

Crinoids from the Silurian of Western Estonia

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The Silurian crinoids of Estonia are re-evaluated based on new collections and museum holdings. Nineteen species-level crinoid taxa are now recognized. All crinoid names applied to Estonian Silurian crinoids during the middle 19th century are disregarded. Especially significant is the fauna reported herein from the Pridoli because coeval crinoids are very poorly known from the Baltic region and elsewhere. One new genus and four new species are described from Estonia, namely *Calceocrinus balticensis* sp. nov., *Desmidocrinus laevigatus* sp. nov., *Eucalyptocrinites tumidus* sp. nov., and *Saaremaacrinus estoniensis* gen. et sp. nov.

Key words: Echinodermata, Crinoidea, Pridoli, Silurian, Estonia, Baltica.

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Introduction

Wenlock and Ludlow crinoids are well known from the Baltica paleocontinent with the extensive faunas from Gotland, Sweden. This fauna was monographed by Angelin (1878) and has been studied subsequently by Ubaghs (1956a, b, 1958a, b), Franzén (1982, 1983), and Franzén-Bengtson (1983). However, there is very little known about other Silurian crinoids from Baltica. In this study we evaluate and describe Silurian crinoids from Estonia, including one new genus and four new species. These crinoids include the only known crinoid from the Llandovery of Estonia, *Calceocrinus balticensis* sp. nov. Further, the number of known Pridoli crinoids from Baltica is now ten species-level taxa.

The Silurian witnessed the recovery and eventual adaptive radiation of crinoids following the end-Ordovician biosphere collapse (Eckert 1988; Donovan 1988, 1989). Crinoids underwent a single significant extinction interval at the close of the Katian that corresponded to the beginning of the Hirnantian glaciation (Peters and Ausich 2008). This extinction event separated the Early from the Middle Paleozoic Crinoid Macroevolutionary Fauna (CMF) (Baumiller 1994; Ausich et al. 1994). Assemblages from the Ordovician, Early Paleozoic CMF were commonly dominated by diplobathrid camerate, disparid, and hybocrinid crinoids. Ordovician crinoids commonly occurred in paleocommunities comprised of several pelmatozoan classes, and a reasonable degree of biogeographic endemism existed. In contrast, crinoids from the Middle Paleozoic CMF (Silurian through middle Mississippian) occurred commonly in paleocommunities domi-

nated by monobathrid camerates, cladids, and flexibles. These paleocommunities typically contained relatively fewer non-pelmatozoan echinoderms (especially after the Silurian), and crinoid faunas became more cosmopolitan.

The new Estonian crinoids reported here add important information about Silurian faunas on Baltica. The recovery and radiation of the Middle Paleozoic CMF can now be better characterized on another paleocontinent.

Institutional abbreviations.—TUG, University of Tartu, Estonia; GIT and TTÜGI, Institute of Geology, Tallinn University of Technology, Estonia.

Other abbreviations.—CMF, Crinoid Macroevolutionary Fauna; CD, posterior interradius; P-3, primanal followed by three plates.

Historical background

Eichwald (1840) described the first Silurian crinoids from Estonia. His work was completed within two decades by Miller (1821), who separated the Crinoidea from starfish as a distinct group of echinoderms. The primary focus of Miller (1821) was Mississippian crinoids from England, and Eichwald (1840) applied these Mississippian crinoid names to the Silurian fauna from Estonia. Thus, the Eichwald (1840) faunal list (Table 1) is a list of names unsuitable for Silurian crinoids. Furthermore, Eichwald (1840) had no illustrations; and his specimens, deposited in Saint Petersburg, are presumably lost. Webster (2003) listed the Miller (1821) crinoid

Table 1. Crinoids attributed to the Silurian of Estonia by Eichwald (1840). The recommendation herein is to disregard these names as crinoids from Estonia.

<i>Actinocrinites granulatus</i> (non Goldfuss, 1831) in Eichwald, 1840
<i>Actinocrinites</i> aff. <i>triacontadactylus</i> Miller, 1821 in Eichwald, 1840
<i>Cupressocrinites pentaporus</i> Eichwald, 1840 (columnals only)
<i>Cyathocrinites planus</i> Miller, 1821 in Eichwald, 1840
<i>Cyathocrinites quinquangularis</i> Miller, 1821 in Eichwald, 1840
<i>Platycrinites</i> aff. <i>laevis</i> Miller, 1821 in Eichwald, 1840
<i>Poteriocrinites crassus</i> Miller, 1821 in Eichwald, 1840

names; however, he noted that most of these assignments were incorrect. We concur and conclude that the seven names in Table 1 should be disregarded in reference to Silurian crinoids of Estonia, and there is no way to determine to which crinoids these names were applied. Jaekel (1900) described two crinoid species from the upper Silurian of Estonia, *Lagarocrinus osiliensis* Jaekel, 1900 and *Lagarocrinus scanicus* Jaekel, 1900. These two species were studied by Rozhnov (1981) and redescribed as *Cicerocrinus osiliensis* (Jaekel, 1900) and *Cicerocrinus scanicus* (Jaekel, 1900). Both of these species were listed by Rozhnov (1981) from the Pridoli Ohesaare Stage of Estonia. In addition, Rozhnov and Männil in Rozhnov et al. (1989) reported Wenlock pisocrinids from several cores across Estonia. These are all Wenlock in age and include *Pisocrinus* (*Granulosocrinus*) *lanceatus* Rozhnov and Männil in Rozhnov et al., 1989; *Pisocrinus* (*Granulosocrinus*) sp.; *Pisocrinus* (*Pisocrinus*) *tria-lobus* Rozhnov and Männil in Rozhnov et al., 1989; *Pisocrinus* (*Pocillocrinus*) *pilula* de Koninck, 1858; and *Pisocrinus* (*Pocillocrinus*) *rubeli* Rozhnov and Männil in Rozhnov et al., 1989.

Raukas and Teedumäe (1997) reported additional Silurian crinoids; however, it is not clear what specimens were used for these identifications. Nestor (1997: 105) reported *Crotalocrinites rugosus* (Miller, 1821) from the Pridoli. Hints and Stukalina (1997: 241) listed *Crotalocrinites*, *Myelodactylus*, and *Glyptocrinus* from the Adavere Stage; *Pisocrinus* from the Jaani and Jaagarahu Stages; *Crotalocrinites* from the Paadla, Kuressaare, and Kaugatuma Stages; *Anthinocrinus*, *Eucalyptocrinites*, and *Leptocrinites* from the Kaugatuma Stage; and *Cicerocrinus* and *Hexacrinites* from the Ohesaare Stage.

To date, we are unable to confirm the occurrences of *Crotalocrinites*, *Glyptocrinus*, and *Hexacrinites* in the Silurian of Estonia. Although we recognize *Myelodactylus* from the Ohesaare Formation, we have not been able to confirm it from the Adavere Stage. *Leptocrinites* is a rhombiferan, and *Anthinocrinus* is a columnal. These latter two taxa are not discussed further.

Based on our fieldwork, the most common Silurian crinoid from Estonia is *Eucalyptocrinites* (see below). It is thus surprising that this crinoid was not reported from Estonia until Hints and Stukalina (1997).

Geological setting

During the Silurian, the paleocontinent of Baltica was located in equatorial latitudes drifting northward (Melchin et al. 2004). The pericontinental Baltic paleobasin of modern Estonia was characterized by a wide range of tropical environments and diverse biotas (Hints 2008). According to the facies model developed by Nestor and Einasto (1977), five depositional environments can be recognized in the Baltic Silurian Basin: tidal flat/lagoonal, shoal, open shelf, transitional (basin slope), and a basin depression. The first three environments formed a carbonate shelf or platform, and the latter two formed a deeper pericratonic basin with fine-grained siliciclastic deposits (Raukas and Teedumäe 1997). In the outcrop area, including Saaremaa Island, the Silurian succession is represented by shallow shelf carbonate rocks rich in shelly faunas. In the subsurface of southwestern Estonia, Latvia, and Lithuania, deeper-water facies occur. These are represented predominantly by various argillaceous rocks, from calcareous marlstone to graptolitic shale (Hints 2008).

The Silurian of Estonia has been studied since the middle 19th century. Outlines of the Silurian stratigraphy were established by Schmidt (1881), Bekker (1925), and Luha (1933). More recently, various aspects of the Silurian System in Estonia have been discussed in detail by Kaljo (1970), Nestor (1997), Nestor and Einasto (1997) (see Hints 2008), and Cramer et al. (2011). The Silurian of Estonia is subdivided into ten regional stages (from Rhuddanian to Pridoli) (Fig. 1). All the international stages of the Silurian System are represented by sedimentary rocks in the Estonia. The regional stages of the Silurian are correlated using biostratigraphy and, at some levels, K-bentonites and stable isotope curves. Graptolites are typically rare in the carbonate succession of Estonia; and hence, shelly faunas have been traditionally used as the main biostratigraphic tools. However, in recent decades, microfossils have become useful, and detailed chitinozoan, conodont, and vertebrate biozonal schemes have been elaborated. These microfossil groups also enable correlation with the standard graptolite zonation and with the global timescale (Mõtus and Hints 2007).

Silurian exposures on Saaremaa are the best in Estonia. They are mostly represented by coastal cliffs. All Baltic Silurian environments, except the basin depression, occur in the Silurian of Saaremaa, which is dominated by carbonates, mostly dolomite, limestone, and marlstone. The exposed strata have a stratigraphic range from Sheinwoodian (Jaani Stage) to Pridoli (Ohesaare Stage) (Fig. 2). Geographic and stratigraphic details of Saaremaa and Hiiumaa localities are given in Appendix 1.

Methods

Terminology follows Ubahgs (1978a) with modifications from Ausich et al. (1999). Open nomenclature follows

