). Algal fossils have been described from the Sinsk Formation of Siberia (Krassilov, 2005), the Burgess Shale Formation of Canada (Walcott, 1919) and from the Kinzers (Resser and Howell, 1938), Conasauga (Schwimmer and Montante, 2007), Marjum (Brett et al., 2009; LoDuca et al., 2015) and Wheeler (Cornway Morris and Robinson, 1988; LoDuca et al., 2015) formations of the USA. Five genera (*Doushantuophyton*, *Konlingiphyton*,

Sinocylindra, *Enteromorphites*, *Chuaria*) have been described as appearing in the Neoproterozoic and continuing in the Cambrian.

The Ordovician noncalcified macroalgal fossils differ markedly from those of the Cambrian and Neoproterozoic. The cylindrical and spherical forms are missing, monopodial forms (e.g., *Medusaegraptus*, *Chaetocladus*) and dichotomously branched (e.g., *Manitobia*, *Winnepegia*) forms are now dominant (LoDuca et al., 2017). From the Ordovician, 17 genera and 24 species have been documented and described (LoDuca et al., 2017). The majority of findings come from the USA, Canada and China (Fry, 1983; Lamsdell et al., 2016; Lin, 1984; Mu et al., 1979; Ruedemann, 1909; Whitfield, 1894). The fossils discovered are assigned to Chlorophyta (mainly dasycladalean algae) and Rhodophyta. The dasycladalean algal genera are *Medusaegraptus*, *Chaetocladus*, *Callithamnopsis* and *Archaeobatophora*. *Leveilleites hartnageli* (Foerste, 1923), described from the Manitoulin Formation (originally as of early Llandovery age, but argued by Bergström et al. (2011) to be of the latest Ordovician (Hirnantian) rather than of the earliest Silurian age), is now redescribed as Rhodophyta (PAPER III).

Silurian noncalcified algal fossils are similar in form to the Ordovician fossils. Different monopodial forms (e.g., *Medusaegraptus*, *Chaetocladus*, *Leveilleites*, *Kalania*, *Heterocladus*) and dichotomously branched forms (e.g., *Palaeocymopolia*, *Buthotrephis*) are dominating. Five genera (*Chaetocladus*, *Leveilleites*, *Manitobia*, *Medusaegraptus* and *Buthotrephis*) have been described as appearing in the Ordovician and continuing in the Silurian. Most of the Silurian noncalcified macroscopic algal fossils have been discovered from two continents: Laurentia and Baltica and just a few individual findings come from Siberia and Gondwana (Fig. 1). The majority of the Silurian macroalga-bearing deposits accumulated within 30 degrees from the palaeoequator (LoDuca et al., 2017). Altogether, 37 thallophytic algal deposits have been discovered from the Silurian (LoDuca et al., 2017). About 40% of reported Silurian algal fossil genera are described as dasyclads. Two species have been described as putative Rhodophyta (PAPER III; White, 1902), one species has been attributed to Chlorophyta (Wang et al., 2014b) and several species are considered simply as noncalcified macroscopic algae because of the lack of any specific details preserved in thallus morphology that could help to identify these fossils even at the phylum level (Edwards, 1977; Nitecki and Spjeldnaes, 1993). Silurian noncalcified algal remains have been discovered and described in Estonia (PAPERS I–III; Tinn et al., 2009), Canada (LoDuca, 1997; LoDuca et al., 2011, 2013; Tetreault, 2001; Wang et al., 2014b), the USA (Ehlers and Kesling, 1957; LoDuca, 1990; LoDuca, 1997; LoDuca et al., 1999,2003; Ruedemann, 1925; Taggart and Parker, 1976; White, 1902), Norway (Høeg, 1926, 1937, 1940), Sweden (Kenrick and Vinther, 2006; Nitecki and Spjeldnaes, 1993), the Czech Republic (Bouček, 1941), the UK (Edwards, 1977; Elliott, 1971), Russia (Korde, 1993), Ukraine (Ishchenko, 1984, 1985) and Australia (Douglas, 1983; Lucas, 1927) (Fig. 1).
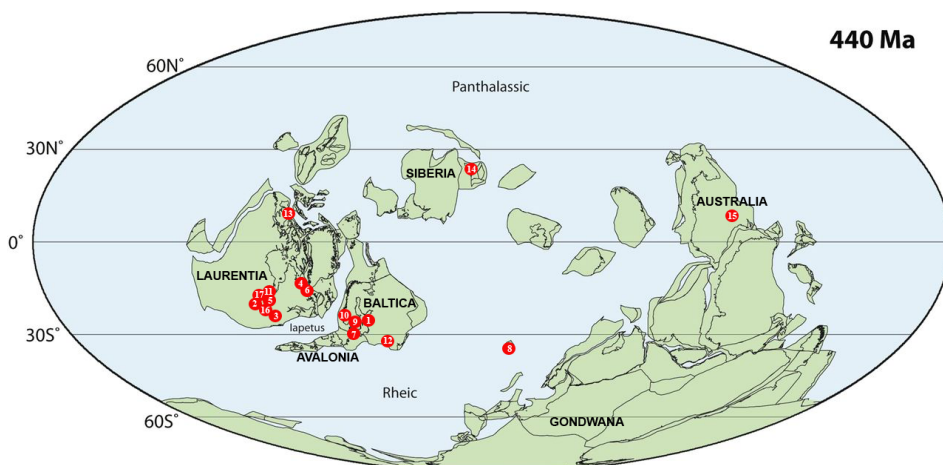
Figure 1. Occurrences of the Silurian noncalcified algal fossils, plotted on a 440 Ma world map reconstruction (adopted from Torsvik and Cocks, 2013). Key to localities: 1, Estonia; 2, USA, Illinois; 3, USA, New York; 4, Canada, New Brunswick; 5, Canada, Ontario; 6, Canada, Anticosti; 7, England; 8, Czech Republic; 9, Sweden, Gotland; 10, Norway; 11, USA, Wisconsin; 12, Ukraine; 13, Canada, Cornwallis Island; 14, Russia, Eastern Sayan; 15, Australia; 16, USA, Indiana; 17, USA, Michigan.

3.2. Algal fossils from Estonia

No comprehensive research has been carried out on Estonian algal material, and mostly individual calcareous algal species have been reported and described so far. The first record was made by Schlotheim (1820), who described *Escharites fomiculosus* from Reval (Tallinn), which has been argued (Nitecki et al., 1999) to be conspecific with the Ordovician *Fisherites orbis*. Eichwald (1860) described and illustrated many Estonian fossils, including receptaculitids such as *Receptaculites orbis* (now *Fisherites orbis*) from the Lasnamägi Stage. The other problematic genus *Cyclocrinites* (Eichwald, 1840), a putative calcified alga is common in the Upper Ordovician strata. Many palaeontologists (Beadle, 1988; Nitecki et al., 1987, 1999; Pia, 1920; Stolley, 1898) consider cyclocrinitids to belong to Dasycladales. *Mastopora* (Eichwald, 1840), *Coelosphaeridium* (Roemer, 1885), *Dasyporella* (Stolley, 1893), *Rhabdoporella* (Stolley, 1893) and *Vermiporella* (Stolley, 1893) have been described as green algae (Shuyskiy, 1987) and are also known from the Upper Ordovician and Silurian strata of Estonia. Eichwald (1855) originally described the ribbon-like films of *Laminarites antiquissimus* from the Ediacaran Valday series from the St. Petersburg area in Russia. This species is now regarded as the synonym for *Vendotaenia antiqua* (Gnilovskaya, 1971). The problematic *Vendotaenia antiqua* has also been reported from the Ediacaran Kotlin Formation of Estonia (Mens and Pirrus, 1980). Kõrts (1991) studied the stratigraphic distribution of calcareous algae in the Wenlock–Ludlow boundary beds in Saaremaa, mentioning

several taxa such as rhodophyte genera *Parachaetetes* and *Solenopora* and the dasycladalean genus *Rhabdoporella*.

Although the Estonian researchers have collected a large number of algal fossils, which are now stored in the geological collection of Estonia, their systematic treatment is poor. The data about fossil algae can be accessed through the geological collections (www.Geokogud.info) database. The majority of the Estonian Ordovician and Silurian calcareous algal fossils in the database are tentatively classified as green algae.

4. GEOLOGICAL SETTING

During the Silurian Period, large parts of the Earth's landmasses were located in the Southern Hemisphere – the largest of them was the supercontinent of Gondwana. The continents of Baltica, Avalonia and Laurentia approached each other near the equator and collided in a complex sequence of tectonic events known as the Caledonian orogeny (Cocks and Torsvik, 2005; Torsvik and Cocks, 2013; van Staal et al., 2009), which finally led to the formation of the supercontinent of Laurussia by the Devonian. The climate, which due to the global cooling had stabilized by the Aeronian (Cocks and Torsvik, 2005, 2011).

During the early Silurian, the Baltic Palaeobasin was located in the tropics, approximately 10–20 degrees south of the equator, and the climate was relatively stable and warm. The Baltic Palaeobasin (Fig. 2A) at the margin of the Baltica continent was a shallow, epicontinental sedimentary basin. The territory of present-day Estonia at the southern margin of the Fennoscandian Shield was part of the northern flank of a shallow cratonic sea in the western Baltica continent. Silurian strata are exposed in western, central and eastern Estonia. Further to the south, the Silurian successions are covered by terrigenous rocks of Middle Devonian age (Nestor, 1997).
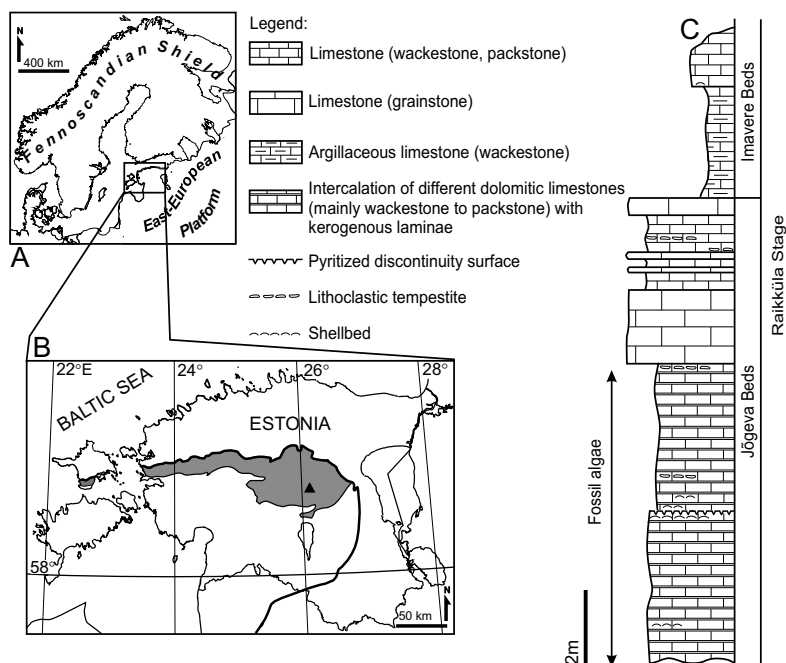

Figure 2. (A and B) Location of the Kalana quarry (black triangle). Grey colour indicates the outcrop area and the thick line the boundary of the distribution area of the Raikküla Regional Stage. (C) The stratigraphical column, combined from the eastern and western parts of the quarry, illustrates the geological section in Kalana (modified after Tinn et al., 2015 – PAPER II).

