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Thallophytic algal flora from a new Silurian Lagerstätte

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Abstract. Algae have always been the most diverse and numerous eukaryotic autotrophs in marine ecosystems. Both fossil and molecular data point to an early Proterozoic origin for algae. Although known for their long evolutionary history, the fossil record of algae is sparse and mainly remains of taxa with heavily calcified thalli are preserved. However, fossils of noncalcareous algae, known as extremely sporadic and occasional finds from different parts of the world, provide important insights into the palaeobiology of algal flora in the Earth's past. Here we describe highly diverse flora of noncalcareous thallophytic algae from a Silurian age deposit.

Key words: Silurian, Konservat-Lagerstätte, thallophytic algae, Estonia.

INTRODUCTION

Numerous calcareous algae have constituted an important part of lime-secreting and rock-forming organisms during the Earth's history. Skeletal debris of some heavily calcified macroalgae, like members of the extant orders Dasycladales among Chlorophyta (green algae) and Corallinales among Rhodophyta (red algae), abound in some intervals of sedimentary rocks. However, non-calcified plant-like macroalgae or seaweeds, also referred to as thallophytic algae (LoDuca 2001), are rarely preserved. Our present knowledge of noncalcareous algal flora and its place and importance in the early Palaeozoic ecosystems is still rather incomplete.

The early Palaeozoic noncalcified algal floras are best known from a group of distinctive Konservat-Lagerstätten, termed as thallophytic-algal-dominated biotas (LoDuca 1998) that have largely preserved delicate algal morphology. One of the most diverse floras was described by Ruedemann (1925) and LoDuca & Brett (1997) from the Ludlovian deposits (late Silurian) in eastern North America. It is known as the *Medusaegraptus* epibole, after an unusually abundantly occurring dasyclad algal genus. Altogether these deposits have yielded four species of noncalcified algae. The same number of species had previously been recorded from the Silurian of the entire Baltica palaeo-continent (Nitecki & Spjeldnaes 1993; LoDuca et al. 2003).

A new and highly diverse flora of noncalcareous thallophytic algae was recovered from the Kalana quarry, central Estonia (Fig. 1). The material comes from a series of shallowing-upward shelf carbonates of early Aeronian (Llandovery, Silurian, ca 440 m.y.) age. The lower part of the limestone succession contains abundant noncalcified thallophytic algal remains. Most of the material occurs within the light to dark brown organic-rich, microlaminated, partly dolomitized lime-stones, which form 1–20 mm thick laminae on the bedding planes of micritic limestone layers. The other faunal remains in the kerogenous intercalations comprise monograptid and diplograptid graptolites, scolecodonts, bryozoans, sponges, and crinoids. The section also contains occasional lenses with abundant shelly fauna (tempestites), including gastropods, ostracods, and brachiopods. An important characteristic of the kero-genous intercalations is the absence of ichnofossils.

Organic remains of poorly preserved macroalgae from the Silurian of Estonia have formerly been described by Obut & Rytzk (1958) and Obut (1960), but Obut attributed them to dendroid graptolites. He established two new genera, *Estoniocaulis* and *Rhadinograptus*, although the preservation of fossils was extremely poor. This material was redescribed and discussed by Mierzejewski (1991), who excluded these fossils from Graptolithina and treated them as *incertae sedis*.

MORPHOLOGY AND AFFINITIES OF THE ALGAL REMAINS

The Kalana Lagerstätte contains two types of algal fossils. The first type occurs as pale brown to dark brown kerogenous and carbonized compressions on bedding