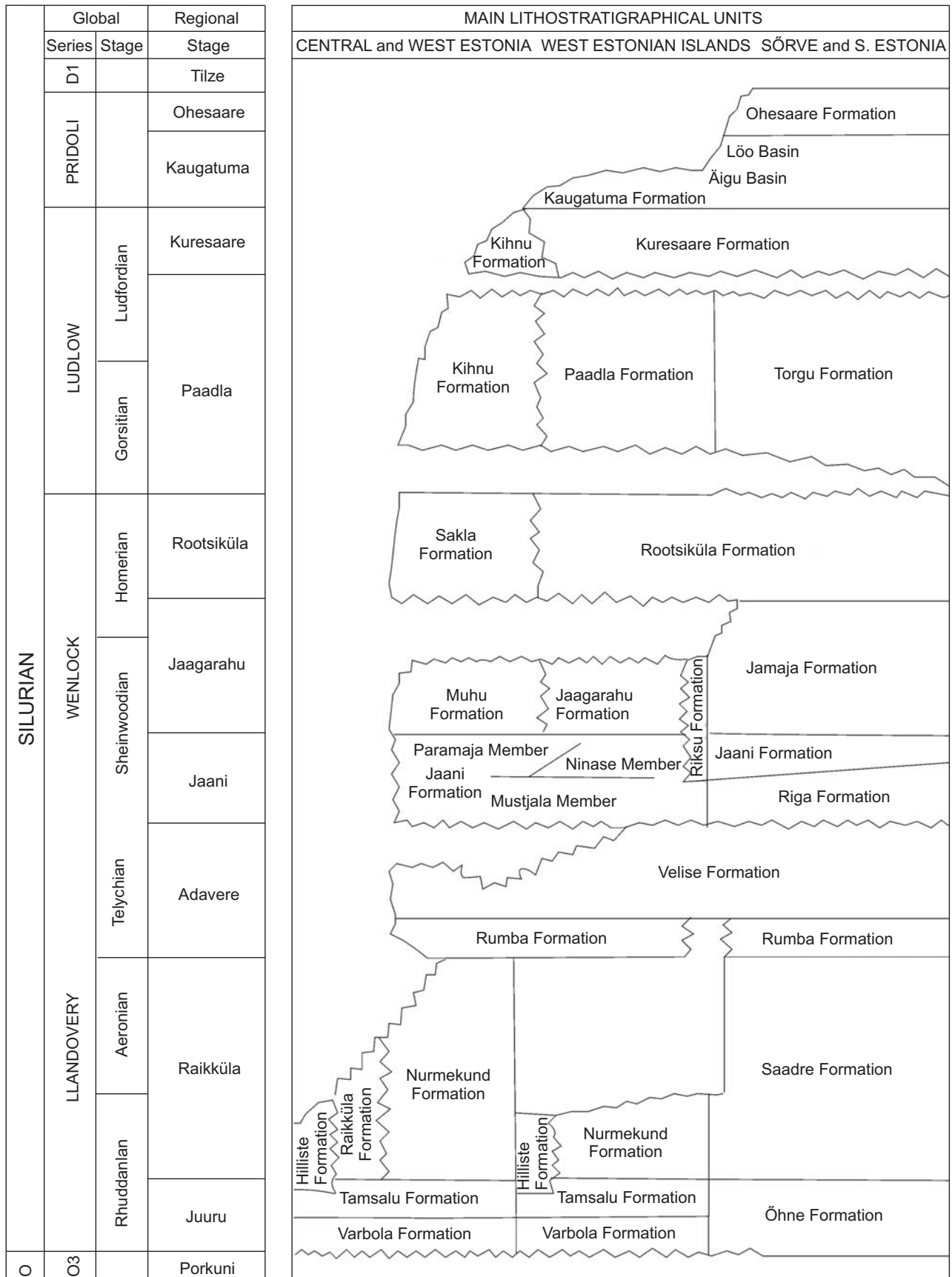


Fig. 1. Silurian stratigraphy of Estonia. The majority of the new fossil material is from the West-Estonian islands, represented in the middle of the chart of lithostratigraphic units (based on Hints 2008). D1, Lower Devonian; O, Ordovician; O3, Upper Ordovician.

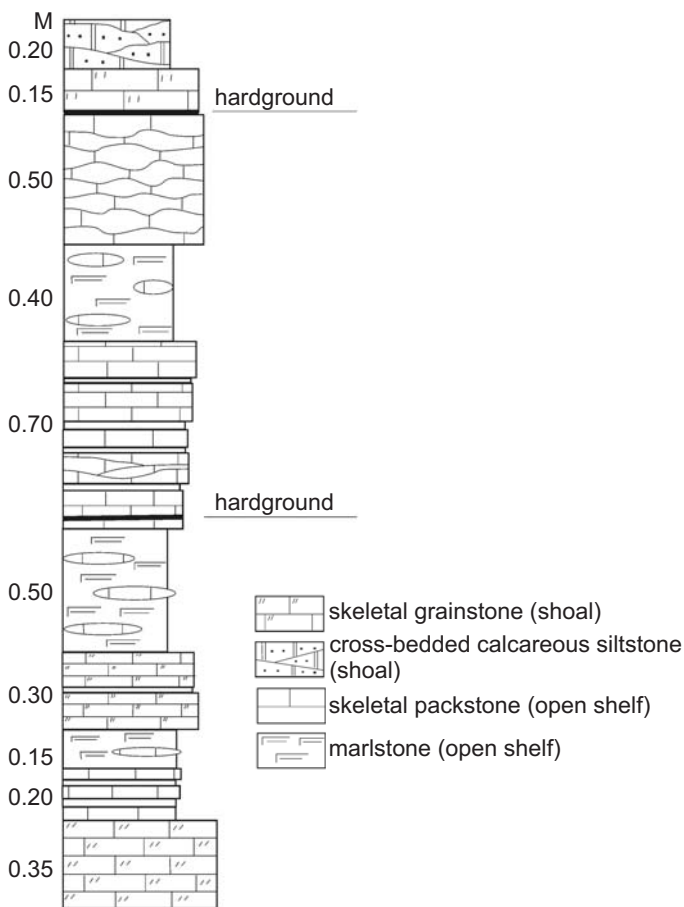


Fig. 2. Stratigraphic section at the Ohesaare Formation at Ohesaare Cliff, Saaremaa, Estonia (modified after Nestor 1990).

Matthews (1973) and Bengtson (1988). The scheme for defining relative proportions of the calyx follows Ubaghs (1978a: fig. 72). All measurements are in mm, unless otherwise noted. Asterisk indicates a crushed or broken specimen.

Systematic paleontology

Class Crinoidea Miller, 1821

Subclass Camerata Wachsmuth and Springer, 1885

Order Monobathrida Moore and Laudon, 1943

Suborder Compsocrinina Ubaghs, 1978b

Superfamily Periechocrinoidea Bronn, 1849

Discussion.—In order to understand the oldest periechocrinids from the Brassfield Limestone (Aeronian) of southwestern Ohio, USA, Ausich (1987) emended the diagnosis of the family. This emended diagnosis was needed to accommodate morphological variability in the primitive Brassfield periechocrinids. Stratigraphically younger forms, as defined by Ubaghs (1978b), had more stable, basic morphology. Following Ausich (1987), six Silurian periechocrinid genera are now recognized, including *Acacocrinus* Wachsmuth and

Springer, 1897; *Ibanocrinus* Ausich, 1987; *Periechocrinus* Morris, 1843; *Stiptocrinus* Kirk, 1946; *Tirocrinus* Ausich, 1987; and a new genus from Estonia, *Saaremaacrinus*.

Among these genera, only *Periechocrinus* and *Saaremaacrinus* gen. nov. have a biseries of alternating plates in the regular interrays. In contrast, *Acacocrinus*, *Ibanocrinus*, *Stiptocrinus*, and *Tirocrinus* have interrarial plates above the first interrarial plate arranged into more distinct ranges symmetrical about the interray midline. Furthermore, both *Periechocrinus* and *Saaremaacrinus* have more fixed brachials, interradials, and intraradials than other Silurian periechocrinids. *Saaremaacrinus* is also similar to *Stammocrinus* and *Pyrioxocrinus* from the Devonian. However, these two Devonian forms have 20 free arms and *Saaremaacrinus* has only 10.

This new periechocrinid is consistent with Ausich and Kammer (2008) in that the periechocrinids were only present on Baltica during the Silurian. *Saaremaacrinus* extends this range into the Pridoli. This new genus should be nested within the clade containing *Periechocrinus*, as discussed in Ausich and Kammer (2008).

Genus *Periechocrinus* Morris, 1843

Type species: *Periechocrinus costatus* Austin and Austin, 1842; Dudley, England; Wenlock, Silurian.

Periechocrinus longimanus (Angelin, 1878)

Fig. 3E.

1878 *Actinocrinites longimanus* sp. nov. Angelin, 1878: 6, pl. 15: 17; pl. 26: 16; pl. 28: 5, 5a, 6.

1881 *Periechocrinus longimanus* (Angelin, 1878); Wachsmuth and Springer 1881: 132 (306).

1943 *Periechocrinites longimanus* (Angelin, 1878); Bassler and Moodey 1943: 599.

1983a *Periechocrinus longimanus* (Angelin, 1878); Franzén 1983: 6.

2003 *Periechocrinus longimanus* (Angelin, 1878); Webster 2003.

Material.—Two Estonian specimens are assigned to *P. longimanus*: GIT 405-4-1 and GIT 405-4-2 from lower Wenlock, Jaani Formation.

Description.—Calyx small for the genus and is high bowl or globe shaped (Fig. 3E). Calyx plates are gently convex and smoothly sculpted with thin median ray ridges beginning on the first primibrachials. Basal circling is relatively low, truncate proximally, visible in side view. Three basal plates are subequal in size. Radial circling is approximately 1.8 times higher than the basal circling; interrupted in the posterior; radial plates five, hexagonal, and approximately 1.5 times higher than wide. In normal interrays, the first interrarial is hexagonal, approximately as high as wide but tapers distally, and smaller than radials and first primibrachials. The second range of plates in normal interrays comprised of two plates, but more distal plating is not preserved. The first primibrachial is fixed, hexagonal, approximately 1.2 times wider than high, and smaller than radial plates. More distal ray plates, tegmen, free arms, and column are not preserved.

Discussion.—*Periechocrinus* is a cosmopolitan Silurian crinoid that characterizes many Silurian faunas. Franzén (1983)