The majority of the studied material was collected in the Kalana (Otisaare) quarry (Fig. 2B) located in central Estonia. The quarry opens a succession of carbonates of mid-Aeronian (mid-Llandovery, early Silurian) age. Biostratigraphically, the layers with exceptionally preserved fossils in Kalana correlate with the *Pranognathus tenuis* Conodont Biozone and *Pribylograptus leptotheca* Graptolite Biozone (Männik et al., 2016). The succession is characterized by a series of shallowing-upward shelf carbonates representing the Raikküla Regional Stage. The Raikküla Stage consists of a variety of carbonate rocks, the most characteristic of which are micro- and cryptocrystalline limestones that are cyclically interbedding with marl- or mudstones in the distal facies, and wacke-, pack- and grainstones in the nearshore areas (Männik et al., 2016; Nestor, 1997). The Raikküla Stage carbonates in the outcrop area are mostly 20–75 m thick and the thickness of the stage in core sections varies from 16.3 m in northwestern to 176.3 m in southwestern Estonia (Nestor, 1997). Lateral facies changes in the Raikküla succession from shallow- to deeper-shelf carbonates have resulted in the erection of different lithostratigraphical units – the Raikküla, Nurmekund and Saarde formations, replacing each other from north to south (Männik et al., 2016). The Nurmekund Formation consists of five sedimentary cycles. In ascending order, the cycles are termed the Järva-Jaani, Vändra, Jõgeva, Imavere and Mõhküla beds. The first, third and fifth cycles from below are thicker and more complete, the second and fourth being thinner and less typical (Nestor, 1997).

The Kalana quarry opens only part of the Raikküla Stage – the upper part of the Jõgeva Beds and the lower part of the Imavere Beds of the Nurmekund Formation are exposed (Ainsaar et al., 2014). The Jõgeva and Imavere beds entail wavy-bedded to nodular grey-coloured limestones and secondary dolostones intercalating with thin laminae of dolomitic marlstone. The geological section indicates that sediments of at least two facies belts – open shelf and shoal are distinguished in the Kalana area. In addition to typical normal marine nearshore sediments and fauna, a few beds show thin lamination, layers with desiccation cracks, abundant leperditiid crustaceans and occasional eurypterid remains, suggesting short-term periods of shallow lagoonal environments (Tinn et al., 2009), especially in the upper part of the section. The carbonate rocks in the Kalana quarry show a dip up to 8–9° and are gently folded, a trait which is quite unusual within the Estonian bedrock strata (Männik et al., 2016). Thus, the oldest part of the succession that yields the exceptionally preserved algal flora is exposed only in the eastern part of the quarry, in the lowermost part of the Jõgeva Beds characterized by normal marine nearshore pack- and wackestone carbonates (Fig. 2C).

The locality has revealed rich biota. The beds with fossilized noncalcified flora contain also a number of calcitic or partly dolomitized, rarely silicified or pyritized, faunal fossils – the benthic, nektic and planktic faunas are preserved. However, the preservation of different groups, depending upon their lifestyle and skeletal mineralogy, is rather variable. Rhynchonelliformean brachiopods and gastropods as part of the normal marine shelly carbonate fauna occur

mostly in well-sorted coquina lenses, which vary from one to several centimetres in thickness and are up to several metres in lateral extent. The shelly fauna in these accumulations was most probably transported and/or piled up by storm events, and as a rule, does not occur together with algal fossils. Occasional rugose and tabulate corals, sponges, nautiloids, crinoids and bryozoans, but also rare trilobites, linguliformean brachiopods and even an osteostracan vertebrate are represented in the locality (PAPERS I–III; Männik et al., 2016; Tinn et al., 2009; Tinn and Märss, 2018). Some surfaces reveal abundant dendroid graptolites and the micropalaeontological samples yield low-diversity conodont, graptolite, scolecodont and ostracod fauna. The majority of samples reveal no bioturbation or show rare discrete isolated traces only. Even while a few beds might exhibit a higher degree of bioturbation, as a rule, the trace fossils do not occur together with well-preserved algal thalli.

5. MATERIAL AND METHODS

5.1. Algal material from the quarries and drillcores in Estonia

Different drillcore sections and quarries have yielded numerous specimens of noncalcified algae from the Late Ordovician and early Silurian strata in Estonia. (Fig. 3; Table 1 supplementary).
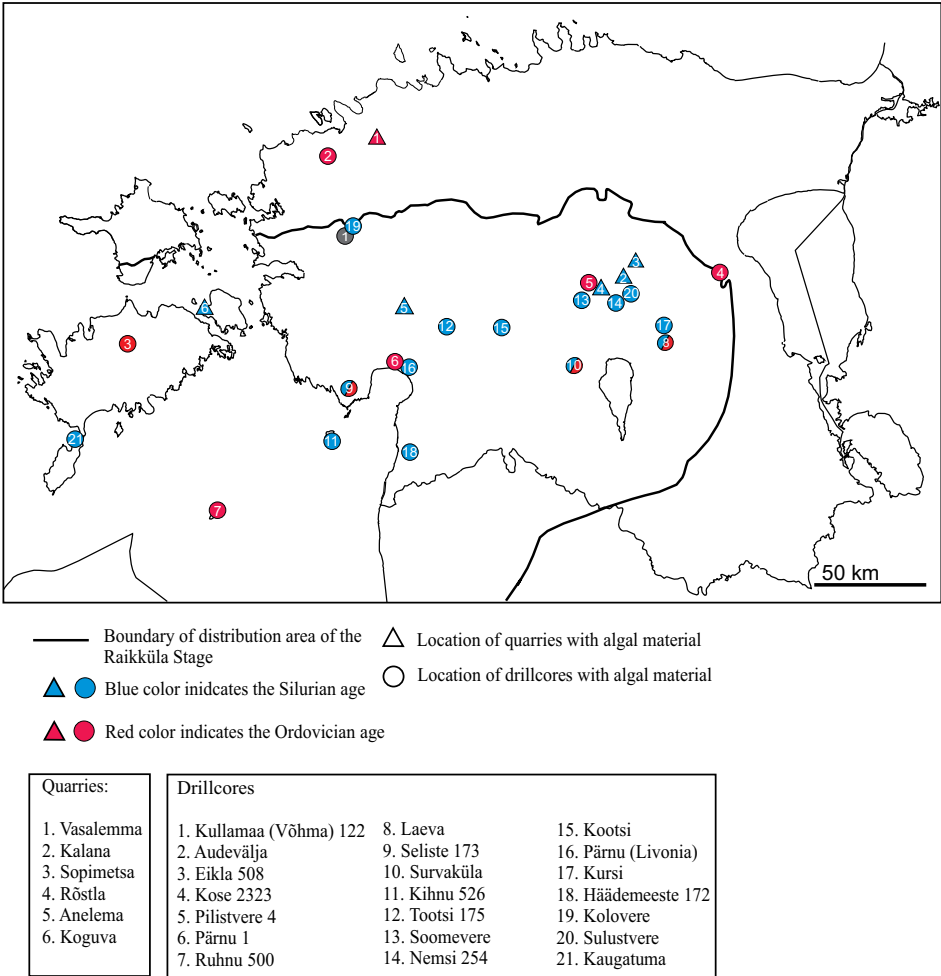

Figure 3. Noncalcified algal material from Estonian quarries (triangles) and drillcores (circles).

By far the highest concentration of algal fossils has been recorded in the Kalana (Otisaare) quarry (Fig. 4), where specimens were collected during the field seasons of 2006 to 2018. In this locality, the quarrying company 'Kaltsiit' produces limestone aggregate with the help of explosives. The loose blocks acquired as a result of blasts were examined by teams of geologists from the University of Tartu and blocks with fossils were selected and collected for further research in the Department of Geology. As the blasted loose carbonate rock material was in piles, it is hard to specify the exact levels where the individual fossils were originally located. This kind of collecting gives a generalized, but considering the uniqueness of the fossils, a detailed and representative enough picture of the palaeoecosystem.

Individual algal finds (PAPER III) collected from the Rõstla quarry 16 km SW of Kalana, which exposes the Mõhküla Beds (upper part of the Nurmekund Formation, upper Raikküla Stage, upper Aeronian) (Männik, 2014), were also used in the study. Rocks in the Rõstla quarry are heavily dolomitized and the preservation of fossils is mostly poor. However, the material used supplemented the data on the stratigraphic and areal distribution of algal fossils. In addition, some of the algal fossils were loaned from the collections of the Institute of Geology, Tallinn University of Technology (PAPER I; PAPER III).

Figure 4. The orthophoto of the Kalana quarry (maaamet.ee, 2017). The red line indicates the location of the Kalana *Lagerstätte*.

The noncalcified algal fossils occur as black or dark brown carbonaceous compression fossils. They include complete intact thalli, as well as fragments of different size and states of preservation. Counting individual thalli on rock slabs can be difficult as they are often tangled or fragmented. Therefore, the number of 'rock samples', typically including several to tens of individual specimens, is used, which gives at least some estimation about the amount of the studied material.

The collection of *Palaeocymopolia silurica* (PAPER I) consists of more than 77 rock samples. Two drillcores from different parts of Estonia (Fig. 1, in PAPER I) have also revealed rare *P. silurica* specimens: Laeva (at 38.3 m depth) and Kullamaa (Võhma) (at 53.55 m depth). The collection of *Kalania pusilla* (PAPER II) includes about 80 rock samples, all found from the Kalana quarry. The collection of *Leveilleites hartnageli* (PAPER III) is based on material from the Kalana and Rõstla quarries and from several drillcores. The collection consists of more than one hundred rock samples. Several drillcores from different parts of Estonia have also revealed fragments of *L. hartnageli*: Kihnu (depth 241.3 m), Tootsi (depth 69.1 m), Soomevere (depth 53.5 m) and Nemsi (depth 29.9 m) (Fig. 4, in PAPER III). We also studied part of the type material of *L. hartnageli* originally described by Foerste (1923). This material is stored in the Smithsonian National Museum of Natural History, USA. The described and photographed Estonian material is housed at the University of Tartu Natural History Museum, Estonia, as collections TUG 1269 and TUG 1713. The core material is housed at the Institute of Geology, Tallinn University of Technology.