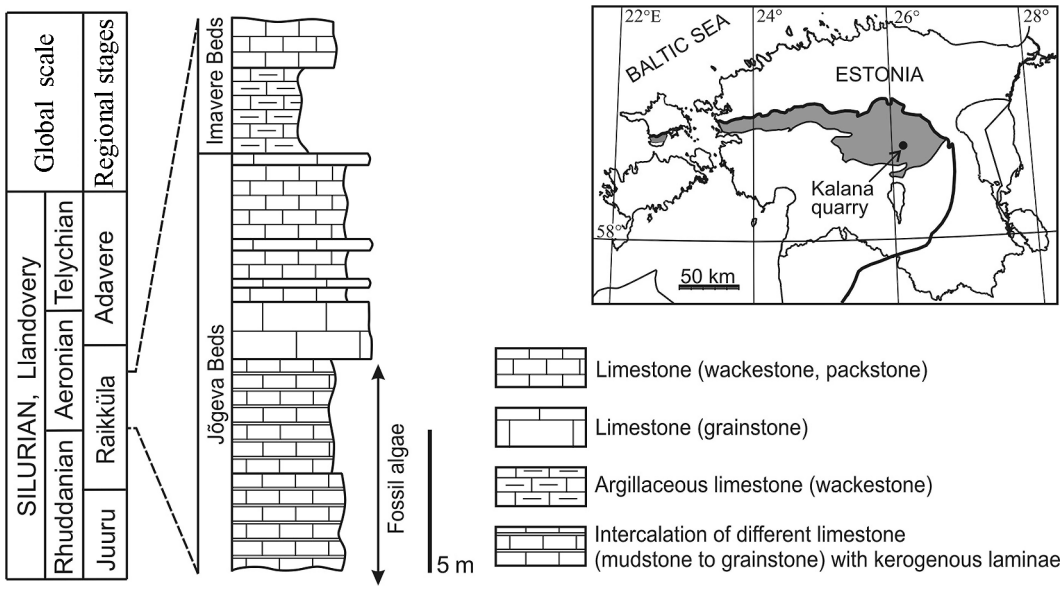

Fig. 1. Geographic location and stratigraphic position of the Kalana quarry section. Outcrop area (grey) and boundary of the distribution area of the Raikküla Stage (thick line) are shown on the map.

planes. No details of cellular level have been detected so far. The second type occurs as three-dimensional carbonaceous material and is represented by slightly compacted black-coloured 'stems' and sporangia, but occasionally also by laterals or entire thalli. The Kalana fossils do not show any evidence of calcification that could have occurred during their lifetime. While there are several algal taxa that produce an external coating of calcium carbonate, it is expected that in the case of a fossil specimen, it could be preserved as an external mold.

Systematics of fossil algae is complicated due to morphologies which are common to the majority of algal groups and to the lack of preserved cellular structures in most cases. In the material from Kalana we could preliminarily distinguish up to ten morphological groups (species). This marks a considerably higher diversity than has been up to now documented from the Cambro-Silurian strata.

A particularly abundant fossil in the Lagerstätte is a form that resembles *Leveillites hartnageli* (Foerste) (Fig. 2A), which was originally described from the lowermost Silurian in southern Ontario (Foerste 1923, p. 61) as a doubtful alga, sponge or 'some group of animals not yet discriminated from those recognized so far'. Although this taxon was included in the Graptoloidea (Ruedemann 1947), most graptolite workers (Bulman 1955, 1970) take this assignment with caution. The thalli of this form are up to 7 cm high, with a 1–2 mm wide central axis. Each specimen has 10–20 primary branches, most of them about equal in length and 12–25 mm long. These branches bear 10–30 so-called tufts, consisting of 20–30 up to 1 mm long laterals and arranged in either side of the 1st-order laterals. Although the present material consists of hundreds of specimens, definite reproductive structures have not been revealed yet.

Of particular interest is an alga with a tape-like thallus, 2–5 mm wide and up to 5 cm long. Part of these thalli are plain narrow lanceolate blades without any detectable structures. However, some specimens show groups of ovoid structures about 50 µm wide and 100 µm long, which we interpret as reproductive structures. In our interpretation there are male plants bearing spermatangia formed on spermatangial mother cells (Fig. 2B, C) and female plants (carposporophytes) bearing carposporangia. Similarly arranged reproductive structures are known in several taxa among Rhodophyta.