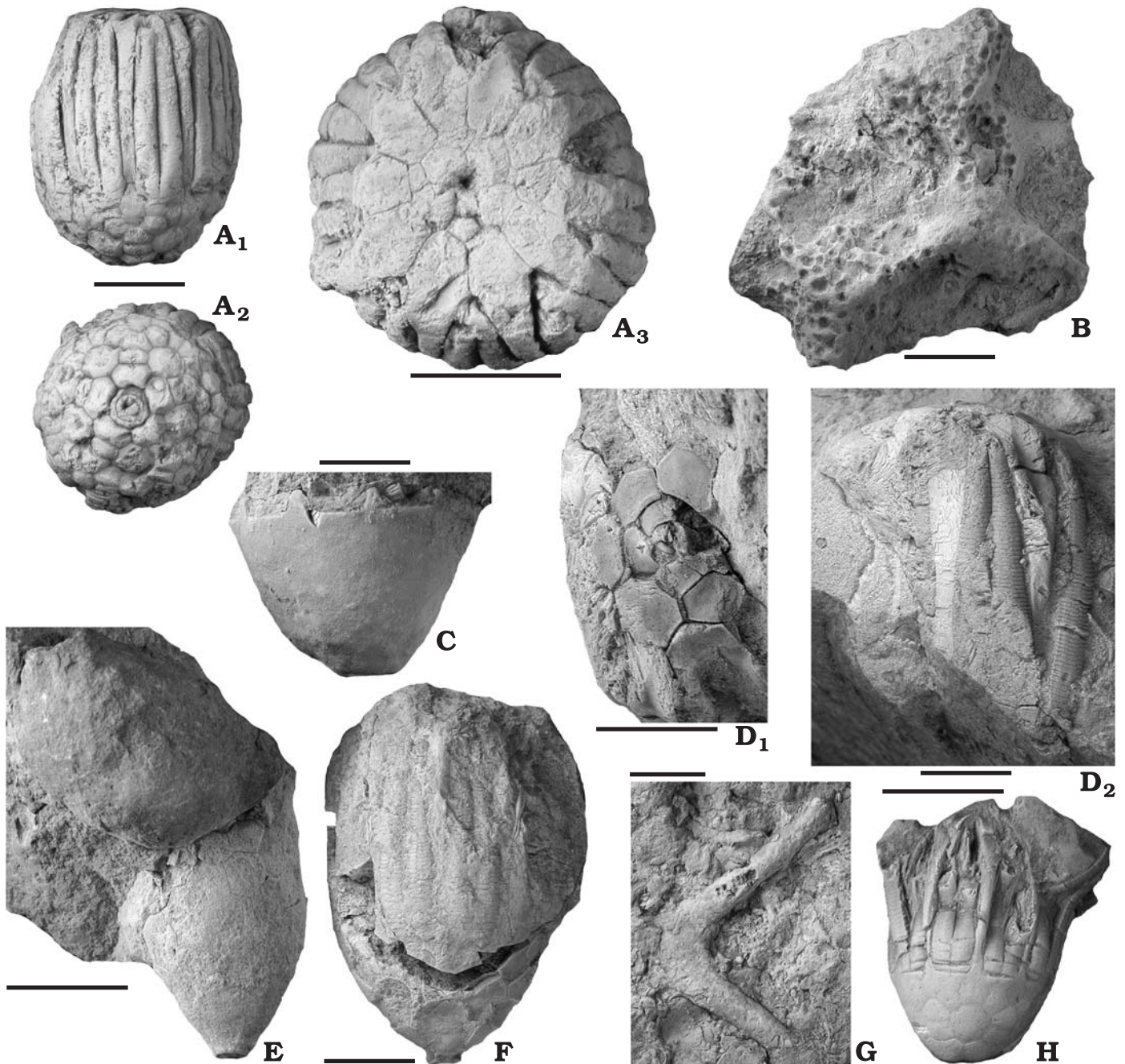


Fig. 3. Camerate crinoids from the Silurian of Estonia. **A, B.** Middle Äigu Beds, Kaugatuma Formation (Pridoli), Kaugatuma Cliff. **A.** *Eucalyptocrinites tumidus* sp. nov., GIT 405-243. A₁, lateral view of crown, note modestly expanding partition plates; A₂, basal view of calyx, note nodose calyx plates; A₃, tegmen view of crown, note flat tegmen top. **B.** *Calliocrinus sedgwickianus* sp. nov., TUG 1395-8. Basal view of a portion of the basal and radial circlets, all circular pits are the trace fossil *Oichnus*. **C.** *Eucalyptocrinites* sp., GIT 405-238, Jaani Formation (Wenlock), Suuriku Cliff. Lateral view of calyx. **D.** *Eucalyptocrinites* sp. 2., TUG 1395-13, Ninase Member, Jaani Formation (Wenlock), Panga Cliff. D₁, tegmen view of crown; D₂, B-ray view of partial crown, note deep elongate groove on well-preserved partition plate. **E.** *Periechocrinus longimanus* (Angelin, 1878), GIT 405-4-1, Jaani Formation (Wenlock), Janni Cliff. Lateral view of partial calyx, calyx sutures very indistinct. **F.** *Eucalyptocrinites* sp. 1, TUG 1375-3, Jaani Formation (Wenlock), Undva Cliff. Lateral view of broken crown. **G.** *Calliocrinus* sp., TUG 1395-6, Ninase Member, Jaani Formation (Wenlock), Suuriku Cliff. Broadly bifurcating spine. **H.** *Eucalyptocrinites* sp. 1, TUG 1375-2, Jaani Formation (Wenlock), Undva Cliff. Lateral view of crown of juvenile. Scale bars 10 mm.

listed twelve species of *Periechocrinus* from Gotland, Sweden. Only two of these species are characterized by smooth calyx plating, *P. grandiscutus* and *P. longimanus*. From Angelin's (1878) illustrations, *P. grandiscutus* has much more convexity to the radial plates than *P. longimanus* and the two

Estonian specimens. Thus, Wenlockian specimens from Saaremaa are assigned to *P. longimanus*. The preserved portion of the calyx is approximately 15 mm wide and 17 mm high. Calyx plating is not evident on either specimen. Thus, the illustration (Fig. 3E) only illustrates the calyx outline.

Geographic and stratigraphic range.—Franzén (1983) reported *P. longimanus* from the Wenlock (Sheinwoodian) Höglint Formation and Slite Group of Gotland, Sweden. Similarly, the Estonian specimens are from the lower Wenlock, Jaani Formation, Jaani Shore, Saaremaa Island, Estonia.

Genus *Saaremaacrinus* nov.

Etymology: Named for the island of Saaremaa.

Type species: *Saaremaacrinus estoniensis* gen. et sp. nov., by monotypy.

Diagnosis.—Calyx shape medium bowl, basal concavity absent, no calyx lobation. Calyx plates thick, broad median ray ridges present. Basal plate circlet relatively high. Radial plates higher than wide, orientation of radials subvertical, radial circlet only open in CD interray, fixed first primibrachial wider than high, axillary second primibrachial pentagonal. Fixed brachials divide isotomously, fixed rays symmetrical, highest fixed brachials fifth secundibrachial. Numerous interradiation plates, regular interray plating in an alternating biseries, normal interrays not depressed. CD interray proximal plating P-3, anitaxial ridge present, CD interray wider than regular interrays. Tegmen low, tegmen robust, tegmen slightly depressed interradiationally. Ambulacral and orals not differentiated on tegmen, anal tube absent, anus positioned slightly eccentrically. (Characters of the free arms, and presence or absence of the goniopores unknown.)

Description.—See species description below.

Discussion.—Relationships of *Saaremaacrinus* gen. nov. to other Silurian periechocrinids is described in the discussion of the family, above.

Geographic and stratigraphic range.—Pridoli, Late Silurian, Estonia.

Saaremaacrinus estoniensis sp. nov.

Figs. 4A, 5B.

Etymology: After Estonia.

Holotype: TUG 1395-3.

Type locality: Kaugatuma Cliff, Saaremaa Island, Estonia.

Type horizon: Äigu Beds, Kaugatuma Formation, Pridoli, Late Silurian.

Material.—Holotype only.

Diagnosis.—As for genus.

Description.—The calyx is medium in size for the family, and it has a medium bowl shape (Fig. 4A₄) with a slight proximal protrusion of the basal circlet. The basal concavity is absent; no calyx lobation is present; arms are grouped (Fig. 5B₂); and calyx plates are gently convex, have smooth sculpturing, and are relatively thick. Calyx plates in rays are more broadly convex yielding a slightly raised, broad ray ridge (Fig. 5B₁). Basal circlet has a slight protrusion proximally, is relatively high, is visible in side view, and is approximately 10% of calyx height. The three basal plates are subequal in size. The radial circlet is approximately 18% of calyx height, interrupted in posterior by primanal, and is comprised of five, hexagonal radial plates that are approximately 1.1 times

wider than high and subvertical in orientation. Normal interrays are in contact with the tegmen. The first interradiation is hexagonal, approximately as high as wide, smaller than radials, and slightly smaller than first primibrachials. The second range has two plates of unequal size. Normal interray plating is 1-2-2-2-2 in alternating ranges yielding a biseries of alternating plates (Fig. 4A₁). The CD interray is wider than others and not depressed. The primanal is heptagonal, approximately 1.1 times higher than wide, smaller than radial plates; and it interrupts the radial circlet. Plating in the CD interray is P-3-3-3- (Fig. 4A₃) with at least five ranges of plates in CD interray. The anitaxis is defined by more elongate plates through the CD interray, but an anitaxial ridge is absent. The CD interray is in contact with the tegmen. The first primibrachial is fixed, hexagonal, approximately 1.3 times wider than high, and approximately the same size as radials. The second primibrachial is axillary and pentagonal. Commonly five secundibrachials are fixed in the calyx. First secundibrachials in sutural contact medially. Fixed rays are symmetrical. Intrabrachial plates are in the center of the ray, begin on upper shoulder of first secundibrachials (Fig. 4A₂), and are in contact with tegmen.

The tegmen is low and robust, has an inverted cone shape (Fig. 5B₁), and is slightly depressed interradiationally. The tegmen is composed of small, slightly convex plates with smooth sculpturing. The anal opening is slightly eccentric, and the anal tube interpreted to be absent.

There are 10 free arms but further details unknown.

Only the proximal few, immature columnals are preserved but poorly preserved. They are circular and holomeric, and the columnal height of the most-proximal columnals is variable. The lumen is circular.

Discussion.—The holotype is a complete theca that is in part weathered or has a dark calcite overgrowth so that distinction of the plating is not always possible. However, the posterior interray, other interrays, and enough rays are adequately preserved to permit the plating of this new crinoid to be confidently determined.

Measurements.—TUG 1395-3: calyx height, 11.5; calyx width, 12.0; radial plate height, 3.4; radial plate width, 3.6; first primibrachial height, 2.6; first primibrachial width, 2.8; primanal height, 3.4; primanal width, 3.4; and tegmen height, 5.4.

Suborder Glyptocrinina Moore, 1952

Superfamily Eucalyptocrinitoidea Roemer, 1855

Family Eucalyptocrinitidae Roemer, 1855

Genus *Eucalyptocrinites* Goldfuss, 1831

Type species: *Eucalyptocrinites rosaceus* Goldfuss, 1831; Eifel, Germany; Eifelian.

Discussion.—*Eucalyptocrinites* spp. are the most abundant crinoids from the Silurian of Estonia. On many beach sections, dozens of calyxes are preserved in limestone beds and are readily identifiable to genus, which, as mentioned above,

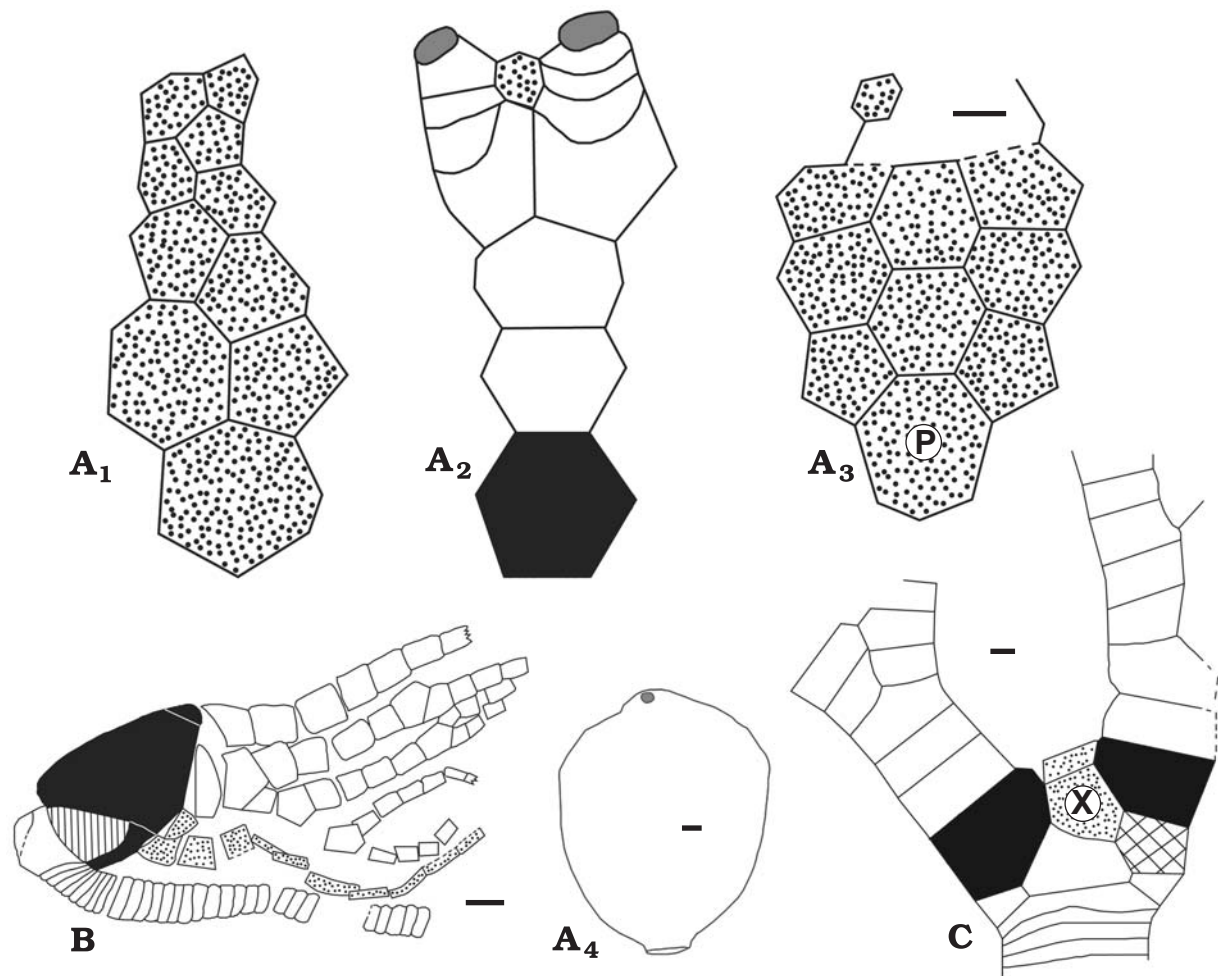


Fig. 4. Plate diagrams of Estonian crinoids. **A.** *Saaremaacrinus estoniensis* gen. et sp. nov., TUG 1395-3, middle Äigu Beds, Kaugatuma Formation (Pridoli), Kaugatuma Cliff. Normal interray plating (A_1), C-ray plating (A_2), CD-interray plating (A_3), and lateral outline of theca (A_4). **B.** *Calceocrinus baliticensis* sp. nov, GIT 405-212, Juuru Stage (Llandover), Heltermaa. D-ray view of crown. **C.** *Protaxocrinus salteri*? (Angelin, 1878), TUG 1395-4, Ninase Member, Jaani Formation (Wenlock), Suuriku Cliff. Lateral outline. Plate designations: black, radial plate; ruled, inferradial plate; cross-ruled, radial plate; stippled, interradiial plates or anal plates; P, primanal; X, anal X plate; grey, openings into theca. Scale bars 1 mm.

makes it all the more surprising that this cosmopolitan crinoid was not reported from Estonian until Hints and Stukalina (1997). *Eucalyptocrinites* is known currently from the Wenlock and Pridoli of Estonia. Both the calyx and tegmen are very distinctive in this genus. *Eucalyptocrinites* is taphonomically robust whether the theca is preserved intact or separated into the calyx and tegmen. Many juveniles, as well as adults, are preserved. Unfortunately, most specimens are only preserved calyces, a portion of the arms with partition plates, a broken crown, or some broken combination.