In addition to the Kalana and Rõstla quarries, noncalcified algal material has been discovered from the Vasalemma (Ordovician), Sopimetsa, Koguva and Anelema (all Silurian) quarries. The oldest well-preserved (not yet described) macroalgae were found from the Vasalemma quarry (Late Ordovician, Keila Stage). Also, investigations of Ordovician drillcores prove that algal material, especially fragments of *P. silurica*, are represented in the upper Ordovician Keila (Audevälja 321), Pirgu (Kose 2323; Pilistvere 4) and Porkuni (Pärnu 1) regional stages (Fig. 5).

The Sopimetsa quarry (Llandovery, Raikküla Stage) is located about 7 km north of the Kalana quarry. A few *incertae sedis* specimens have been collected from the Sopimetsa quarry, but the algae-rich layer exposed in the Kalana quarry probably lies below the current excavation level. The Rõstla dolomite quarry (Llandovery, Raikküla Stage) is about 16 km southwest of Kalana and only *L. hartnageli* specimens have been found there. Most of the Silurian drillcore material, where algal fragments have been discovered, comes from the Raikküla Regional Stage, except the deeper intervals of the Laeva, Survaküla and Seliste drillcores, representing of the Juuru Regional Stage (Fig. 5). Material from the Koguva (Wenlock, Jaani Regional Stage) quarry on Muhu Island is sparse, but the few specimens discovered are similar to *K. pusilla*. One specimen of *Challisphenus* sp. B has been described from the Anelema quarry (Wenlock, Jaani Regional Stage) by Nitecki and Spjeldnaes (1993). The Kaugatuma drillcore from Saaremaa Island, western Estonia, proves that algal fossils occur also in the Rootsiküla Regional Stage. Although the drillcore material does not reveal complete thalli, it provides a valuable insight into the distribution of algal fossils in Estonia.

SERIES		REGIONAL STAGE	AGE Ma	*P. silurica*	*K. pusilla*	*L. hartnageli*
LOWER SILURIAN	Wenlock	**ROOTSIKÜLA**	423			
		JAAGARAHU				
		JAANI	428		◊	
	Llandovery	ADAVERE				
		RAIKKÜLA		✿	◊	❊
		JUURU	443			
UPPER ORDOVICIAN		**PORKUNI**		✿		
		PIRGU		✿		
		VORMSI	449			
		NABALA				
		RAKVERE				
		OANDU				
		KEILA		✿	◊	
		HALJALA				
		KUKRUSE	460			

Figure 5. Estonian regional stages and discoveries of *Palaeocymopolia silurica*, *Kalania pusilla* and *Leveilleites hartnageli*.

5.2. Analytical methods

The described algal material, reported in Papers I–III, was photographed with Canon EOS 450D, and measured and studied in detail under the Leica M205A microscope and with a Zeiss EVO MA15 scanning electron microscope (SEM) at the University of Tartu. For SEM analyses, the sample surfaces were coated with a 3–5 nm thick layer of platinum, and in order to make the study of details easier, both regimes – the backscattered electron (BSE) and the secondary electron detectors were used in parallel.

With *L. hartnageli* material we used also the SEM-BSE detector regime to highlight the carbonaceous type of preservation. In the SEM-BSE regime, the beam of primary electrons interacts with the sample surface where electrons change their trajectories due to elastic scattering that is controlled by the average atomic number of elements in the sample.

Elemental analysis (EDS mapping) was performed with *L. hartnageli* material on the same SEM with the Oxford X-MAX 80 energy dispersive detector system and Aztec Energy software.

6. RESULTS

Generally, there are two basic methods for the identification of algal species: (a) morphological, which uses various features observed under a microscope and (b) molecular, which uses a variety of gene regions. In the case of fossil algae, the only available characteristics are morphological features. The identification of fossils is not always straightforward and even exceptionally preserved fossils may pose a challenge. Algal fossils are not an exception. A large part of them do not provide distinctive features: fossilized thalli are often compressed and/or broken, in some cases with secondary mineral overprint, and reproductive structures, which could give a hint about the systematic position, are typically perished (Nitecki and Spjeldnaes, 1993). Morphological characteristics could also be misleading, directing to other fossil groups, such as graptolites and sponges, or even trace fossils, which could exhibit morphologically similar structures. Algal fossils that resemble modern organisms (PAPER I) are easier to classify taxonomically. However, there are fossil organisms which do not have analogues among living organisms (PAPER III), and the determination of their taxonomic relation with other organisms can be challenging.

6.1. Dasyclads from the Kalana quarry

The order Dasycladales is represented by unicellular, tropical to subtropical shallow-marine green algae which are the most common algae in Kalana *Lagerstätte* and have a long and highly diverse fossil record dominated by calcareous forms (Berger and Kaever, 1992; Kenrick and Vinther, 2006). Finds of dasyclads that are the most common algae in the fossil record extend back to the Cambrian.

The main characteristics of this order are the radially symmetrical thallus architecture and the siphonous bodyplan of the cell (Lee, 2008). The classification of the dasyclads is based on three main criteria: the arrangement of primary laterals, the position of cysts (reproductive structures) at the maturity of the thallus and the presence/absence of the branching of the laterals (Berger and Kaever, 1992; Deloffre and Genot, 1982). The primary laterals, which are the basis of the first criterion, do not show any particular positioning in the aspondyl type, but are arranged in verticils around the main axis in the euspondyl type; in the metaspondyl type the primary branches in verticils are grouped into clusters (Berger and Kaever, 1992). The second criterion is the position of the reproductive structures when the cell reaches maturity. It has been argued that the endospore type, where the cysts remain in the main axis (i.e. *Yakutina aciculata*, *Seletonella mira*) is the most primitive and evolutionarily the earliest (LoDuca et al., 2011; Pia, 1920). In the more advanced cladospore type, the cysts are produced in the laterals. In the choristospore type,

23

the cysts are produced in specialized structures called gametophores and in the umbrellospore type, the reproductive bodies are formed inside the cuplike arrangement of gametophores (Berger and Kaever, 1992). The third criterion is the presence or absence of the branching of the laterals. Laterals can vary in shape and size. They arise at the main axis in different arrangement, number and forms that can be used for systematic classification.

6.1.1. *Palaeocymopolia silurica*

Palaeocymopolia silurica (PAPER I) is assigned to the green algal (division Chlorophyta) order Dasycladales on the basis of its distinctive thallus architecture – the serially segmented thallus with a central cylindrical main axis (Fig. 6).
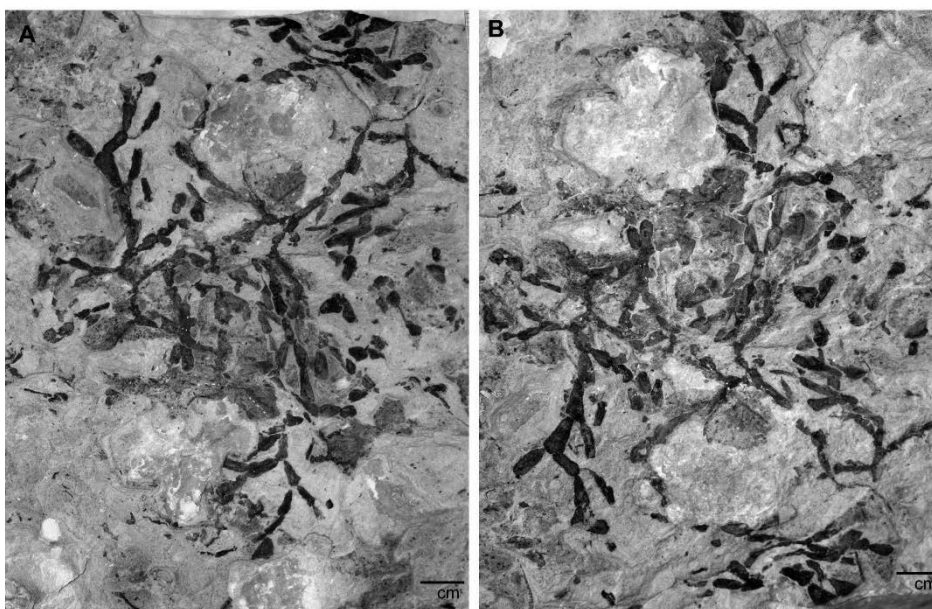
Figure 6. *Palaeocymopolia silurica*. (A) Holotype (TUG 1269–9) and (B) (TUG 1269–11) are counterparts of slabs with a nearly complete branching of thalli (from Mastik and Tinn, 2015 – PAPER I).