Some taxa within the Kalana flora exhibit thallus architecture diagnostic of the Chlorophyte (green algae) order Dasycladales. Dasyclads are unicellular and radially symmetrical macroalgae with siphonous organization. This highly diverse group has a long geological history, but is dominated by calcareous forms (Berger & Kaever 1992). In the Kalana quarry the fossils of dasycladalean affinity resemble *Medusaegraptus* sp. (Fig. 2D), *Chaetocladus* sp. (Fig. 2E), and *Inopinatella* sp. (Fig. 2F). All these uncalcified dasyclad taxa that have earlier been reported from the Silurian of Sweden (Kenrick & Vinther 2006), England (Elliott 1971), and North America (LoDuca 1990, 1997) occur in minor quantities at Kalana.

The overall morphology of another species, *Cympolia*? sp., resembles a recent dasyclad *Cympolia* and the species is therefore tentatively attributed to the

dasycladaleans (Fig. 2I). A repeatedly branching thallus probably reached the height of 6–10 cm. The central axis, visible in several specimens, is encased into a series of bell-shaped forms, up to 1 cm long and 3–5 mm wide. The branches terminate with a bundle of slender hair-like filaments.

A number of other morphologies (Fig. 2G, H) tentatively identified in this material allows us to conclude that the locality contains not less than eight but perhaps more than ten different species of non-calcified thallophytic algae. Altogether 14 species of noncalcified dasycladalean algae have been reported from the entire Silurian system (LoDuca et al. 2003; Kenrick & Vinther 2006). In this context, material from the Kalana quarry is a major contribution to the fossil record in this group. The new locality apparently represents the richest Silurian Lagerstätte of thallophytes recorded so far.

PALAEOGEOGRAPHIC REMARKS

Although noncalcified algal floras were probably widespread in the Palaeozoic seas, the extraordinary preservation of such a material seems to be extremely rare. During early Silurian times the Baltic palaeobasin was located approximately 10–20 degrees south of the equator (Cocks & Torsvik 2005). Given this position, the climate was likely tropical to subtropical. Although special taphonomic studies need to be carried out, it is obvious from the accompanying fauna (palaeocopid ostracods, rhynchonelliformean brachiopods) and primary description that the material was deposited in the conditions of normal marine salinity, but probably in extremely shallow water protected from direct wave action. Similar conditions dominated in the Laurentia palaeocontinent, on the other side of the Iapetus ocean, where the algal flora of the *Medusaegraptus* epibole and similar Konservat-Lagerstätten of North America were described (LoDuca & Brett 1997).

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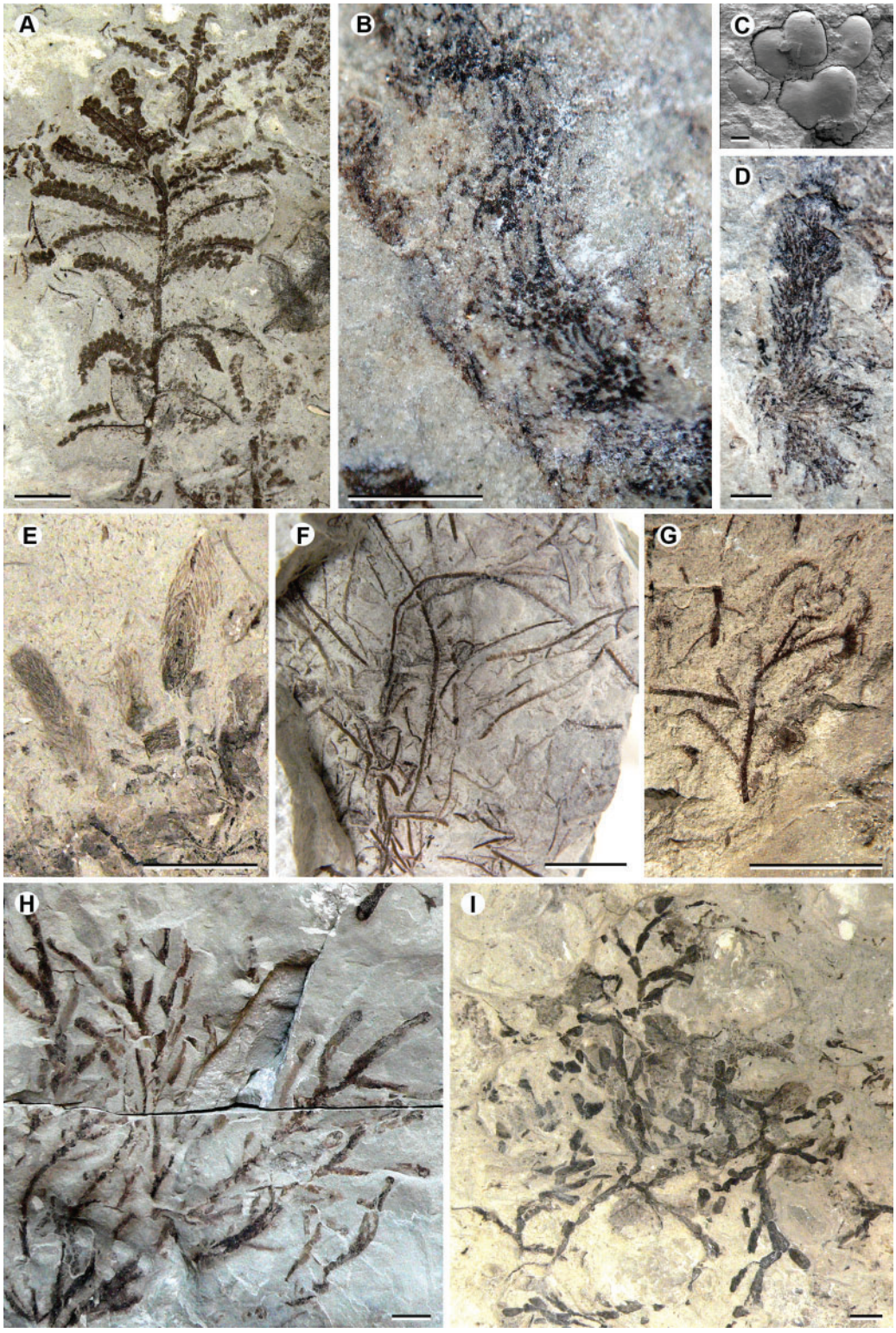