Species distinctions within *Eucalyptocrinites* include variability in calyx shape; relative height of the basal circler; calyx, tegmen, and arm plate sculpturing (smooth, nodose, or other types of sculpturing); shape of partition plates; shape of the distal tegmen; spinosity of the partition plates; presence or absence of an anal tube; and spinosity or other sculpturing around the anal opening at the summit of the tegmen. The only other Silurian *Eucalyptocrinites* reported from Baltica are from the Wenlock through Ludlow of Gotland, Sweden.

On Gotland, Franzén (1983) recognized ten species, whereas Webster (2003) listed only nine. Based on the illustrations of Gotland specimens in Angelin (1878), *Eucalyptocrinites* can be divided into species with smooth or with variously sculptured calyx plates. Those with smooth calyx plates are of three types: (i) *E. plebejus* (Angelin, 1878), *E. regularis* (Hisinger, 1840), and *E. rigens* (Angelin, 1878) have smooth calyx plate sculpturing, low cone-shaped calyx, flat or convex base, basals not visible, and partition plates conspicuously widened; (ii) *E. minor* (Angelin, 1878) has smooth calyx plate sculpturing, low bowl-shaped calyx, very low convex base, basals visible, and partition plates conspicuously widened; and (iii) *E. ovatus* (Angelin, 1878) has smooth calyx plate sculpturing, low bowl-shaped calyx, very low convex base, basals not visible, and partition plates not conspicuously widened. In addition, some species from Gotland have distinctive calyx plate sculpturing, including *E. decoratus* (Angelin, 1878), *E. elegantissimus* (Angelin, 1878), *E. excellentissimus* (Angelin, 1878), and *E. speciosus* (Angelin, 1878).

Three species-level taxa of *Eucalyptocrinites* are now recognized from Estonia. One has distinctive calyx plate sculpturing, *Eucalyptocrinites tumidus* sp. nov., which is described below. Those with smooth plate sculpturing are difficult to evaluate and are referred to here as *Eucalyptocrinites* sp. 1 and *Eucalyptocrinites* sp. 2. Complete specimens are needed to evaluate all species-level characters; and, typically, only an isolated calyx or an isolated partition plate assembly is preserved. Furthermore, a wide size range exists among known specimens. Perhaps the most common preservational mode is for a calyx, all or partly visible, to be preserved upside-down on a bedding surface. If partially buried to preserve only the proximal-most calyx, it appears that the calyx shape has a lower height-to-width ratio than if the entire calyx was exposed.

The majority of known specimens have smooth calyx plates, and the majority of these are isolated calyces or tegmen. Thus, the majority of Estonian *Eucalyptocrinites* specimens are not preserved sufficiently well enough to identify beyond *Eucalyptocrinites* spp.

Eucalyptocrinites tumidus sp. nov.

Fig. 3A.

Etymology: From Latin *tumidus*, swollen; refers to the convex, swollen appearance of the calyx plates.

Holotype: GIT 405-243.

Type locality: Kaugatuma Cliff, Saaremaa Island, Estonia.

Type horizon: Middle Äigu Beds, Kaugatuma Formation, Pridoli, Late Silurian.

Material.—Holotype only.

Diagnosis.—*Eucalyptocrinites* with low, bowl-shaped calyx. Very convex calyx plates. Basal plates not visible in lateral view, completely hidden beneath the proximal columnal. Partition plates expand distally but only modestly; central groove along distal partition plates absent; flat-topped tegmen; anal tube absent. Distal arms do not extend above distal tegmen.

Description.—The calyx is relatively small for the genus and has a low bowl shape (Fig. 3A₁). The base of calyx is truncate with basal plates in a small basal concavity and hidden by the proximal column. The calyx plate sculpturing is nodose to very nodose, and sutures are broadly impressed (Fig. 3A₂). The basal circlet is hidden. The radial circlet is complete and approximately 12% of calyx height. The 5 radial plates are pentagonal and approximately 2.8 times wider than high. Normal interrays are in contact with the tegmen partition plates. The first interradyal plate is decagonal, higher than wide, and much larger than the radial plates or first primibrachials. The second range has two adjacent plates sutured to the interradyal tegmen partition plates. Each interradyal plate of the second range is approximately 2.3 times higher than wide. The posterior interradyal is indistinguishable from normal interrays (Fig. 3A₂). The first primibrachials are tetragonal, approximately 1.5 times wider than high, and smaller than radial plates and primaxils. The second secundibrachial is axillary in all rays, yielding four arms per ray. One fixed intrabrachial occurs dis-

tally with the partition plate above. The fixed intrabrachial is approximately 1.5 times higher than wide.

The tegmen is composed of ten partition plates that extend to the top of the tegmen. The tegmen is higher than the full height of the arms (Fig. 3A₁). Partition plates expand in width distally to less than twice the proximal width. The tegmen is flat topped (Fig. 3A₃) and formed primarily of partition plates, but the center of the distal tegmen is composed of two irregular circlets of five plates each. The anal opening is flush with the tegmen surface, and the anal tube is absent.

The 20 free arms are atomous, pinnulate; and approximately the first five tertibrachials are uniserial cuneate with remainder of the brachials biserial. Arms taper distally and do not extend beyond the flat top of the distal tegmen.

Proximal column circular, holomeric, heteromorphic, other details not known.

Discussion.—Because other Baltic species of *Eucalyptocrinites* have smooth or ridged calyx plate sculpturing, the very convex calyx plate sculpturing of *E. tumidus* is unique.

Measurements.—GIT 405-243: crown height, 28.1 (to top of tegmen); maximum crown width, 23.5; calyx height, 6.2; calyx width at distal-most calyx, 20.2; radial plate height, 1.8; radial plate width, 4.1.

Geographic and stratigraphic range.—Middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island, Estonia.

Eucalyptocrinites sp. 1

Fig. 3F.

Material.—TUG 1375-2, Janni Formation, Undva Cliff; TUG 1375-3, Janni Formation, Undva Cliff; TUT 1395-10, Ninance Member, Janni Formation, Liira Cliff; TUT, 1395-11, middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff. All are from Saaremaa Island.

Description.—The calyx is small to medium size for the genus. It has a low cone to bowl shape, and the base of calyx is convex with basals not visible in lateral view. Calyx plate sculpturing is smooth. The basal circlet is in a small basal concavity and is hidden by the proximal columnal. The radial circlet is 16–20% of the calyx height. The five radial plates are pentagonal. In smaller specimens the radial plate is 1.4 times wider than high, but in medium-sized specimens it is approximately as wide as high. Normal interrays are in contact with tegmen partition plates. The first interradyal plate is decagonal, higher than wide, somewhat larger than radial plate, and much larger than first primibrachial. The second range has two plates that are sutured to the interradyal tegmen partition plates. The posterior interradyal is indistinguishable from normal interrays. The first primibrachials are tetragonal, approximately 1.3 times wider than high, smaller than radial plates, and approximately the same size as the primaxil. The second secundibrachial is axillary in all rays. There are four arms per ray. One fixed intrabrachial is sutured distally with a partition plate, and in smaller specimens the fixed intrabrachial is approximately two times higher than wide.

In the smallest specimen (TUG 1375-2), the tegmen is comprised of ten partition plates that extend to base of the anal tube and rise to the full height of the arms. In the smallest specimen (TUG 1375-2) the distal partition plates expand slightly and curve inward toward the anal tube and the distal tegmen is narrow convex. A short anal tube is framed by two five-plate circlets (the distal tegmen may be different in the larger specimens assigned to this taxon). The largest specimen (TUG 1395-11) has partition plates of equal width along the entire length (Fig. 3F).

Free arms are 20 in number, atomous, pinnulate, cuneate uniserial through first six primibrachials, and thereafter biserial. Arms reach to distal extent of partition plates.

The proximal column is circular, heteromorphic, but other details are unknown.

Discussion.—Four specimens with both smooth calyx plate sculpturing and partition plates of uniform width throughout or slightly expanded do not correspond to any Angelin (1878: pl. 5: 1) illustration. The only Gotland species with these characters is *E. ovatus*, which has a much flatter base than the Estonian specimens. However, only one juvenile and three partial adult specimens are known, so description of a new species is considered premature. Therefore, this taxon is referred to herein as *Eucalyptocrinites* sp. 1.

The most complete specimen is the smallest (TUG 1375-2), and it is not clear what aspects of this specimen reflect only juvenile characters. This specimen is a very slightly compressed, nearly complete crown with arms attached. Of intermediate size are TUG 1395-10 and TUG 1375-3. Specimen TUG 1395-10 is a crushed and mostly buried crown with a column mostly buried, calyx crushed with missing plates, and a few arms and partition plates partially visible. Specimen TUG 1375-3 is nearly one half of a crushed and fractured crown. The largest specimen (TUG 1395-11) is one half of a crushed crown with the lower half of the calyx missing.

As noted above, without a more complete understanding of the morphology of this smooth-sculptured form from Estonia and definitive diagnoses of *Eucalyptocrinites* species from Gotland, *Eucalyptocrinites* sp. 1 cannot be described as a new nominal taxon, if appropriate. Below we assign the majority of *Eucalyptocrinites* specimens to *Eucalyptocrinites* sp.; however, we suspect that most of the Estonian specimens may be *Eucalyptocrinites* sp. 1, potentially making this the most abundant taxon from the Silurian of Estonia, except perhaps locally, such as at Kaugatuma Cliff where *Enallocrinus* holdfasts are very abundant.

Measurements.—TUG 1375-2: crown height, 22.0; calyx width, 13.7*; calyx height, 8.0. TUG 1375-3: crown height, 39.8*; calyx width, 21.0*; calyx height, 11.3. TUG 1395-11: crown height, 40.0* (at least one half of calyx and distal tegmen missing).

Geographic and stratigraphic range.—In older collections, this taxon is known from the Jaani Formation (Ninase Member), Wenlock, Silurian, at Undva Cliff. New collections from the present study are from the Ninase Member of the

Jaani Formation at Liiva Cliff and the middle Äigu Beds of the Kaugatuma Formation at Kaugatuma Cliff. All are from the Saaremaa Island, Estonia.

Eucalyptocrinites sp. 2

Fig. 3D.

Material.—TUG 1395-12, Mustjala Member, Janni Formation, Suuriku Cliff; TUG 1395-13, Ninase Member, Janni Formation, Panga Cliff; TUG 1395-14, Ninase Member, Janni Formation, Suuriku Cliff; TUG 1395-15 and TUG 1395-16, Ninase Member, Janni Formation, Undva Cliff. All are from Saaremaa Island.