The main axis (Fig. 7.6–7.7) generates numerous regularly positioned branched laterals, arranged in regular whorls. The thallus branches dichotomously at every second to fifth repetitive element (segments) up to six repetitive elements after the last branching. The repetitive elements are barrel-shaped to pyriform (Fig. 7.4–7.5), with an average length of 6.1 mm and an average width of 2.7 mm. At the growing tips of some 'branches', small rounded structures can be observed (Fig. 7.4 arrow) which probably represent the growing tips of

branches or hair-like filaments. Between the last segments and the growing tips, the branches terminate with bundles of fine hair-like filaments (Fig. 7.1–7.3). The filaments are up to 3 mm long and 0.03 mm wide. Some individual filaments show bifurcations (Fig. 7.2). A number of specimens show polygonal structures on the segments (Fig 7.8–7.9).
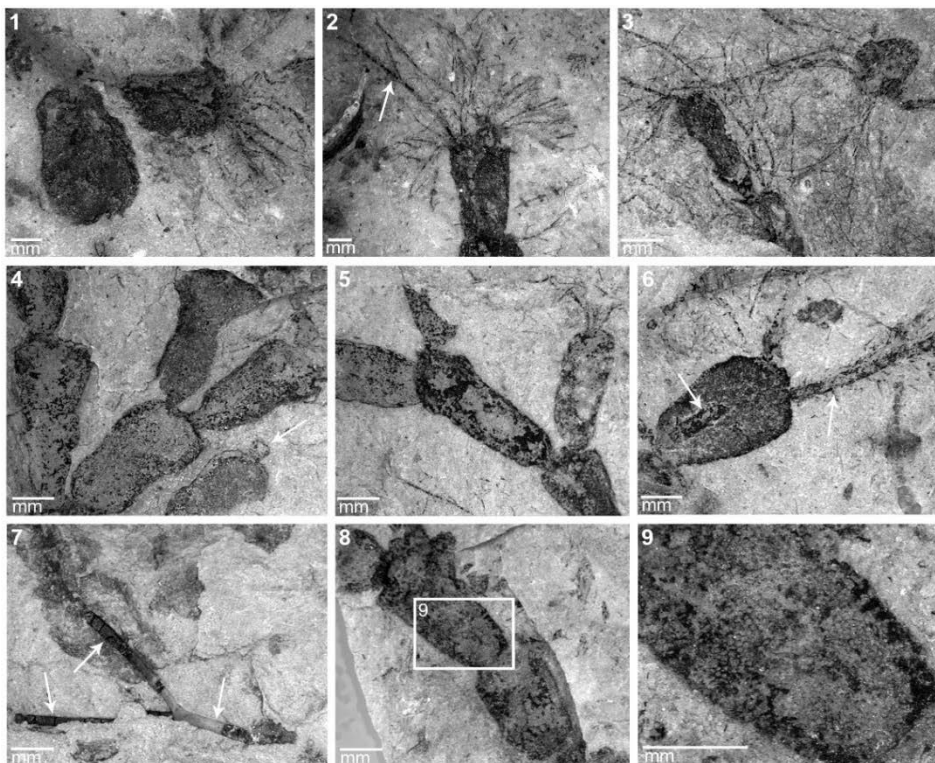
Figure 7. Details of *Palaeocymopolia silurica.* (1) TUG 1269–15, (2) TUG 1269–19 and (3) TUG 1269–16, different branches terminating with bundles of fine filaments; (2) shows also the bifurcation of the hair-like filaments, pointed out with an arrow. (4) TUG 1269–14, the growing tip of *P. silurica* is pointed out with an arrow; (4) and (5) TUG 1269–17 show different shapes of repetitive elements. (6–7) TUG 1269–18, variously preserved main axes pointed out with arrows. (8) Polygonal structures on the segments that could be interpreted as facets. (9) Enlargement of the box in Figure 8 (TUG 1269–14) (from Mastik and Tinn, 2015 – PAPER I).

The genus *Palaeocymopolia* (LoDuca et al., 2011) is assigned to the family Triploporellaceae, known from the Middle Ordovician to the Eocene (Berger and Kaever, 1992; LoDuca, 1997), on the basis of an inferred euspondyl thallus form and endospore (with reproductive bodies formed within the main axis) or cladospore (with reproductive bodies formed within ramifications) type of formation of gametangia. *Palaeocymopolia nunavutensis*, described by LoDuca et al. (2011) from Arctic Canada, and *P. silurica* from Estonia are closely similar,

thus the new species was described within the same genus. However, the new species was erected due to several details which were not observed in the Canadian material. The abundant and well-preserved specimens from Kalana have not revealed any features that could suggest endospore formation of gametes. Several specimens of *P. silurica* show well-preserved polygonal structures on the segments, which could be interpreted as facets covering the reproductive structures and are similar to the structures seen in extant *Cymopolia barbata*. Therefore, it is equally possible that gametangia are not preserved in our material and the specimens were of choristospore type of morphology.

6.1.2. *Kalania pusilla*

Kalania pusilla (PAPER II) is a small and narrow leaf-like (as a compressed fossil but was club-shaped as a living organism) dasycladalean algal fossil, with simple external morphology but unique internal anatomy. The unbranched cylindrical thallus is straight or gently curved (Fig. 8A). The average length of the complete thallus is 40 mm, average diameter 3.1 mm. The thallus ends with a bundle of short fine filaments (Fig. 8C, D). A few specimens show a well-preserved carbonaceous central axis (Fig. 8A, B, E) and up to six whorls of primary laterals (Fig. 8E, pl) with the distance between two successive whorls of about 500 µm. The diameter of the central axis is around 190 µm. The length of the primary laterals is ~ 85 µm and the diameter (measured at the tip) ~70 µm. Each of the primary laterals branches to form sterile, about 2 mm long slender secondary laterals (Fig. 8E, sl).
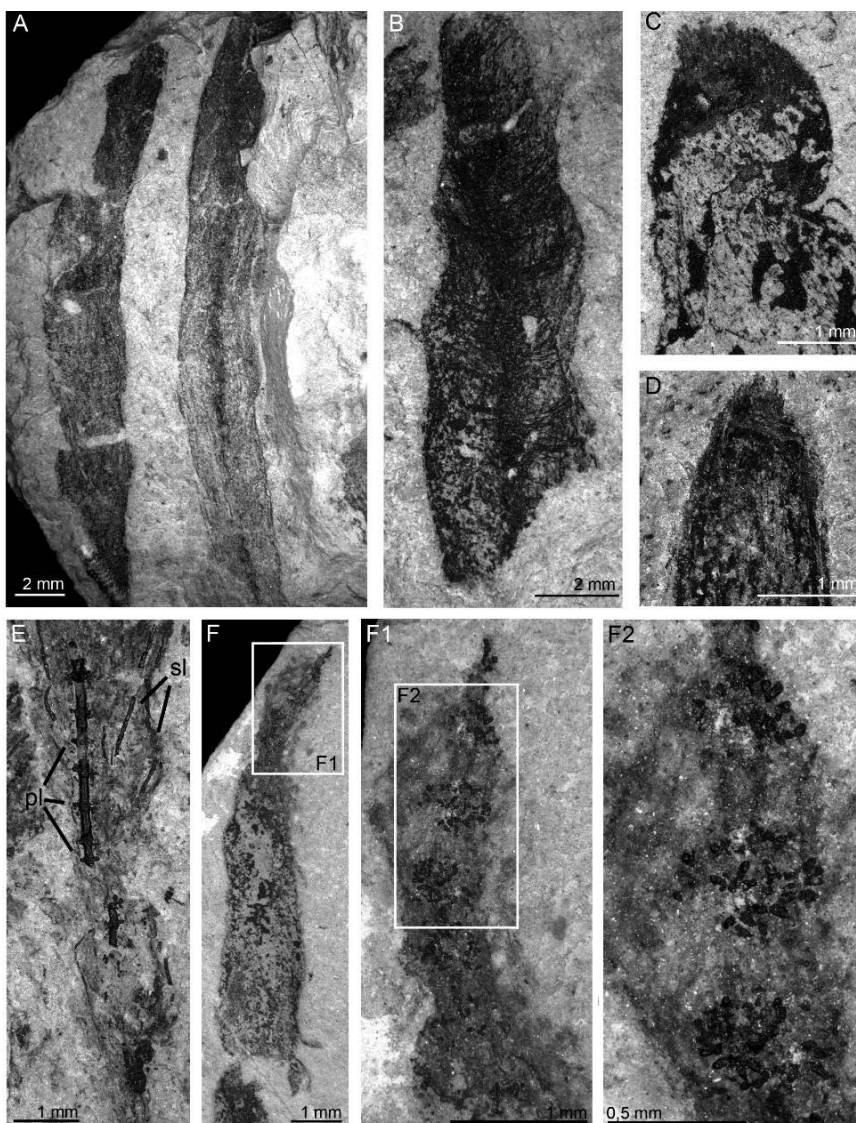
Figure 8. *Kalania pusilla* from the Aeronian of Estonia. (A) TUG 1269–27 (left) and TUG 1269–28 (right); two almost complete specimens, the specimen on the right demonstrating a partly preserved central axis. (B) TUG 1269–29, specimen showing well-preserved second-order laterals. (C) TUG 1269–30, specimen showing a tuft of short filaments at the top of the thallus. (D) TUG 1269–31, specimen showing a tuft of short filaments at the top of the thallus. (E) TUG 1269–32, specimen showing a well-preserved central axis, whorls of primary laterals (pl) and fragments of second-order laterals (sl). (F–F2) TUG 1269–33, specimen showing a noncalcified thallus in the upper part and gametophores near the tip of the thallus (from Tinn et al., 2015 – PAPER II).

The euspondyl type of arrangement of the laterals can be seen on the SEM images (Fig. 9B), which means that the laterals are arranged in whorls. The SEM images demonstrate that the whorls consist of six short perpendicularly positioned primary laterals in pyriform shape (Fig. 9A, A1). The position of gamete production is of choristospore type, where the reproductive structures are arranged at the sides of the first-order laterals (Fig. 9A2) and presumably they are organized in clusters at the sides of the first-order branch (Fig. 9C). According to the lateral arrangement and reproductive structure positions, *K. pusilla* is assigned to the family Dasycladaceae. Although Berger and Kaever (1992) describe this family from the Jurassic to Recent, the new data prove that this family existed already in the early Silurian (PAPER II).

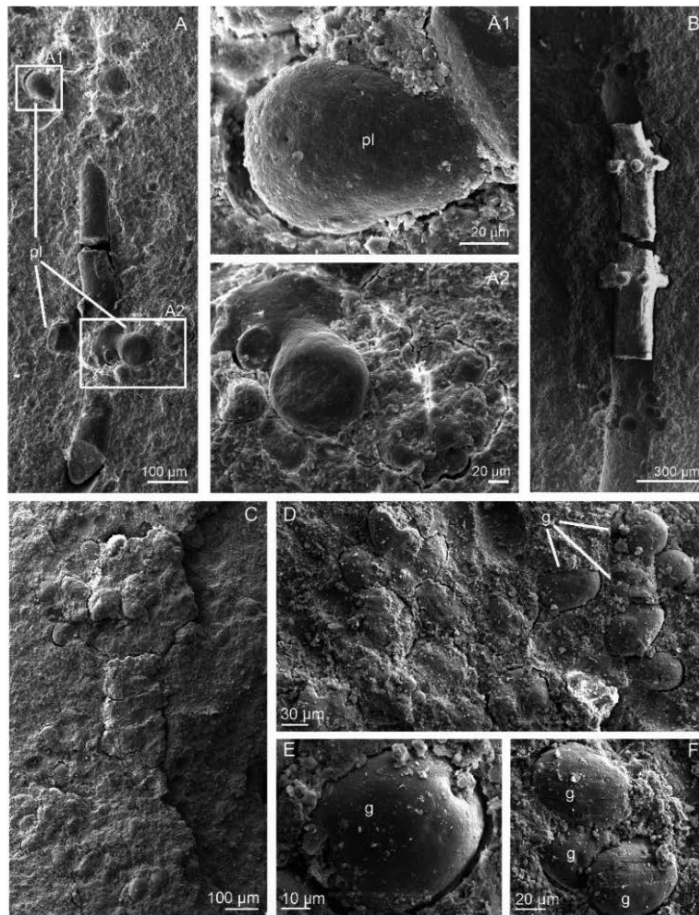**Figure 9.** Scanning electron microscope images of *Kalania pusilla*. (A) TUG 1269–34, central axis with whorls of primary laterals (pl). (B) TUG 1269–35, central axis with whorls of primary laterals and imprints of gametophores. (C) TUG 1269–36, fragment of *K. pusilla* showing clusters of gametophores on the rock. (D–F) TUG 1269–36, close images of gametophores (g) (from Tinn et al., 2015 – PAPER II).