Fig. 2. Algal fossils of Aeronian (Llandovery, Silurian) age from Kalana, Estonia. **A**, a form that resembles *Leveillites hartnageli*, scale 1 cm (Tartu University Natural History Museum, specimen number TUG 1269-1); **B**, alga with a tape-like thallus, scale 1 mm (TUG 1269-2); **C**, SEM picture of organic-walled reproductive structures, scale 20 µm (TUG 1269-3); **D**, a specimen resembling *Medusaegraptus* sp., scale 1 mm (TUG 1269-4); **E**, a specimen resembling *Chaetocladus* sp., scale 1 cm (TUG 1269-5); **F**, a specimen resembling *Inopinatella* sp., scale 1 cm (TUG 1269-6); **G**, noncalcified thallophytic alga, scale 1 cm (TUG 1269-7); **H**, noncalcified thallophytic alga, scale 1 cm (TUG 1269-8); **I**, *Cympolia*? sp., scale 1 cm (TUG 1269-9).

Tallofüütsed vetikad uuest, Siluri-ealisest Lagerstättest

Oive Tinn, Tõnu Meidla, Leho Ainsaar ja Tõnu Pani

Tänapäevastes ökosüsteemides on vetikad kõige mitmekesisem ja arvukaim autotroofsete organismide rühm. Kuigi vetikad on tuntud oma pika evolutsioonilise ajaloo poolest, mis on leidnud kinnitust ka molekulaarsete meetoditega, on vetikafossiilid haruldased ja enamasti on säilinud vaid tugeva kaltsiitse tallusega organismid. Vaid harvad üksikud kaltsifitseerumata vetikafossiilide leiud annavad meile pildi vetikafloorast Maa geoloogilises minevikus. Artiklis on kirjeldatud Siluri-ealisest leiukohast pärinevaid, märkimisväärse detailsusega fossiilsena säilinud kaltsifitseerumata vetikaid. Rikkaliku ja mitmekesise flooraga Lagerstätte leidmine Balti paleobasseinis näitab Siluri madalmerelise keskkonna suurt mitmekesisust ning tõstatab intrigeeriva küsimuse pikaajalistest, erakordset säilimist soodustavatest keskkonnatingimustest Siluri paleotroopikas.