Description.—The calyx is large for the genus. It is probably low cone shaped, but the base of the calyx and plating from basals through radials are unknown. The normal interrays are in contact with the tegmen partition plates. The first interradial is decagonal, higher than wide. The second range of the normal interray has two plates that are sutured to the interradial tegmen partition plates. Fixed primibrachials are not known. The second secundibrachials are axillary as known, yielding four arms per ray. One fixed intrabrachial plate is sutured distally with the partition plate. The tegmen partition plates extend to the base of anal tube, are gently convex on upper tegmen surface, extend to full height of crown, and are higher than the arms. Two circlets of plates frame the anal opening, with the tube probably absent (Fig. 3D₁). Distal partition plates expanded to nearly four times proximal width with broad, deep longitudinal groove (Fig. 3D₂).

Free arms atomous, pinnulate. First three or four brachials are cuneate uniserial, then biserial distally. Arms do not reach the full extent of the partition plates.

Column unknown.

Discussion.—Three very large and one smaller, very incomplete specimens have significant distal widening of the partition plates. Further, the wide distal portion of the partition plates have a broad groove along the center. Calyx sculpturing is inferred to be smooth based on two specimens. Specimen TUG 1395-16 has the distinctive partition plates, but the calyx is badly beach-worn. It is possible that the inferred sculpturing of this specimen is erroneous. Specimen TUG 1395-15 has smooth plate sculpturing, and the distal partition plates are not visible. However, the medial portion of the partition plates are expanding consistent with this morphology. Based on illustrations in Angelin (1878), this morphology could match one of the following species: *E. minor* (Angelin, 1878), *E. plebejus* (Angelin, 1878), *E. regularis* (Hisinger, 1840), or *E. rigens* (Angelin, 1878). The details of calyx shape are necessary to distinguish among these species, so this taxon is also left in open nomenclature.

Measurements.—TUG 1395-16: crown height, 60.0* (proximal calyx missing); calyx width, 35.0*. TUG 1395-12: arm-tegmen complex width, 30.5.

Geographic and stratigraphic range.—All occurrences of this taxon are from Saaremaa Island, Estonia, with new collections from the Ninase Member of the Jaani Formation at

Suuriku Cliff and the Ninase Member of the Jaani Formation at Panga Cliff, Suuriku Cliff, and Undva Cliff. All of these occurrences are Wenlock, Silurian.

Eucalyptocrinites spp.

Fig. 3C.

Material.—Numerous examples of *Eucalyptocrinites* sp. occur, including TUG 860-1736, TUG 860-1737, TUT 405-238 to GIT 450-240, and GIT 1395-17 to TUG 1395-37 from the Ninase Member, Jaani Formation, Wenlock, Silurian at Suuriku Cliff and Undva Cliff, and from the Kaugatuma Formation at Kaugatuma Cliff.

Discussion.—As discussed above, specimens assigned to *Eucalyptocrinites* sp. are so assigned because most lack preservation of both calyx plate sculpturing and the shape of the partition plates are known (Fig. 3C). Unfortunately, these are the majority of *Eucalyptocrinites* specimens known. As mentioned above, we suspect that the majority of specimens assigned to *Eucalyptocrinites* sp. may belong to *Eucalyptocrinites* sp. 1.

Genus *Calliocrinus* d'Orbigny, 1850

Type species: *Eugeniocrinites? costus* Hisinger, 1837; Gotland, Sweden; Wenlock, Silurian.

Calliocrinus sedgwickianus Angelin, 1878

Fig. 3B.

1878 *Calliocrinus sedgwickianus* sp. nov. [sic.]; Angelin 1878: 15, pl. 1: 5.

1943 *Calliocrinus sedgwickianus* Angelin, 1878; Bassler and Moodey 1943: 349.

2003 *Calliocrinus sedgwickianus* Angelin, 1878; Webster 2003.

Material.—A single specimen (TUG 1395-8) is known from Estonia.

Discussion.—Only the proximal portion of one specimen of *Calliocrinus sedgwickianus* Angelin, 1878 is recognized from Estonia. However, this specimen had long, robust spines (now broken) projecting outward from both the basal and radial plates (Fig. 3B). This resulted in a distinctive pattern that characterizes only a few species of this genus. Although this specimen is heavily bored with *Oichnus* Bromley, 1981, it is evident that a single ridge projects from the base of the basal plates toward the column attachment, which is characteristic of *C. sedgwickianus* (see Angelin 1878: pl. 1: 3).

Geographic and stratigraphic range.—This taxon was identified from the Middle Äigu Beds, Kaugatuma Formation at Kaugatuma Cliff, Saaremaa, Estonia.

Calliocrinus sp.

Fig. 3G.

Material.—TUG 1395-5 and TUG 1395-6 are examples of this plate with a bifurcating spine from the Ninase Member of the Jaani Formation, Wenlock, Silurian at Suuriku Cliff, Saaremaa, Estonia.

Discussion.—Isolated, long (approximately 25 mm) and wide (approximately 35 mm) bifurcating spine plates (Fig. 3G) oc-

cur at localities in the Ninase Member of the Jaani Formation. These are assigned herein to the genus *Calliocrinus* d'Orbigny, 1850, which is a eucalyptocrinitid in which many species have long, spinose plates. Depending on the species, taxa from the Wenlock and Ludlow of the Isle of Gotland (Angelin 1878) may have prominent spines from radial plates, first interrational plates, proximal tegmen plates, or as a "parasol" on the distal-most plates of the anal tube. Angelin (1878: pl. 28: 15) only illustrated a single species, *C. purchisonianus* Angelin, 1878 with bifurcating plates; although broadly similar, the new Estonian material has a much more obtuse angle of spine divergence compared to the Gotland specimen. Thus, the Estonian spine plates are retained in *Calliocrinus* sp. until more complete specimens become available.

Superfamily Carpcrinoidea de Koninck and Le Hon, 1854

Family Carpcrinidae de Koninck and Le Hon, 1854

Genus *Desmidocrinus* Angelin, 1878

Type species: *Desmidocrinus pentadactylus* Angelin, 1878; Gotland, Sweden; Wenlock, Silurian.

Desmidocrinus laevigatus sp. nov.

Fig. 5G, H.

Etymology: From Latin *laevigatus*, smooth; in reference to the smooth plate sculpturing.

Type material: Holotype, TUG 1395-1; paratype, TUG 1395-2.

Type locality: Kaugatuma Cliff, Saaremaa Island, Estonia.

Type horizon: Middle Äigu Beds, Kaugatuma Formation, Pridoli, Late Silurian.

Material.—ATUG 1395-1 (holotype), TUG 1395-2 (paratype) from middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island.

Diagnosis.—*Desmidocrinus* with bowl- to globe-shaped calyx. Smooth plate sculpturing. One fixed intrabrachial between primibrachials. Normal interrays plating 1-2. Ten free arms, free arms branch, and biserial brachials.

Description.—The calyx is medium in size for the genus and has a low bowl to globe shape (Fig. 5G₃). Arms are not grouped. The calyx plates are convex with smooth sculpturing, and plate sutures are slightly impressed (Fig. 5H). The basal circling is visible in side view (Fig. 5G₃) and approximately 18% of calyx height. Three basal plates occur and are equal in size. The radial circling averages 32% of calyx height and is interrupted in the posterior. The five radial plates are hexagonal (Fig. 5G₁) and approximately 1.4 times wider than high. The normal interrays are in contact with the tegmen. The first interrational plate is octagonal, approximately 1.1 times wider than high, smaller than radial plates, and much larger than first primibrachials. The first interrational plate extends from shoulders of radial plates to the lower part of the first secundibrachial. Only one other interrational plate fixed in calyx resulting in 1-1 plating. The primanal is hexagonal, approximately equal in height and width, same size as radial plates, and interrupts the radial circling. Plating in the CD

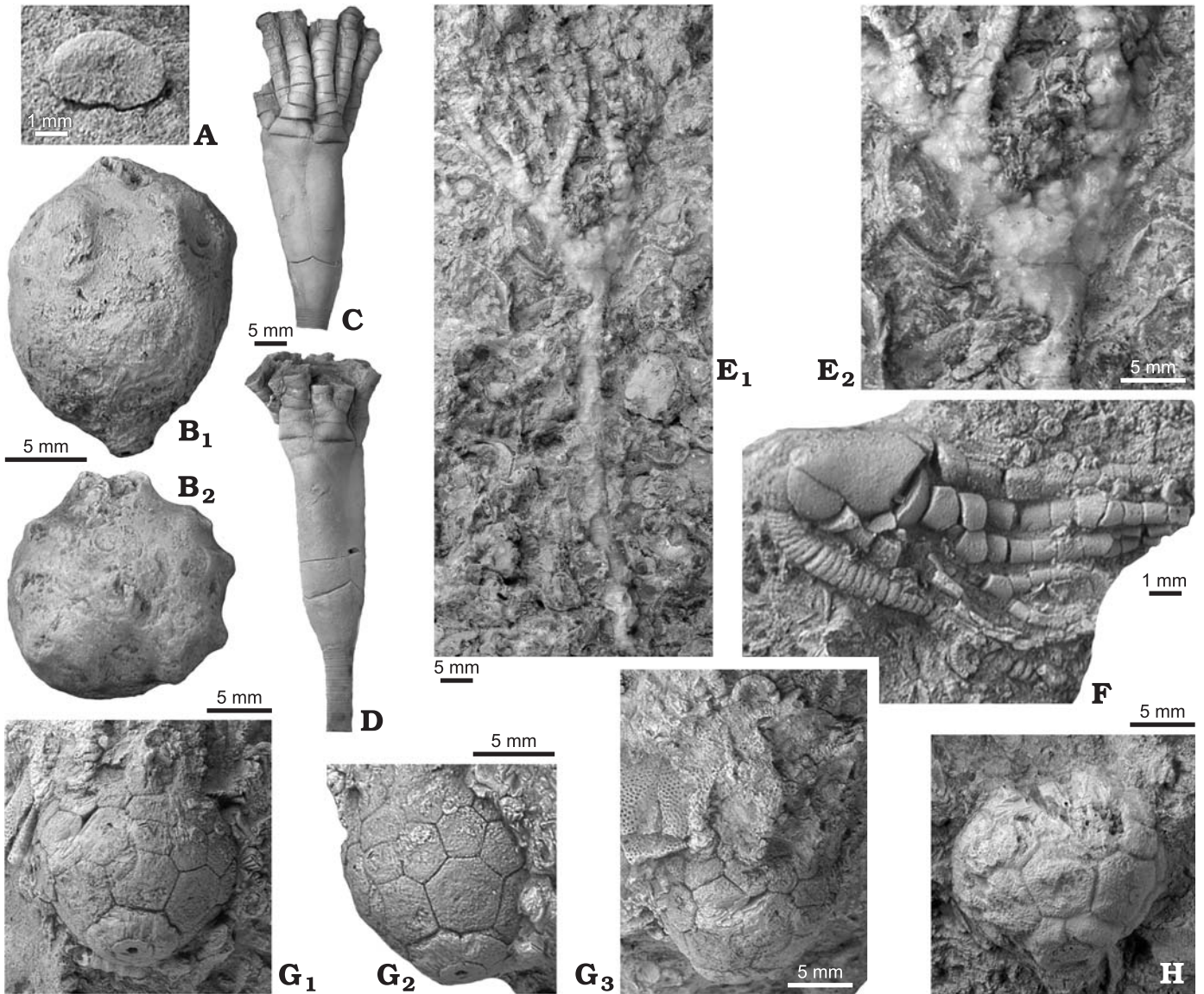


Fig. 5. Camerate, disparid, and flexible crinoids from the Silurian of Estonia. **A.** *Myelodactylus?* sp., TUG 1395-7, Ohesaare Formation (Pridoli), Ohesaare Cliff. Articular facet of columnal. **B.** *Saaremaacrinus estoniensis* gen. et sp. nov., holotype, TUG 1395-3, middle Äigu Beds, Kaugatuma Formation (Pridoli), Kaugatuma Cliff. **B₁**, lateral view of theca, interpretation of plates in Fig. 4; **B₂**, tegmen view of theca. **C, D.** *Cicerocrinus osiliensis* (Jaekel, 1900), Ohesaare Formation (Pridoli), Ohesaare Cliff. **C.** TUG 1376-1. C-ray lateral view of calyx. **D.** GIT 405-242. C-ray lateral view of calyx. **E.** *Protaxocrinus salteri?* (Angelin, 1878), TUG 1395-4, Ninase Member, Jaani Formation (Wenlock), Suuriku Cliff. **E₁**, CD interray view of crown and proximal column; **E₂**, CD interray view of calyx, proximal arms and column, note badly beach-worn preservation. **F.** *Caleocrinus balticensis* sp. nov., GIT 405-12, Juuru Stage (Llandovery), Heltermaa. D-Ray lateral view of crown. **G, H.** *Desmidocrinus laevigatus* sp. nov., middle Äigu Beds, Kaugatuma Formation (Pridoli), Kaugatuma Cliff. **G.** TUG 1395-1, holotype. **G₁**, oblique D-ray lateral view of calyx; **G₂**, CD-interray lateral view of calyx; **G₃**, D-ray lateral view of incomplete crown. **H.** TUG 1395-2, paratype. D-ray lateral view of calyx.