6.2. Rhodophyta

Rhodophytes are almost all multicellular and structurally more complex than other algae, with filamentous, branched, pinnate or flake thalli, and with a complex mode of reproduction (Butterfield, 2000; Verbruggen et al., 2010; Woelkerling, 1990). The main characteristics available for the determination of red algal fossils are the position of reproductive structures and the comparisons with extant algal groups. Some morphological features, like the size and shape of the thallus, may be similar in several algal groups, but specific characteristics, such as the position of reproductive structures, could be helpful in distinguishing between similarly shaped fossil red, brown or green algae (Maggs and Callow, 2002).

6.2.1. *Leveilleites hartnageli*

Leveilleites hartnageli is the most common algal fossil in Kalana (PAPER III) that is assigned to the division Rhodophyta on the basis of its distinctive thallus architecture and the position of the reproductive structures. The complete thallus is composed of a holdfast, axis and laterals with tuft-like appendages (Fig. 10B), but in most cases only the upper part of the thallus is preserved. The irregularly branching thallus is up to 80 mm high, with an up to 2 mm wide axis. The specimens bear 10–25 primary laterals, 12–35 mm long, but mostly of equal length on one specimen.
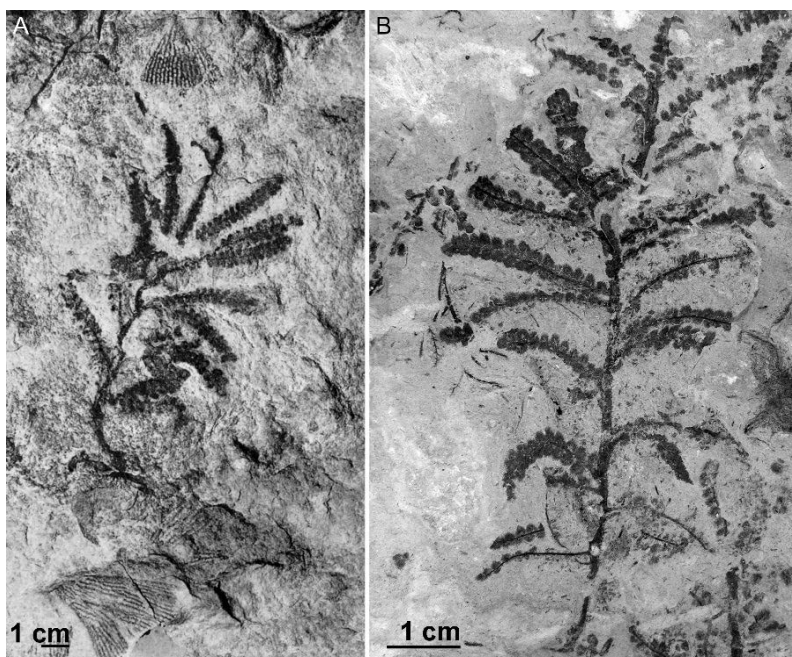

Figure 10. (A) Holotype of *Leveilleites hartnageli* from Credit Forks in Southern Ontario, Canada. (B) TUG 1269–1, nearly complete branching thallus of *L. hartnageli*, from Kalana, Estonia (from Mastik and Tinn, 2017 – PAPER III).

A few specimens show a root-like fibrous holdfast (Fig. 11), which anchors the thallus to the substrate. Generally, the fibres which make up the bushy holdfast are 0.7–1.2 mm long and 0.04–0.14 mm wide.
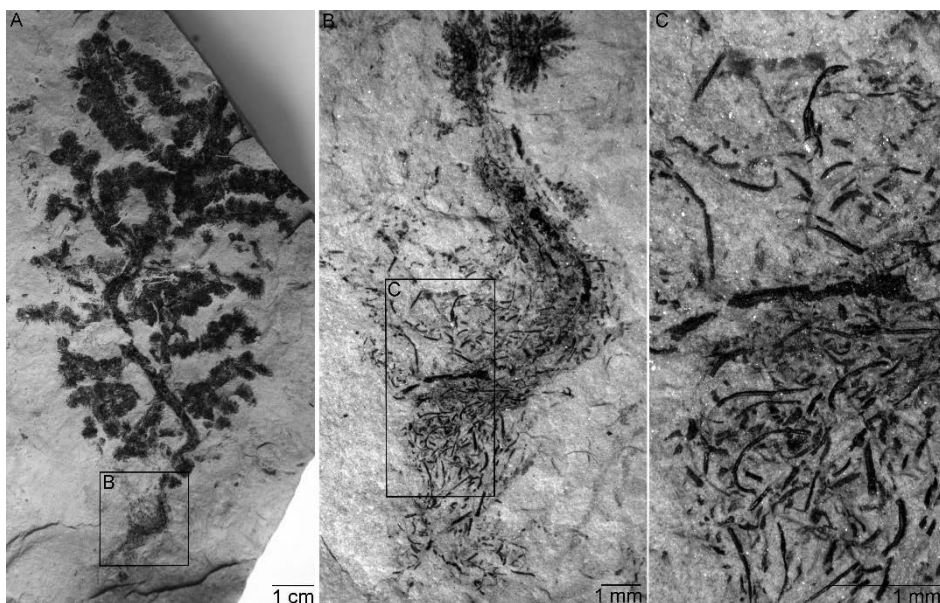
Figure 11. (A) TUG 1269–22, preserved root-like fibrous holdfast, and the details of holdfast fibres (B, C) (from Mastik and Tinn, 2017 – PAPER III).

The type specimen of *L. hartnageli*, as seen in the original photograph by Foerste (1923) (Fig. 10A), and purportedly stored at the Smithsonian National Museum of Natural History has got lost. However, the paratypes – nearly 30 small limestone slabs covered with *L. hartnageli* are in poor condition. The carbonaceous matter which made up the fossils has almost disappeared, and only limited evidence of structures is preserved and could be used for further investigation. Following the rules of *International Code of Nomenclature for algae, fungi, and Plants*, especially Art 9.7 (McNeill et al., 2012) and to maintain nomenclatural stability, the neotype, specimen TUG 1269–1, was designated for *L. hartnageli* Foerste (1923).

Due to compression, the laterals give an impression of irregular arrangement, however, some better-preserved specimens reveal that the laterals come in dyads (Fig. 10B; Fig. 12B, C), commonly at intervals up to 4.5 mm. The laterals bear regularly positioned 10–35 tuft-like appendages (Fig. 12G, I). The attached rounded or ellipsoidal structures inside the tuft-like appendages (Fig. 12G, H), which were interpreted as reproductive structures, indicate a possible relationship with the class Florideophyceae within the division Rhodophyta. Although the size and morphology of these structures are comparable to those of cystocarps on some Recent red or green algae, the structures do not allow more precise determination.
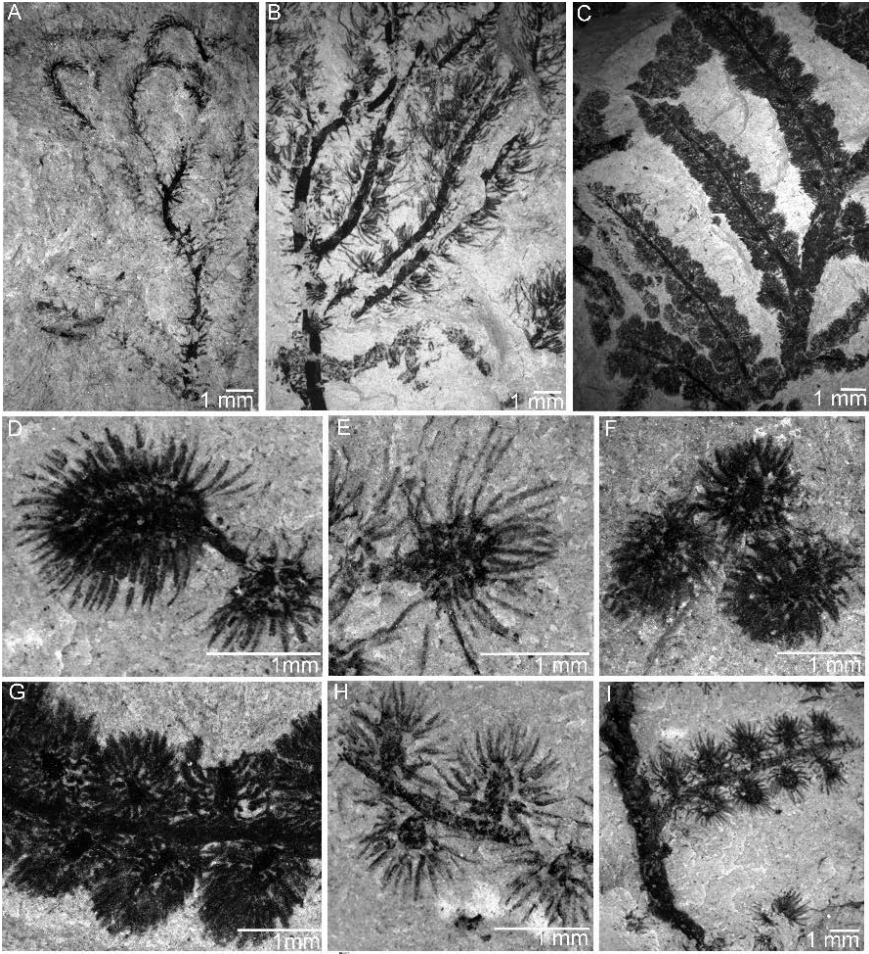
Figure 12. Details of *Leveilleites hartnageli.* (A) TUG1269–23, the early growth stage. (B) TUG 1269–24, the medium stage. (C) TUG 1269–25, the mature stage. (D, E) TUG 1618–1 and (F) TUG 1269–26, different shapes of tuft-like appendages. (G) TUG 1269–27 and (H) TUG 1618–2 different shapes of the dark rounded or ellipsoidal structure. (A–C) and (I) TUG 1618–1 different shape of the axis and laterals (from Mastik and Tinn, 2017 – PAPER III).