interray is P-3-3 (Fig. 5G₂), and an anitaxis of plates without anitaxial ridge. The CD interray is in contact with the tegmen. The first primibrachial is tetragonal, approximately 1.5 times wider than high, much smaller than radial plates, and somewhat smaller than primaxil. The second primibrachial is axillary and pentagonal to heptagonal in shape. The first secundibrachial is fixed and is the distal-most fixed brachial. Adjacent first secundibrachials within a ray are in contact medially. A single intrabrachial plate is in the center of each ray and sutured on upper shoulder of first secundibrachials. Tegmen unknown.

The 10 free arms branch (Fig. 5G₃). The first few free brachials are uniserial and the remainder are biserial. Brachials are aborally very convex. Arms branch on approximately ninth free brachial. Pinnules and other aspects of free arms are unknown.

The most proximal columnal is circular and holomeric with a lumen pentalobate. Other aspects of the column are unknown.

Discussion.—Previously, only five species were recognized in *Desmidocrinus*, including *D. heterodactylus* Angelin,

Table 2. Diagnostic characters among the species of *Desmidocrinus*.

	Calyx shape	Plate sculpturing	Fixed intrabrachial between second primibrachials	Proximal normal interray plating	Free arm number	Free arm branching	Brachials
<i>Desmidocrinus dubius</i>	bowl to globe	smooth	present	[not known]	10	present	uniserial
<i>Desmidocrinus heterodactylus</i>	cone	pitted	absent	1–2	15	absent	uniserial
<i>Desmidocrinus macrodactylus</i>	cone	smooth	absent	1–2	15	absent	uniserial
<i>Desmidocrinus pentadactylus</i>	cone to bowl	pitted	present	1–2	20–30	present	uniserial
<i>Desmidocrinus tridactylus</i>	cone	coarse stellate	absent	1–1	15	absent	uniserial
<i>Desmidocrinus laevigatus</i> sp. nov.	bowl to globe	smooth	present	1–1	10	present	biserial

1878; *D. macrodactylus* Angelin, 1878; *D. pentadactylus* Angelin, 1878; and *D. tridactylus* Angelin, 1878 from the Wenlock Slite Group of Gotland, Sweden. *Desmidocrinus pentadactylus* also occurs in the Ludlow Eke Formation (Franzén 1983). A single North American species, *D. dubius* Springer, 1926 is recognized from the Laurel Limestone of Indiana, USA (Wenlock).

Therefore, *Desmidocrinus laevigatus* sp. nov., from the Pridoli of Saaremaa Island, is the youngest species recognized in this genus. It is the only *Desmidocrinus* with biserial arms and *D. laevigatus* and *D. dubius* are the only *Desmidocrinus* with 10 free arms. *Desmidocrinus laevigatus* is distinguished from its congeners as listed in Table 2.

Measurements.—TUG 1395-1, holotype: calyx height, 9.2; calyx width, 15.1; basal circlet width, 1.4; radial plate height, 3.8; radial plate width, 5.3; first primibrachial height, 2.2; first primibrachial width, 3.1; primanal height, 4.7; primanal width, 4.7.

Geographic and stratigraphic range.—This new species is only known from the middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island.

Subclass Cladida Moore and Laudon, 1943

Order Cyathocrinidida Bather, 1899

Family Crotalocrinitidae Bassler, 1938

Genus *Crotalocrinites* Austin and Austin, 1843

Type species: *Encrinites verucosus* Schlotheim, 1820; Gotland, Sweden; Wenlock, Silurian.

Discussion.—*Crotalocrinites rugosus* was reported from Estonia by Hints and Stukalina (1997); however, to our knowledge, no specimens can be unequivocally assigned to *Crotalocrinites*. Similar to Anticosti Island, Quebec, Canada (Ausich and Copper 2010), we suspect that isolated columnals and pluricolumnals with a wide outside diameter and a wide lumen have been assumed to belong to *Crotalocrinites*. However, this cannot be verified. Instead, Franzén-Bengtson (1983: 292, 296) noted that *Abacocrinus*, *Clonocrinus*, *Crotalocrinites*, and *Enallocrinus* from Gotland had either very wide columnals, wide lumens, or both. However, Franzén-Bengtson (1983: 298) was unable to identify any of these four crinoids based solely on columns or pluricolumnals.

Genus *Enallocrinus* d'Orbigny, 1850

Type species: *Apiocrinites scriptus* Hisinger, 1828; Gotland, Sweden; Wenlock, Silurian.

Enallocrinus sp.

Fig. 6B, C.

Material.—The best examples of this holdfast remain in situ at Kaugatuma Cliff. Specimens deposited in a museum include TUG 1395-38 and TUG 1395-39.

Discussion.—Donovan et al. (2007) identified a distinctive Gotland crinoid holdfast as “probably *Enallocrinus*” (Donovan et al. 2007: fig. 1). We follow this identification, herein.

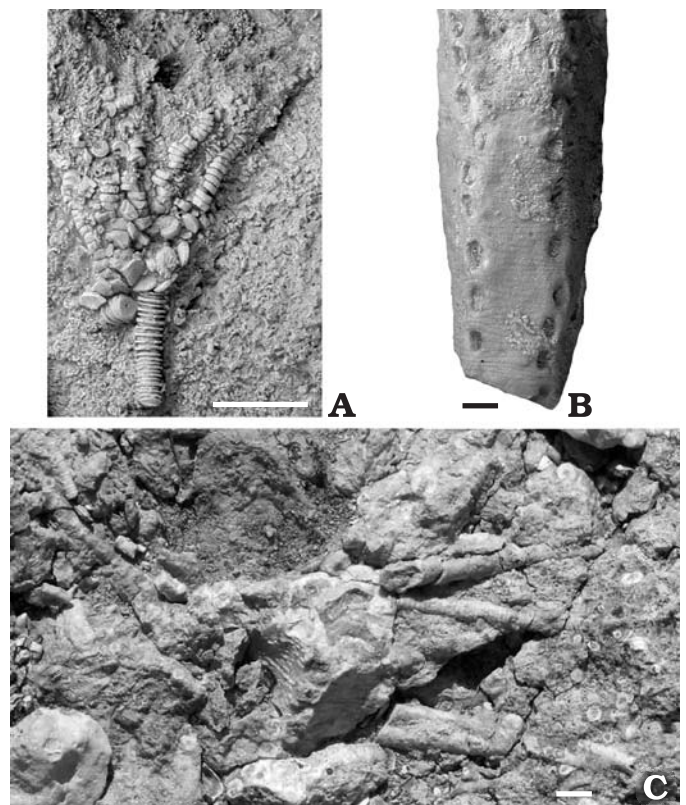


Fig. 6. Crinoids from the Silurian of Estonia, middle Äigu Beds, Kaugatuma Formation (Pridoli, Silurian), Kaugatuma Cliff. **A.** Cladida indet., TUG 1395-9, lateral view of badly disarticulated calyx. **B.** *Enallocrinus* sp. holdfast, TUG 1395-39, column of *Enallocrinus* holdfasts lacking the rhizoids. **C.** Field photograph of an uncollected in situ *Enallocrinus* holdfast. Note wide, pentalobate lumen and long radices of holdfast. Scale bars 10 mm.

This is a striking dendritic radice holdfast (sensu Brett 1981) that can grow to a quite large size. Although incomplete, the largest *Enallocrinus* holdfast has a total diameter in excess of 200 mm, and the largest columnal diameter in the holdfast region exceeds 40 mm.

As discussed in Donovan et al. (2007) for Gotland material (Wenlock), numerous holdfasts may occur along a single horizon with variable sizes (most probably representing multiple generations of settlement). On Saaremaa, horizons with numerous holdfasts occur in the Kaugatuma Formation (Pridoli). Franzén (1977: fig. 2D) regarded this holdfast as a cirriferous holdfast, and in side view it was recognized as a “holdfast with stout cirri” in Franzén-Bengtson (1983: fig. 5). However, note that these are now recognized as radices rather than cirri (Donovan 1993; Donovan and Ewin 2010).

Geographic and stratigraphic range.—On Gotland, Sweden, this holdfast is reported from the Hemse Beds (Gorstian, lower Ludlow) (Franzén 1977) and the lower Klinteberg Formation (Homerian, Wenlock) (Donovan et al. 2007). In Estonia, this *Enallocrinus* holdfast is only known from the middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa, where innumerable holdfasts occur.

Cladida indet.

Fig. 6A.

Material.—TUG 1395-9 from the middle Äigu Beds, Kaugatuma Formation (Pridoli) from Kaugatuma Cliff, Saaremaa Island, Estonia.

Discussion.—An unknown cladid is represented by specimen TUG 1395-9 with column, badly crushed calyx, and partially disarticulated arms. The calyx is much too disarticulated to allow any consideration of its identity (Fig. 6A). The arms are very convex, composed of uniserial brachials, and no pinnules, similar to Silurian cladids and perhaps some flexibles. In contrast, the column is circular, holomeric, heteromorphic with very convex latera on nodals and on the single priminternodals in the mesistele. This column morphology is more typical of camerate crinoids. However, based on the morphology of the arms, this specimen is assigned herein to *Cladida* indet.

Subclass Flexibilia von Zittel, 1895

Order Taxocrinida Springer, 1913

Superfamily Taxocrinoidea Angelin, 1878

Family Taxocrinidae Angelin, 1878

Genus *Protaxocrinus* Springer, 1906

Type species: *Taxocrinus ovalis* Angelin, 1878; by subsequent designation; Gotland, Sweden; Wenlock, Silurian.

Protaxocrinus salteri? (Angelin, 1878)

Figs. 4C, 5E.

Material.—A single specimen (TUG 1395-4) from the Ninase Member, Jaani Formation (Wenlock) at Suuriku Cliff, Saaremaa Island, Estonia is questionably assigned to this taxon.

Description.—The crown is large and expanding (Fig. 5E₁). The aboral cup has a low cone shape, the width to height ratio is approximately 1.6 (Fig. 5E₂), and external plate sculpturing is not preserved. Infrabasal plates are visible in side view, and the infrabasal cirlet is approximately 13% of aboral cup height. The CD basal is the only basal plate fully known; and it is hexagonal, wider than high, and smaller than radial plates. Parts of the C and D radial plates are visible, and they are probably hexagonal and are wider than high. Radial facets are plenary and straight. Three anal plates are in aboral cup (Fig. 4C). The radianal is immediately below the full width of the C radial and smaller than the C radial plate. The anal X is sutured below to CD basal and radianal and sutured laterally to the C and D radials. This fills the entire gap between the C and D radials. One additional anal plate is immediately above the anal X and is sutured laterally with the C radial.

Arms are completely separate above the radial plates and branch. The third primibrachial is axillary on the D-ray arm, and the second primibrachial is axillary on the C-ray arm. The first two or first two and one-half secundibrachials in a ray are sutured medially to the adjacent secundibrachial. On the D-ray arm, the third secundibrachial is axillary and the eighth tertibrachial is axillary. Arm divisions are slightly heterotomous. Brachials are uniserial rectangular, wider than high, with straight sutures. Pinnules are absent.

The column is xenomorphic. The proxistele narrows distally, and proxistele columnals range from approximately 6 to 15 times wider than high. Mesistele columnals are approximately 5 times wider than high.

Discussion.—TUG 1395-4 is an unusual crinoid that is difficult to place systematically. With the radianal occupying the full width beneath the C radial plate, this specimen is most similar to *Protaxocrinus*, and it probably represents a new species with a distinctive CD basal plate. However, the holotype and only known specimen is severely beach-worn, so that plate sculpturing is not preserved and other aspects of its morphology must be inferred with some question.

The exposed portion of the specimen clearly has a column with a proxistele, a dicyclic aboral cup, and a posterior interray, which are all very similar to Silurian *Protaxocrinus*. Because this specimen is so deeply weathered, it is impossible to verify whether the unusual anal plate arrangement is portrayed as it would be on a well-preserved specimen. At least one more, well-preserved specimen is needed to confidently describe this taxon.

The unique aspect of this specimen, which needs verification, is that the distal suture of the CD basal plate does not have an indentation to hold the anal X adjacent to the C radial plate and radianal. Instead, the anal X occupies the full width between the C and D radials (Fig. 4C). If this Estonian specimen is a new species, it would be characterized by this unusual plating in the posterior interray.

Protaxocrinus occurs on Gotland. Franzén-Bengtson (1983) listed four species: *P. distensis* (Angelin, 1878), *P. interbrachiatus* (Angelin, 1878), *P. ovalis* (Angelin, 1878),

and *P. salteri* (Angelin, 1878). *Protaxocrinus distensis* was unlocalized. *Protaxocrinus salteri* occurs in the Höglkint and Slite formations, both Wenlock; *P. interbrachiatus* is only from the Wenlockian Slite Formation; and *P. ovalis* is from the Slite and Eke formations, Wenlock and Ludlow, respectively.

TUG 1395-4 is questionably placed in *P. salteri* because one specimen illustrated by Angelin (1878: pl. 22: 1) appears to have a CD interray quite similar to the Estonian specimen. However, Angelin's (1878) illustration is not definitive, especially because a certain artistic license was commonly employed on these illustrations.

Subclass Disparida Moore and Laudon, 1943

Order Calceocrinida Ausich, 1998

Family Calceocrinidae Meek and Worthen, 1869

Genus *Calceocrinus* Hall, 1852

Type species: Cheirocrinus chrysalis Hall, 1860; Lockport, New York, USA; Wenlock, Silurian.

Geographic and stratigraphic range.—Middle Ordovician (Caradoc) to Late Silurian (Ludlow); Québec, Ontario, Oklahoma, Minnesota, Missouri, Iowa, Illinois, Indiana, Ohio, Tennessee, New York, England, Wales, Czech Republic, and Estonia.

Calceocrinus balticensis sp. nov.

Figs. 4B, 5F.

Etymology: Named in recognition of its occurrence in the Baltics.

Holotype: GIT 405-212.

Type locality: Heltermaa on Hiiumaa, Estonia.

Type horizon: Juuru Stage, Llandovery, Silurian.

Material.—Holotype only.

Diagnosis.—*Calceocrinus* with adorally-aborally compressed aboral cup, smooth aboral plate sculpturing. Trapezoidal radial plate cirlet, radial cirlet higher than wide. (Condition of ligament pit unknown.) E arm unbranched through primibrachial 6. Main axil brachials not constricted. (Condition of anal tube unknown.)

Description.—The crown is recumbent on the column (Fig. 5F). The aboral cup is medium in size, adorally-aborally compressed, and with smooth plate sculpturing. The four basal plates are all in the column concavity and are all part of distal margin of basal cirlet. The radial cirlet is widest proximally and trapezoidal in shape; (ligament pit condition unknown). A and D radials occupy majority of radial cirlet. The E-ray inferradial and superradial are inferred to have short sutural contact. The E superradial is triangular; the E inferradial is narrow, elongate; and the E superradial occupies 100% of the distal aboral cup margin. The distal facet of the D radial supports a lateral arm. The proximal facet articulates with the C inferradial and superradial (presumably analogous relationship of A radial and B inferradial). Anal plates are wider than high, and the anal sac is slender (Fig. 4B).

Only the D and E arms are visible; the A-ray arm is con-

cealed. Arms are slender with aborally convex brachials. The main axil has nonaxillary brachials, divisions are heterotomous, and the first brachial is wedge-shaped. The E-ray arm is unbranched through six brachials, and it is poorly preserved but may branch higher. E-ray brachials are wider than high proximally. The main axils are well developed. Three axillaries are present, each one separated by one nonaxillary brachial (Fig. 4B). The lateral arms have few heterotomous divisions. The primaxil arm bifurcates at least through the axillary alphabrachial, and four nonaxillary brachials occur below the alphabrachial. One division is preserved on the betaaxil arm with four nonaxillary brachials before the bifurcation. The tertaxil arm and the omega ramule are slender and unbranched as known.

The column is homeomorphic, although near the aboral cup the columnals are very thin (Fig. 5F). Beneath the aboral cup columnals are approximately five times wider than high and wedge shaped. More distal columnals are parallel sided with more convex latera, and columnals are approximately less than 2.5 times wider than high. A pentalobate lumen occupies the central 30% of the column diameter, but details of columnal articular facets are unknown.

Discussion.—The calyx and proximal arms of *Calceocrinus balticensis* sp. nov. are reasonably well preserved on a bedding surface with only the D-ray side visible. Late Ordovician and Llandovery species of *Calceocrinus* were diagnosed in Ausich and Copper (2010). *Calceocrinus balticensis* is the sixth known Llandovery species of *Calceocrinus*, including *C. incertus* Foerste, 1936; *C. ontario* (Springer, 1919); *C. pustulosus* Johnson in Brower, 1966; *C. tridactylus* Eckert, 1984; *C. turnbulli* Donovan, 1993; and this new species from Estonia. *Calceocrinus turnbulli* is from southwestern Wales, and the other previously known species are from North America. Thus, *C. balticensis* is the first Llandovery *Calceocrinus* from Baltica. With smooth aboral cup sculpturing, *C. balticensis* is most similar to *C. insertus*; however, it is distinct because the aboral cup shape is rectangular in *C. insertus* and trapezoidal in *C. balticensis*. Both *C. pustulosus* and *C. turnbulli* have a trapezoidal aboral cup shape.

Measurements.—GIT 405-212: preserved crown height, 13.0*; calyx height, 4.5; calyx width, 3.0; calyx depth, 4.1; preserved columnal height, 11.1*.

Geographic and stratigraphic range.—This new species is only known from the Juuru Stage from Heltermaa, Hiiumaa Island.

Order Pisocrinida Ausich and Copper, 2010

Family Pisocrinidae Angelin, 1878

Discussion.—The only previous modern treatment of crinoids from Estonia was by Rozhnov (1981) and Rozhnov et al. (1989), who described Silurian pisocrinids. They studied both *Cicerocrinus* from Pridoli outcrops on Saaremaa Island and *Pisocrinus* from cores drilled throughout Estonia, Latvia, and Lithuania, and the reader is referred to these papers for details of the locality and position within core.

Subfamily Pisocrininae Angelin, 1878

Genus *Pisocrinus* de Koninck, 1858

Type species: Pisocrinus pilula de Koninck, 1858; by monotypy; Dudley, England; Wenlock, Silurian.

Subgenus *Pisocrinus (Pisocrinus)* Rozhnov, 1981

Type species: Pisocrinus pilula de Koninck, 1858; Dudley, England; Wenlock, Silurian.

Pisocrinus (Pisocrinus) pilula de Koninck, 1858

Material.—GIT 240-16, GIT 240-17, GIT 240-26, GIT 240-29, GIT 240-37, and GIT 240-38 from the Jaagarahu Formation, Ikla Core; GIT 240-18 from the Paprenjai Formation, Kakvaruja Core; GIT 240-23 and GIT 240-27 from the Ohesaare Core; GIT 240-25, GIT 240-30, GIT 240-33, GIT 240-34, GIT 240-35, and GIT 240-36 from the Kalvariija Core; GIT 240-31 from the Häädemeete 172 Core (see Rozhnov and Männil in Rozhnov et al. 1989).

Discussion.—*Pisocrinus (Pisocrinus) pilula* is a well-known and geographically widespread pisocrinid and the type species for *Pisocrinus*. Rozhnov and Männil in Rozhnov et al. (1989) reported it from the following cores: Häädemeete 172, Ikla, Kalvariija (Lithuania), and Ohesaare. In Estonia, it occurs exclusively in the Jaagarahu Formation and in Lithuania in the Paprienis Formation (Sheinwoodian). For a complete synonymy and discussion for this species, see Donovan et al. (2009).

Geographic and stratigraphic range.—This taxon is reported from Wenlock through Ludlow strata from Asia, Czech Republic, Estonia, Lithuania, Poland, Russia, Sweden (Gotland), and the United Kingdom. In Estonia, it is in the Jaagarahu Formation.

Pisocrinus (Pisocrinus) trialobus Rozhnov and Männil in Rozhnov et al., 1989

1989 *Pisocrinus (Pisocrinus) trialobus* sp. nov. Rozhnov and Männil in Rozhnov et al. 1989: 75, pl. 1: 2.

1993 *Pisocrinus (Pisocrinus) trialobus* Rozhnov and Männil in Rozhnov et al., 1989 [sic.]; Webster 1993: 92.

2003 *Pisocrinus (Pisocrinus) trialobus* Rozhnov and Männil in Rozhnov et al., 1989; Webster 2003.

Material.—GIT 240-1 (holotype), GIT 240-2, GIT 240-3, and GIT 240-54 from the the Jaagarahu Formation, Ikla Core (see Rozhnov and Männil in Rozhnov et al. 1989).

Discussion.—Rozhnov and Männil in Rozhnov et al. (1989) reported this taxon from the Ikla core in the Jaagarahu Formation.

Geographic and stratigraphic range.—This taxon is known exclusively from the Wenlock Jaagarahu Formation in the subsurface of Estonia.

Subgenus *Pisocrinus (Granulosocrinus)* Rozhnov, 1981

Type species: Pisocrinus granulatus Rowley, 1904; St. Genevieve County, Missouri, USA; Ludlow, Silurian.

Pisocrinus (Granulosocrinus) lanceatus Rozhnov, 1981

1981 *Pisocrinus (Granulosocrinus) lanceatus* sp. nov. Rozhnov, 1981: 74, pl. 16: 6–7; fig. 15o.

1989 *Pisocrinus (Granulosocrinus) lanceatus* Rozhnov, 1981; Rozhnov and Männil in Rozhnov et al. 1989: 79, pl. 1: 3–4.

1993 *Pisocrinus (Granulosocrinus) lanceatus* Rozhnov 1981; Webster 1993: 92.

2003 *Pisocrinus (Granulosocrinus) lanceatus* Rozhnov 1981; Webster 2003.

Material.—GIT 240-12 (holotype) and GIT 240-13 from the Jaagarahu Formation, Ohesaare Core; GIT 240-14 and GIT 240-51 from the Jaagarahu Formation, Kalvariija (see Rozhnov and Männil in Rozhnov et al. 1989).

Discussion.—Rozhnov and Männil in Rozhnov et al. (1989) reported this taxon from the Kalvariija (Lithuania) and Ohesaare cores, where it was collected exclusively from the Jaagarahu Formation.