7. DISCUSSION

The described algal species are unique but do allow the interpretation of their living environments. The fossil material helps us to understand the palaeo-ecological setting of the area. The algal fossils can be used for assessing environmental parameters like water depth, wave action, temperature and character of the substrate. Through the analysis of the preservation of the fossils we can determine if the fossils were buried *in situ* or transported.

7.1. Environmental constraints

7.1.1. Water depth

Various parameters, like temperature, water clarity, depth, bottom sediments, etc., affect the growth of algae in marine environments, but the role of light is the most critical among them (Graham et al., 2009). The Rhodophyceae, for instance, are able to live at greater depth in the ocean than members of many other algal groups. They can live at depths up to 200 m, an ability related to the function of their accessory pigments in photosynthesis (Lee, 2008). However, some algal groups, dasycladaleans among them, inhabit areas with a rather limited depth and temperature range, and can therefore be used to evaluate the original depositional conditions of the Kalana *Lagerstätte*. The extant dasycladalean algae live in tropical to subtropical waters in depths up to 15 m (Berger and Kaever, 1992; Wray, 1977). Presuming that dasyclads have not changed their environmental preferences through geological time, we may expect that the environment which the dasycaladalean species *Palaeocymopolia silurica* (PAPER I) and *Kalania pusilla* (PAPER II) described from Kalana inhabited was a similar, shallow marine (up to 10–15 m) habitat.

7.1.2. Transported or buried *in situ*

The noncalcified thallophytic algae are very delicate and can easily break in the course of transportation. Therefore, algal fossils could be good indicators of transport and/or *in situ* burial. The studied collection contains a large variety of differently preserved algal fossils. Among these, the fossil thalli from the Kalana quarry are most complete and best preserved, suggesting only short-distance transport or no transport at all before burial. This notion is also supported by the excellent preservation of some faunal fossils, which were found together with algal fossils, e.g. complete specimens of crinoids, with undisintegrated stems and the finest pinnules preserved on brachials. The crushed algal material from different core sections outside the Kalana region suggest that this material has gone through at least some transport before burial (PAPER I; PAPER II; Table 1 supplementary).

The relatively complete noncalcified algal fossils have also been found from Ontario, Canada (LoDuca, 1995; LoDuca and Tetreault, 2017), Michigan, the USA (Lamsdell et al., 2016), New York, the USA (LoDuca, 1990, 1995, 1997; LoDuca and Brett, 1997) and Anticosti Island, Canada (Wang et al., 2014b). However, there are some *Lagerstätten* where fossilized algal material is more fragmented, indicating that organisms were transported before burial (LoDuca et al., 2003, 2011, 2013).

7.1.3. Substrate

Most sessile algae have a holdfast, a root-like structure that helps to anchor aquatic organisms to the substrate. Holdfasts vary in shape and form depending on the substrate and species. It is supposed (Thomas, 2002) that the holdfasts of sessile organisms living on muddy substrates often have complex tangles of root-like growths, and organisms that anchor themselves to smooth, hard surfaces like stones or shells have a holdfast with a flat base.

Part of the specimens of *L. hartnageli* (PAPER III) in Kalana show well-preserved complex tangles of a root-like fibrous holdfast (Fig. 11), suggesting that they inhabited soft substrates. Only some of the described well-preserved fossil algae like *Medusaegraptus mirabilis* (LoDuca, 1990), *Heterocladus wauke-shaensis* (LoDuca et al., 2003), *Chaetocladus ruedemanni* (LoDuca, 1997) and *Thalassocystis striata* (Taggart and Parker, 1976) do demonstrate simple rhizoidal structures as a part of their thalli, which may reflect attachment to soft substrates. On the other hand, *Wiartonella nodifera* (LoDuca and Tetreault, 2017) was described as algal fossil with an unusual shape of the rhizoid, where the special shape may reflect attachment to hard substrates, e.g. direct contact with brachiopod shells.

7.1.4. Oxygen and bioturbation

The lower Palaeozoic noncalcified macroalgae-bearing deposits are largely or entirely devoid of trace fossils, thereby pointing to poorly oxygenated substrates (LoDuca et al., 2017). In some Silurian *Lagerstätten*, like New Brunswick (LoDuca et al., 2013), Cornwallis Island (LoDuca et al., 2011), Eramosa (LoDuca and Tetreault, 2017) and also the Kalana *Lagerstätte* (PAPER III), trace fossils are lacking in beds containing well-preserved algal flora, suggesting that the algae were probably buried in low-oxygen environments with rapid influx of sediments or the anoxia was achieved quickly in shallow sediment subsurface. This kind of environment has been described (LoDuca and Brett, 1997) as being typical for poorly circulated areas between reefs, and in tropical bays and lagoons with a restricted connection to open ocean.

7.2. Interpretation of the environment

The environmental setting in Kalana suggests a shallow (maximum 10–15 m), quiet water environment with relatively high sedimentation rates of fine-grained carbonate mud. Given the water depth above the wave base and exceptional preservation of delicate structures, the environment was not an open shelf/shore-face with high hydrodynamic activity, but rather a restricted bay or lagoonal setting behind the reef and/or coastal bar systems. Indeed, in the upper part of the section, just above the algae-rich mudstones, lenses and interbeds of lithoclastic tempestites composed of lithified pebbles of the same mudstone appear and grade into cross-bedded fine-grained grainstone. Lens-like grainstone beds 1–4 m thick are composed mostly of redeposited (rounded) crinoid fragments. Most possibly they represent shoal belts along the palaeo-coastline and create (semi-) restricted lagoons at the shore side of the shelf.

7.3. Distribution

7.3.1. Lateral distribution of the beds with exceptional preservation of the Kalana *Lagerstätte*

The succession yielding the exceptionally preserved fossils is exposed at the eastern end of the Kalana quarry. As the strata in the Kalana region are slightly deformed (Männik et al., 2016), the succession dips westwards and thus these layers are not easily accessible in other parts of the quarry. However, discoveries of algal fossils from quarries and drillcores in different parts of Estonia prove that the extent of the Kalana *Lagerstätte* was larger than the small area in central Estonia and algae were widespread also before and after the Raikküla Age (early Silurian, Llandovery, Aeronian).

7.3.2. Palaeogeographic distribution

Most of the Silurian algal fossils have been reported from the Laurentia and Baltica palaeocontinents. During the early Silurian, Baltica and Laurentia were located approximately 10–20 degrees south of the equator and remained in the tropics, with relatively stable and warm temperatures. Laurentia and Baltica were separated by the narrowing Iapetus Ocean until the mid-Silurian (Ludlow). The presence of closely related species offshore of two different palaeo-continents can be taken as evidence of a broad distribution area of the described algae. For example, the species *P. silurica* in Estonia (PAPER I) and the about 15 million years younger Canadian species *P. nunavutensis* (LoDuca et al., 2011) inhabited the Baltic as well as the Laurentian palaeobasins, indicating wide distribution of dasyclad algal flora on both sides of the Iapetus Ocean. Morphologically indistinguishable specimens of *L. hartnageli* (Foerste, 1923)

from the Hirnantian (Bergström et al., 2011) of Laurentia and the Aeronian of Baltica (PAPER III) allow us to assume that these species inhabited large areas of the epicontinental seas around the Iapetus Ocean. The stratigraphic distribution of *L. hartnageli* in the Late Ordovician and early Silurian proves that the species ranged through the time span of at least 3–5 million years, surviving also the Hirnantian glaciation and the end-Ordovician mass extinction.

7.4. Evolution

The fossilized thalli of *Palaeocymopolia silurica* (PAPER I) are similar to those of the extant dasycladalean alga *Cymopolia barbata*. In both taxa, thalli have dichotomously branching, serially segmented form, similar segment size and shape, also the size and morphology of filaments in the tufts. The only major difference is the absence of a calcium carbonate skeleton. Unfortunately, many of the diagnostic features of the extant genus could not be evaluated for the Silurian material because of their loss in the process of fossilization. The evidence from the Kalana *Lagerstätte* suggests that some of the present-day dasycladalean algae, e.g. *Cymopolia*, may represent the so-called 'living fossils', types of organisms which have maintained their basic morphology for almost 400 million years.

7.5. Biological affinities

Relating fossil algae to living groups may be problematic, as the main groups of algae are distinguished on the basis of a combination of characteristics, including molecular, biochemical and cellular features, many of which are not accessible in fossils (Brodie and Lewis, 2007; Taylor et al., 2009).

Palaeocymopolia silurica (PAPER I) is morphologically similar to the extant species *Cymopolia barbata* and closely similar to the fossil species *Palaeocymopolia nunavutensis* from Arctic Canada (LoDuca et al., 2011). *Palaeocymopolia silurica* and *P. nunavutensis* both have a dichotomously, serially segmented noncalcified thallus, with the cylindrical main axis of the same size range. *Kalania pusilla* (PAPER II) has some similarities with the extant dasyclad genus *Bornetella*, and with the fossil dasyclad genus *Jodotella*. Possibly one of the closest taxa to *K. pusilla* is *Callisphenus gracilis* (Høeg, 1937) from the Silurian (Wenlock) of Norway.

However, there are fossil organisms who do not resemble any living organisms and determining their taxonomic relation to other organisms may be challenging. For example, *L. hartnageli* (PAPER III) has no fossil or modern analogues. Foerste (1923) argued that two modern Rhodophyte species, *Leveillea jungermannioides* and *Polyzonia elegans* from the family Rhodomelaceae, are in some way similar to *Leveilleites*. Some general morphological affinities can also be seen with the genera *Batrachospermum* and *Dasya*. In the past,

Leveilleites has been included in Graptoloidea (Ruedemann, 1947) despite the opposition of graptolite researchers (Bulman, 1955, 1970). The lack of additional fossil material has hindered the exclusion of this taxon from graptolites. The abundant algal material from Estonia and modern analytical methods shed light on this old dispute. The SEM analyses of *L. hartnageli* have proved its algal origin (Fig. 13). No structural details which could support its assignment to Graptoloidea could be detected. *Leveilleites* does not have thecae, fusellar structure or any traces of the stolonal system which would allude to its affinity with dendroid graptolites.
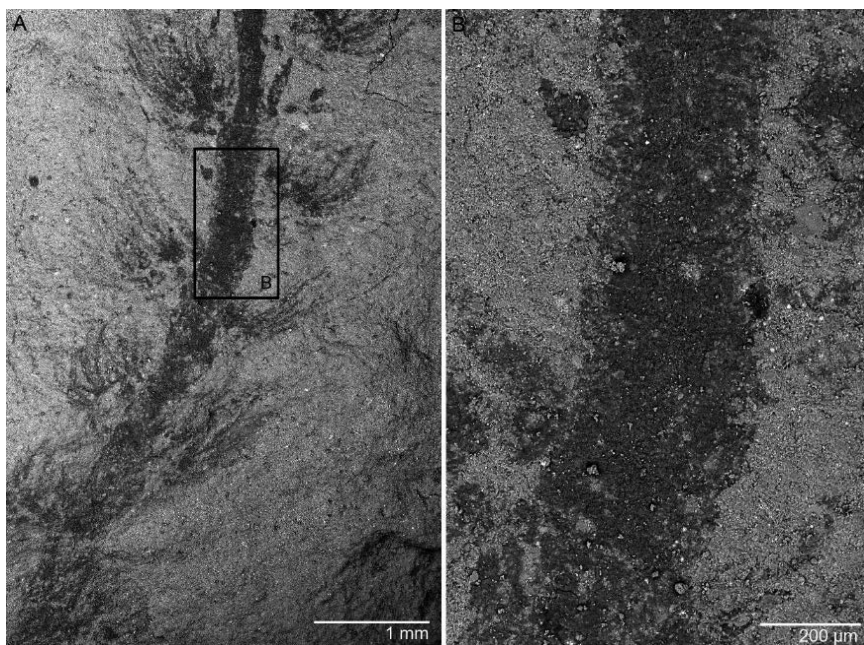
Figure 13. (A, B) TUG 1269–539, SEM (BSE) images showing a first-order lateral with tuft-like appendages (from Mastik and Tinn, 2017 – PAPER III).

7.6. Ontogeny

It is known that during ontogeny, in different growth phases, the morphology of the algal thallus can be rather distinct. The study of a large number of well-preserved specimens available sheds light on the ontogenetic stages of the described algae. Based on numerous *L. hartnageli* specimens (PAPER III), we are also able to designate a sequence of some ontogenetic stages in the life cycle of this species (Fig. 12A–C). During the early stage, the axis and 'spiny' laterals start to roll out in a spiral mode (Fig. 12A). The filaments start to grow and form 'tufts'. In the next stage, when the axis has grown more massive, it looks 'less hairy', filaments become shorter (Fig. 12B) and the 'tufts' on the first-

order laterals grow larger. During the late (mature) stage, the laterals show a dark rounded or ellipsoidal structure attached to the filaments in the centre, which we interpret as a reproductive structure (Fig. 12C).

Earlier literature comprises only a few reports about the ontogeny of fossil algae. One of these fossils is a dasycladalean algal species *Wiartonella nodifera*, reported from Ontario, Canada (LoDuca and Tetreault, 2017). The collection of *W. nodifera* shows three ontogenetic stages: first, thallus with unbranched hair-like laterals only; the early stage, where the laterals are branched; and the late stage, where all second-order lateral segments are shed. Some fossil thalli of *W. nodifera* were surrounded by halos of detected second-order lateral segments. It has been assumed (Berger and Kaever, 1992) that the shedding of second-order lateral segments could be a natural part of the dasycladalean life cycle.

8. SUMMARY AND CONCLUSIONS

The fossil record allows us to understand how life on the Earth looked like in prehistoric times. Unfortunately, the fossil record is highly biased towards organisms with mineralized skeletons, skewing our picture of the past. *Konservat-Lagerstätten* preserving fossils of nonmineralized organisms give us an opportunity to reveal and study the missing components of palaeocommunities. The Kalana *Lagerstätte* is one of such 'windows' that provides us a glimpse to the lower Silurian shallow-water environment.

This thesis gives an overview of the most abundant noncalcified thallophytic algal groups from the Kalana *Lagerstätte*. Three species, *Palaeocymopolia silurica*, *Kalania pusilla* and *Leveilleites hartnageli*, are studied in detail, and the distribution and preservation of algal fossils in the Lower Palaeozoic in Estonia and worldwide are analysed. The *Lagerstätte* materials together with their sedimentological context also enable the interpretation of the environmental conditions where the Kalana *Lagerstätte* was formed.

The main results of this study are as follows:

- The morphological characteristics of the three described and analysed species allow us to assign *Palaeocymopolia silurica* and *Kalania pusilla* to green algae (division Chlorophyta) and *Leveilleites hartnageli* to red algae (division Rhodophyta).

- *Palaeocymopolia silurica* and *K. pusilla* are assigned to the order Dasycladales on the basis of their distinctive thallus architecture. *Palaeocymopolia silurica* is morphologically similar to the extant species *Cymopolia barbata* and closely similar to the fossil species *P. nunavutensis* from Arctic Canada (LoDuca et al., 2011). *Kalania pusilla* has some similarities to the extant dasyclad genus *Bornetella* and the fossil dasyclad genus *Jodotella*. *Callisphenus gracilis* (Høeg, 1937) from the Silurian (Wenlock) of Norway is possibly one of the closest taxa to *K. pusilla*. *Kalania pusilla* specimens show the euspondyl type of arrangement of the laterals and the choristospore type of the position of gamete production. *Leveilleites hartnageli* is the most common algal fossil in Kalana which is tentatively assigned to the division Rhodophyta on the basis of its distinctive thallus architecture and the position of the reproductive structures.

- The relatively complete fragile noncalcified algal fossil thalli from the Kalana *Lagerstätte* suggest *in situ* preservation or only short transport before burial.

- The comparison of allochthonous finds of dasycladalean fossils in the Kalana *Lagerstätte* with well- constrained living conditions of modern dasycladalean algae suggests the water depths up to 10–15 m during the *Lagerstätte* deposition.

- The fibrous root-like holdfasts preserved in few *Leveilleites hartnageli* specimens resemble the holdfasts of organisms that live on muddy substrates, suggesting that algae in the Kalana region inhabited soft substrates.

- The well-preserved dasycladalean fossils and sediment characteristics indicate that the Kalana environment was not an open shelf/shore-face with high hydrodynamic activity, but rather a restricted bay or lagoonal setting behind the reef and/or coastal bar systems.

- The ontogenetic stages in the life cycle of *L. hartnageli*, reconstructed using an exceptionally large number of well-preserved specimens in the collection, show that during the early stage, the axis and 'spiny' laterals start to roll out in a spiral mode, followed by the growth of filaments with 'tuft'-like endings, which become shorter with the growth of the axis whereas the 'tufts' on the first-order laterals grow larger. During the late (mature) stage, the laterals show a dark rounded or ellipsoidal feature attached to the filaments in the centre, which can be interpreted as a reproductive structure.

- Finds of algal fossils from drillcores and quarries in Estonia show that non-calcified algae were widespread in the late Ordovician and early Silurian marine environments. Most of the Silurian drillcore material, where algal fragments have been discovered, represents the Raikküla Regional Stage.

- Most of the Silurian noncalcified thallophytic algal fossils have been discovered from the Laurentia and Baltica continents and described as dasycladalean algae, which indicates the distribution of noncalcified dasyclad algal flora on both sides of the Iapetus Ocean.

- The stratigraphic distribution of *L. hartnageli* in the Late Ordovician and Early Silurian proves that the species survived the Hirnantian glaciation and the end-Ordovician mass extinction.

SUPPLEMENTARY MATERIAL

Table 1. Estonian algal material from different drillcores. The core material is housed at the Institute of Geology, Tallinn University of Technology.

No.	Drillcore	Number (GIT)	Depth (m)	Material	Strat.
1	Kullamaa (Võhma) 122	353-3539	53.55	*P. silurica*	?
2	Audevälja 321	353-3557	60.7	*P. silurica*? *K. pusilla*?	Keila
3	Eikla 508	353-2177	239.8	Algal fossil	Pirgu
4	Kose 2323	539-38	60.3	*P. silurica*	Pirgu
5	Pilistvere 4	353-2157	133.35	*P. silurica*?	Pirgu
5	Pilistvere 4	353-2156	132.6	*P. silurica*? + crushed material	Pirgu
5	Pilistvere 4	353-2153	126.4	Crushed material	Pirgu
5	Pilistvere 4	353-2151	123.1	Crushed material	Pirgu
5	Pilistvere 4	353-2148	120.5	Crushed material	Pirgu
6	Pärnu 1	353-56	246.9	*P. silurica*?	Porkuni
7	Ruhnu 500	353-1697	615.6	*Medusaegraptus* sp.	Porkuni
8	Laeva *	353-2301	93.75	Crushed material	Juuru
9	Seliste 173	353-2044	284.3	Algal fossil + crushed material	Juuru
10	Survaküla	353-2122	80.4	Algal fossil	Juuru
8	Laeva *	353-2290	38.3	*P. silurica*	Raikküla
9	Seliste 173	353-2033	195.6	crushed material	Raikküla
9	Seliste 173	353-2031	194.55	Algal fossil + crushed material	Raikküla
9	Seliste 173	353-2030	194.5	Algal fossil + crushed material	Raikküla
9	Seliste 173	353-2029	194	Algal fossil	Raikküla
10	Survaküla	353-2120	67.4	Algal fossil	Raikküla
11	Kihnu 526	353-2187	241.3	*L. hartnageli* + algal fossil	Raikküla
11	Kihnu 526	353-2188	242.4	Crushed material	Raikküla
12	Tootsi 175	353-2069	69.1	*L. hartnageli* + crushed material	Raikküla
13	Soomevere	353-2415	53.5	*L. hartnageli*	Raikküla
14	Nemsi 254	353-2483	19.48	*L. hartnageli*?	Raikküla
14	Nemsi 254	353-3106-2	29.9	*L. hartnageli*	Raikküla
15	Kootsi	353-2198	57.37	Algal fossil + crushed material	Raikküla
16	Pärnu (Livonia)	353-3547	137.26	Algal fossil + crushed material	Raikküla
16	Pärnu (Livonia)	120-5	133.95	Algal fossil + crushed material	Raikküla
17	Kursi	353-2107	48.7	Crushed material	Raikküla
18	Häädemeeste 172	353-2010	266.1	Crushed material	Raikküla
19	Kolovere	353-3554	3.85	Algal fossil + crushed material	Raikküla
20	Sulustvere	1747-19	58.9	Algal fossil + crushed material	Raikküla
21	Kaugatuma*	353-3478	116.95	Crushed material	Rootsiküla

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SUMMARY IN ESTONIAN

Siluri makroskoopilised lubistumata vetikafossiilid
Kalana *Lagerstättest*

Vetikatel on tähtis roll tänapäeva Maa süsteemis, eriti olulised on nad vee-öko-süsteemides ning on tõenäoline, et vetikad mängisid veel tähtsamat rolli geoloogilises minevikus, aidates kaasa vaba hapniku moodustumisele atmosfääris ning karbonaatkivimite kujunemisele.