Geographic and stratigraphic range.—This taxon is known exclusively from the Wenlock Jaagarahu Stage, Jamaja Formation in the subsurface of Estonia and Lithuania.

Pisocrinus (Granulosocrinus) sp.

Material.—GIT 240-19 from Ruhnu 500 Core and GIT 240-20 from Kalariija Core (see Rozhnov and Männil in Rozhnov et al. 1989).

Discussion.—Specimens of *Pisocrinus (Granulosocrinus)* that were not identifiable to species were isolated from the Jaani Formation in the Ruhnu core.

Geographic and stratigraphic range.—This taxon is known exclusively from the Wenlock Jaani Formation in the subsurface of Estonia. Webster (2003) also lists this crinoid from the Jaagarahu Stage, Jamaja Formation.

Subgenus *Pisocrinus (Pocillocrinus)* Rozhnov, 1981

Type species: Pisocrinus pocillum Angelin, 1878; Gotland, Sweden; Wenlock, Silurian.

Pisocrinus (Pocillocrinus) rubeli Rozhnov and Männil in Rozhnov et al., 1989

1989 *Pisocrinus (Pocillocrinus) rubeli* sp. nov. Rozhnov and Männil in Rozhnov et al. 1989: 78, pl. 1: 5–7.

1993 *Pisocrinus (Granulosocrinus) lanceatus* Rozhnov 1981; Webster 1993: 92.

2003 *Pisocrinus (Granulosocrinus) lanceatus* Rozhnov 1981; Webster 2003.

Material.—GIT 240-4 (holotype), GIT 240-5, GIT 240-6, GIT 240-7, GIT 240-8, GIT 240-9, GIT 240-11, and GIT 240-32 from the Jaani Formation, Häädemeete 172 Core; GIT 240-10 from the Paprenjai Formation, Baltinava 17 Core; GIT 240-15 (questionably the Jaagarahu Formation, Kalvariija Core); GIT 240-24 and GIT 240-33 (questionably from the Jaagarahu Formation, Balinava 17 Core) (see Rozhnov and Männil in Rozhnov et al. 1989).

Discussion.—Rozhnov and Männil (1989) reported this pisocrinid from the Häädemeete 172 core, where it occurs in the

Wenlock Jaani Formation. This taxon was questionably identified from the Baltinava 17 (Latvia) and Kalvariija (Lithuania) cores.

Geographic and stratigraphic range.—This taxon was reported from the Jaani and Jaagarahu formations (Wenlock) in the subsurface of Estonia, and probably also from Latvia and Lithuania.

Genus *Cicerocrinus* Sollas, 1900

Type species: Cicerocrinus elegans Sollas, 1900; Oesel, Russia; Pridoli, Silurian.

Cicerocrinus osiliensis (Jaekel, 1900)

Fig. 5C, D.

1900 *Lagarocrinus osiliensis* sp. nov.; Jaekel 1900: 486, figs. 1, 2.

1938 *Lagarocrinus osiliensis* Jaekel, 1900; Bassler 1938: 120.

1943 *Cicerocrinus osiliensis* (Jaekel, 1900); Bassler and Moodey 1943: 364.

1981 *Cicerocrinus osiliensis* (Jaekel, 1900); Rozhnov 1981: 111, pl. 24: 6; fig. 21z.

1988 *Cicerocrinus osiliensis* (Jaekel, 1900); Webster 1988: 55.

2003 *Cicerocrinus osiliensis* (Jaekel, 1900); Webster 2003.

Material.—GIT 405-242 and TUG 1375-1 from the Ohesaare Formation, Ohesaare Cliff, Saaremaa Island.

Discussion.—Two well preserved crowns of this species are available (Fig. 5C, D).

Geographic and stratigraphic range.—Ohesaare Formation at Ohesaare Cliff, Saaremaa, Estonia.

Cicerocrinus scanicus (Jaekel, 1900)

1900 *Lagarocrinus scanicus* sp. nov.; Jaekel 1900: 486, figs. 3, 4, 6, 7.

1943 *Lagarocrinus scanicus* Jaekel, 1900; Bassler and Moodey 1943: 364.

1981 *Cicerocrinus scanicus* (Jaekel, 1900); Rozhnov 1981: 111, fig. 21i.

1988 *Cicerocrinus scanicus* (Jaekel, 1900) [sic]; Webster 1988: 55.

Discussion.—Specimens of this species were not studied in the current project.

Stratigraphic and geographic range.—*Beyrichia* Limestone, Sweden; Ohesaare Formation, Estonia.

Order Myelodactylida Ausich, 1998

Family Myelodactylidae Miller, 1883

Myelodactylus? sp.

Fig. 5A.

Material.—The columnal on which this identification is based is TUG 1395-7 from the Ohesaare Formation at Ohesaare Cliff, Saaremaa, Estonia.

Discussion.—One apparently elliptical columnal from Ohesaare Formation was exposed with the articular facet parallel to bedding. The only common Silurian crinoids to have elliptical columnals are the myelodactylids. This columnal (Fig. 5A) has radially disposed crenulae on half of the columnal facet, and the other half of the columnal facet is damaged. This facet is not similar to Gotland myelodactylids illustrated by Donovan and Franzén-Bengtson (1988); thus this identifi-

cation is considered tentative. Myelodactylids have very small and inconspicuous crowns. They are normally identified from pluricolumnal segments that have some degree of planispiral coiling and bilaterally symmetrical columnals.

Conclusions

In this study we surveyed Silurian crinoids of Estonia using museum collections and our own new field collections. We recognize 19 species-level crinoid taxa from western Estonia, which includes one new genus and four new species. Wenlock crinoids from Estonia are consistent with crinoids known from Gotland, Sweden, and at least one Wenlock species from Gotland ranges upward into the Pridoli of Estonia. However, based on the new Estonian material, there is clearly a rich diversity of Llandovery and Pridoli fauna yet to be discovered on the Baltica paleocontinent.

Eichwald (1840) reported seven Silurian crinoids from Estonia. His specimens are not known, and we follow Webster (2003) in disregarding these reported occurrence. Further, the report (Webster 2003) of *Haplocrinus mespiliformis* (Goldfuss, 1831) from the Silurian of Estonia is considered erroneous, and we follow Bassler and Moodey (1943) and others by concluding that this species occurs in the Devonian of Germany and not the Silurian of Estonia.

This work provides additional information about the paleogeographic component of the diversification of crinoids following the Katian extinction event so that we can now better understand the early rise of the Middle Paleozoic Crinoid Macroevolutionary Fauna (Baumiller 1994; Ausich et al. 1994). Because the Silurian strata of Baltica are so well constrained by biostratigraphic and chemostratigraphic data (see Cramer et al. 2011), this new crinoid taxonomic and distribution information can be correlated with global Silurian faunal patterns.

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Appendix 1

Locality details.

Hiiumaa Island.—Heltermaa exposure is situated on Hiiumaa Island, on the eastern coast of Sarve Peninsula, 0.5 km south from Heltermaa harbor (58°51'43"N, 23°02'59"E). The outcrop is located on the beach having up to 1 m thick section of grainstone rocks of Juuru Stage (Varbola Formation). In the upper part of the section ripple marks and conglomerate with faunal concentrations occur (Lembit Põlma unpublished field notes). Most abundant are brachiopods, gastropods, rugosans, tabulates, and stromatoporoids.

Saaremaa Island.—Jaani shore is located at the eastern end of the northern coast of Saaremaa Island, about 1 km west of Jaani church (58°36'56"N, 22°53'51"E). Calcitic marlstone with argillaceous marlstone interlayers of the upper part of the Jaani Stage are exposed here. The cliff (about 2 m high) and the pebbly coast lying immediately east of it (the so-called Jaani shore), is known as a rich fossil locality. Typical fossils in marlstone are brachiopods, trilobites and corals. Skeletal fragments and burrows are commonly pyritized. Lithologic composition of rocks, common articulated brachiopods, and trilobite carapaces refer to a quiet-water environment at the boundary of the open shelf and transitional facies zone (Hints 2008).

Kaugatuma cliff.—2.5 m high, situated on the western coast of the Sõrve Peninsula, some kilometers south from its neck and about 100 m from the sea (58°7'22"N, 22°11'36"E). Rocks (Kaugatuma Stage, Äigu Beds) of two different facies types in the regressive succession can be seen. The lower 0.5+ m of the section contains greenish-grey nodular argillaceous wackestone of open shelf origin. Skeletal debris consists mostly of echinoderm and brachiopod fragments (Hints 2008). This layer is very rich in large crinoid holdfasts, some in life position. The upper 1.5+ m contains yellow-grey, coarse-grained, wavy-bedded crinoidal limestone of forereef origin (Hints 2008).

Liiva cliff.—Situated in the northern coast of Saaremaa, a few hundred meters from the road between Võhma and Leisi (58°34'36"N, 22°21'35"E). It is about a kilometer long and only 1.5 m high coastal cliff. The Ninase Member forms the most part of the cliff section (1 m thick) above the Mustjala Member. Two different types of environments occurred in the Jaani Stage (Wenlock), the shoal (Ninase Member) and the open shelf (Mustjala Member). Ninase Member consists of grainstone rocks with the fragments of brachiopods and crinoids. The Mustjala Member above sea level is approximately 0.5 m containing marlstone beds with interlayers and nodules of biomicritic limestone. It is rich in tabulate corals, stromatoporoids,

rugosans corals, brachiopods and crinoidal debris (Mõtus and Hints 2007).

Ohesaare cliff.—Located on the western coast of the Sõrve Peninsula near Ohesaare village, 2.5 km southwest of Jämaja church (58°0'2"N, 22°1'10"E). It is the youngest Silurian outcrop in the whole Baltic area and contains rich association of different fossils including fishes, molluscs, ostracods, and conodonts. The Ohesaare cliff is over 600 m long and up to 4 m high, it is located immediately by the sea in the zone of storm abrasion. The total thickness of the exposed bedrock is 3.5 m, whereas the thicknesses of separate layers are rather variable throughout the outcrop. The section is characterized by the intercalation of thin-bedded limestone and marlstone. In the middle part of the section skeletal packstone dominates, but in its upper and especially in the lower parts of the section biosparitic skeletal grainstone occurs. The section ends with a layer of fissile wavy- to cross-bedded-laminated calcareous siltstone up to 200 mm thick. It is underlain by a 50–150 mm thick interbed of light-grey silty skeletal grainstone, the upper surface of which bears large ripple marks and the lower boundary displays a hardground (Hints 2008). The rocks of Ohesaare cliff were formed in open shelf to shoal environments.

Suuriku cliff.—Located in the northeastern coast of the Tagamõisa Peninsula in Saaremaa (58°30'26"N, 22°0'6"E). The outcrop is 1.6 km long and up to 8 m high. In this locality the Mustjala and Ninase members of the Jaani Stage (Sheinwoodian, Wenlock) are exposed. Coarse-grained skeletal grainstone beds with interlayers of marlstone of the Ninase Member form the main, upper part of the section. The rock is mainly composed of pelmatozoans fragments. Brachiopods and gastropods are abundant, rugose corals are less common. Bioherms with abundant bryozoans (*Ceramopora*, *Lioclema*) occur in the middle part of the Ninase Member (Hints 2008). Clayey interlayers of Ninase Member contain relatively abundant remains of crinoid calyxes, some well preserved and retaining columnals (OV personal observation) The lower part of the Suuriku section consists of marlstones of the Mustjala Member (Hints 2008).

Undva cliff.—Situated in the northern end of the Tagamõisa Peninsula, a few kilometers north from the Suuriku cliff (58°31'1"N, 21°55'7"E). The cliff is about 350 m long and up to 2.5 m high, and the Mustjala and Ninase members of the Jaani Stage (Sheinwoodian, Wenlock) are exposed. The 1.5 m thick Ninase member consists of coarse-grained skeletal grainstone with interlayers of marlstone (Hints 2008). Fragments of crinoid calyxes are common in the grainstone of the Ninase Member.