Olles veekogudes esmase orgaanilise aine tootjateks ning enamiku toidu-ahelate aluseks, on vetikatel looduses märkimisväärne roll. Fotosünteesi käigus eritavad vetikad keskkonda hapnikku, arvestuslikult võib kuni 40% globaalsest fotosünteesist olla seotud vetikate elutegevusega (Andersen, 1992). Tänapäeval Maal elavate vetikaliikide täpne arv ei ole teada, hinnangud varieeruvad 36 000 (John and Maggs, 1997) kuni 10 miljonini (Norton et al., 1996).

Vanimad, üksikud makroskoopilised (mõne mm suurused) vetikafossiilid on teada juba Mesoproterosoikumist (Bengtson et al., 2017; Butterfield, 2000; Kumar, 2001) kuid vetikafloora suurem mitmekesistumine toimus Neoprotero-soikumi lõpus. Punavetikate hulka kuuluvat 1,2 Ga aasta vanust *Bangiomorpha pubescens*'i peetakse üheks vanimaks kindlalt aktsepteeritud vetikafossiiliks, samuti peetakse seda ka vanimaks teadaolevaks eukarüootseks organismiks (Butterfied, 2000). Hiljuti (Bengtson et al., 2017) kirjeldati aga veelgi vanemaid (~ 1,6 miljardit), niitjaid punavetikatele sarnaseid fossiilseid organisme.

Vaid väike osa taimedest ja loomadest säilib pärast surma fossiilidena, kuna organismide säilmed hävivad enne settesse mattumist ning suurima tõenäo-susega säilivad kivististena tugeva skeletiga organismid.

Säilivus-*Lagerstätted* ehk erakordse säilivusega fossiilide leiukohad on üli-malt oluliseks „aknaks", mis võimaldavad inimkonnal heita pilku möödunud aegadesse ning saada aimu minevikus elutsenud pehmekehaliste organismide mitmekesisusest. *Lagerstätted* on geoloogilises ajas ebaühtlaselt jaotunud (Muscente et al., 2017). Üks ühine tingimus harukordse säilivusega materjali kujunemiseks näib olevat see, et elusolendite jäänused mattuksid väga kiiresti ja nõnda, et nii hapniku kui ka bakterite juurdepääs oleks edaspidi takistatud.

Kesk-Eestist, Kalana (Otisaare) lubjakivikarjäärist leitud haruldased Siluri-vanuselised (~ 440 miljonit) vetikafossiilid ei ole säilinud tänu tugevale lubi-skeletile, vaid on fossiliseerunud mustjaspruunide söestunud kelmetena.

Eesti ala asus Siluri ajastul lähistroopilises kliimavöötmes – ekvaatorist lõuna pool, ning oli kaetud madala rannikumerega, mida asustas lisaks vetika-floorale ka suur hulk veeloomi. Välitööde käigus on geoloogid karjäärist kogu-nud suurel hulgal skeletiga organisme – nautiloide, tigusid, koralle, meriliiliaid, käsijalgseid, käsnasid, trilobiite ja graptoliite. Kalana lubjakivid ja dolomiidid sisaldavad hulgaliselt ka mikroskoopilisi kivistisi – skolekodonte, konodonte, karpvähke ning sammalloomade ja käsnade mikroskoopilisi osiseid (Tinn et al.,

2009). Karjäärist on leitud ning kirjeldatud ka maailma vanim luukilbiline lõuatu (Tinn and Märss, 2018).

Käesoleva doktoritöö eesmärkideks oli uurida Kalana *Lagerstättest* leitud vetikate kooslust, leitud vetikaliikide põhjal interpreteerida merekeskkonda, kus *Lagerstätte* kujunes (sügavus, temperatuur, põhja iseloom) ning anda ülevaade Siluri vetikate levikust Eestis ning maailmas.

Tänapäeval kasutatakse vetikate määramiseks ja kirjeldamiseks kaht põhilist meetodit: esiteks detailseid morfoloogilisi uuringuid erinevate mikroskoopidega ning teiseks molekulaarseid meetodeid. Vetikafossiilide puhul on võimalik kasutada vaid morfoloogiliste tunnuste analüüsi. Üksnes välistunnuseid kasutades peab olema aga ülimalt ettevaatlik, sest üksteisega sarnase tallusega ning ilma iseloomulike lisatunnusteta vetikaid leidub kõigis suuremates vetikarühmades. Kalanast on tänaseks leitud üle kümne morfotüübi, mida võib pidada eri liikideks: *Palaeocymopolia silurica*, *Kalania pusilla, Leveilleites hartnageli, Medusaegraptus mirabilis*, *Chaetocladus* sp, *Inopinatella* sp. (Mastik and Tinn, 2015; Mastik and Tinn, 2017; Tinn et al., 2009, 2015), lisaks vähemalt viis seni uurimist ootavat (*incertae sedis*) vetikaliiki.

Töös detailselt kirjeldatud kolmest vetikaliigist kaks (*Palaeocymopolia silurica* ja *Kalania pusilla*) kuuluvad rohevetikate (Chlorophyta) seltsi Dascycladales. Dasycladales on suurte üherakuliste vetikate selts, kelle esindajaid elab ka tänapäeval, ning kes peamiselt asustavad troopilisi madalmeresid. Dasüklaade võiks nimetada nende pika geoloogilise ajaloo tõttu lausa „elavateks fossiilideks" ning tänu iseloomulikule ehitusele ning radiaalsümmetrilisele tallusele on neid võrreldes teiste vetikarühmadega lihtsam eristada. Lisaks eelnevale aitavad määramisele kaasa kõrvalharude ning paljunemisstruktuuride asendi uurimine. Kolmas Kalanast kirjeldatud liik on *Leveilleites hartnageli,* mis oma välismorfoloogiliste tunnuste ja võimalike paljunemisstruktuuride asetuse järgi on määratud punavetikaks klassist Florideophyceae.

Lagerstätte materjal koos sedimentoloogiliste andmetega võimaldab interpreteerida vetikate võimalikku elukeskkonda, samavanuselised sarnased leiud kogu maailmast annavad ülevaate liikide levikust ning mitmekesisusest. Vetikate juurelaadsed kinnitusorganid, mis tavapäraselt fossiilsena ei säili, aitavad anda hinnangut sette/põhja iseloomu kohta. Nii näiteks viitavad harunevad niitjad kinnitusorganid pehmele substraadile, lamedad ja massiivsed aga kõvale pinnasele. Üksikud terviklikud *L. hartnageli* talluse leiud näitavad, et Kalana vetikad kinnitusid niitjate kinnitusorganitega pehmele substraadile. Kuna pehmekehalised vetikad on väga õrnad ning lainetuskeskkonnas kergesti purunevad tuleneb, et Kalanast leitud peaaegu terved vetikatallused on mattunud *in situ* ning rahulikus normaalsoolsusega laguunikeskkonnas. Vetikafossiilide ümbriskivim, peen teralis-mudaline lubjakivi/dolomiit viitab samuti rahulikule settekeskkonnale. Tänu dasüklaadifossiilidele Kalanas oleme võimelised hindama ka kunagist veesügavust ning temperatuuri. Tänapäeva dasüklaadid elavad troopilises ja lähistroopilises kliimavööndis, limiteeritud veesügavuses (vahemikus 10–15 m), seega eeldusel, et Kalanast leitud terved vetikafossiilid on mattunud oma elupaigas, sai vee sügavus seal olla maksimaalselt 15 meetrit. Analoogia

põhjal tänapäevaste dasükladide elukeskkonnaga järeldame, et vee temperatuur selles piirkonnas võis püsida umbes 20 °C juures. Suur hulk kogutud *L. hartnageli* eksemplare võimaldas kirjeldada selle liigi erinevaid kasvustaadiume, näidates talluse arengut noorest lihtsa morfoloogiaga organismist täiskasvanud suguküpse organismini.

Siluri vanusega tallofüütsete mittelubistunud vetikate leiukohti on maailmast kokku kirjeldatud 37, neist 22 on nimetatud vetika-*Lagerstättedeks* (Loduca et al., 2017) ning suur osa nendest on leitud Baltica või Laurentia kontinentidelt. Kõige tuntumad Siluri vetika-*Lagerstätted* on kirjeldatud Põhja-Ameerikast (LoDuca and Brett, 1997; LoDuca et al., 2003) ja Kanadast (LoDuca et al., 1995, 2011, 2013).

Vetikafossiilide uurimisele on Eestis seni väga vähe tähelepanu pööratud. Enamik kogutud vetikafossiile on mineraliseerunud skeletiga ning ootavad Tallinna Tehnikaülikooli ja Tartu Ülikooli Loodusmuuseumi geoloogilistes kollektsioonides detailsemaid kirjeldusi.

Lisaks Kalana ja Rõstla karjäärile on sarnase säilivusega vetikafossiile leitud veel Sopimetsa, Koguva, Anelema (kõik Silurist) kui ka Vasalemma karjäärist (Ordoviitsium). Tänu puuraukudest leitud vetikafossiilide andmestikule näeme, et vetikad olid alam-Siluris levinud üle kogu Eesti. Täiendavad puuraukude uuringud on tulevikus kindlasti vajalikud, selgitamaks välja nende täpsem levik.

Praegu on Kalana leiukoht kõige rikkalikum vetika-*Lagerstätte* kogu maailmas. Arvatavasti olid lubistumata vetikad Siluri ajastu meredes niisama tavalised ja levinud kui tänapäevalgi, kuid säilisid erakordselt harva. Iga uus *Lagerstätte* suurendab meie arusaama geoloogilises minevikus kooseksisteerinud organismidest, ning Kalana *Lagerstätte* annab olulise panuse Siluri vetikafloora mitmekesisuse uurimisse. Kalana *Lagerstätt*e ja selle säilimispõhjuste uurimine nõuab paljude erinevate erialaspetsialistide – paleontoloogide, sedimentoloogide, mineraloogide, geokeemikute ja geofüüsikute koostööd ning see töö kestab veel aastaid (Eensaar et al., 2017a, 2017b; Gaškov et al., 2017; Männik et al., 2016; Tinn et al., 2009; Preeden et al., 2008).

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