

Wenlock and Pridoli (Silurian) crinoids from Saaremaa, western Estonia (Phylum Echinodermata)

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Abstract.—Study of new collections of the Wenlock and Pridoli, Silurian, crinoids from Saaremaa, western Estonia, result in taxonomic revision, expanded ranges, and new taxa. *Eucalyptocrinites regularis* and *Periechocrinus laevis* are recognized outside of Sweden for the first time. *Desmidocrinus laevigatus* Ausich et al., 2012 is reassigned to *Methabocrinus*. Because the type species of *Methabocrinus* was previously known only from glacial sediments, the age and provenance of this genus are constrained for the first time. A new crotalocrinitid, *Velocrinus coniculus* new genus and species, is described. Although the Pridoli faunas of western Estonia contain only twelve species-level taxa assigned to nine genera, this fauna is one of the four richest Pridoli faunas known.

Introduction

Pridoli crinoids are poorly understood globally, with the richest fauna known from western Tennessee (USA). With the material reported by Ausich et al. (2012) and the new material reported here, the fauna from the Kaugatuma Formation (Saaremaa, western Estonia Islands) is among the four most diverse Pridoli faunas worldwide. *Velocrinus coniculus* n. gen. and sp. is described here, and *Periechocrinus laevis*? is reported from Estonia for the first time. Based on additional material and better-preserved specimens, *Desmidocrinus laevigatus* Ausich et al., 2012 is reassigned to *Methabocrinus* Jaekel, 1918. Previously, *Methabocrinus* was known exclusively from the holotype of the type species (*M. erraticus* Jaekel, 1918), which was collected from a glacial deposit in Germany. The age and provenance of this genus is constrained for the first time. In addition, new occurrences from the Wenlock of Saaremaa are also reported, including *Calliocrinus* sp. and *Protaxocrinus*? sp.; the most common Wenlockian *Eucalyptocrinites* from Saaremaa is recognized herein as *E. regularis* (Hisinger, 1840a).

Saaremaa crinoid assemblages

Wenlock.—The Wenlock crinoid fauna from Estonia has a low taxonomic richness with only ten species-level taxa assigned to seven genera (Table 1). However, *Calliocrinus*, *Eucalyptocrinites*, *Periechocrinus*, and *Pisocrinus* are among the most characteristic Wenlock crinoids both in Baltica (Gotland faunas) and North America. With the exception of *Eucalyptocrinites*, Wenlock crinoid specimens are quite rare in Estonia. *Pisocrinus* is only known from cores, where it is reasonably abundant.

Pridoli.—Similar to the Wenlock, Pridoli crinoids from Estonia are low in taxonomic richness: twelve species-level taxa

assigned to nine genera. However, globally this is a substantial Pridoli fauna. The Estonian Pridoli fauna includes both genera that ranged up from the Wenlock and Ludlow (*Calliocrinus*, *Cicerocrinus*, *Enallocrinus*, *Eucalyptocrinites*, *Myelodactylus*, and *Protaxocrinus*) as well as genera with first occurrences in the Pridoli (*Methabocrinus*, *Saaremaacrinus*, and *Velocrinus*).

Globally, the Pridoli crinoid fauna from Saaremaa is among the four most diverse Pridoli faunas known. Determination of Pridoli crinoid faunas worldwide is problematic because these faunas are commonly reported from stratigraphic units listed as latest Silurian to earliest Devonian. Thus, the lack of precision from which faunas occur is a source of confusion. As presently understood, Pridoli crinoids are well documented from three paleocontinents, Baltica, Laurentia (Decatur Limestone, Tennessee; Henryhouse Formation, Oklahoma), and the Perunica microcontinent, Bohemia (Pozary Formation). The faunas from Estonia are known from both the Ohesaare Formation and the Kaugatuma Formation, the latter with the highest richness (Table 2).

The Estonian Pridoli fauna is comprised of both cosmopolitan and endemic genera and is more similar to Laurentian faunas than to those from Perunica, with which it shares no genera. The Baltic fauna (Estonia) shares the cosmopolitan genera *Eucalyptocrinites* and *Myelodactylus* with the Pridoli of Laurentia. *Calliocrinus* also occurs in the Wenlock to Ludlow of Baltica, the Wenlock of Laurentia, and the Lower Devonian of the Ural Mountains. *Cicerocrinus* is also known from the Ludlow of Avalonia, and *Enallocrinus* is also known from the Wenlock of Avalonia and the Wenlock and Ludlow of Baltica. *Methabocrinus*, *Saaremaacrinus*, and *Velocrinus* occur exclusively in the Pridoli of Baltica.

A reasonably large Pridoli fauna was reported from the Humevale Formation (eastern Australia) by Jell and Holloway (1983) and Jell (1999). However, similar to elsewhere in the world in late Silurian to early Devonian strata, chronostratigraphic

Table 1. Wenlock and Pridoli crinoids from Saaremaa, Estonia.

Pridoli	
Ohesaare Formation	
<i>Cicerocrinus osiliensis</i> (Jaekel, 1900)	
<i>Cicerocrinus scanicus</i> (Jaekel, 1900)	
<i>Myelodactylus?</i> sp. in Ausich et al., 2012 (columnals only)	
Kaugatuma Formation (middle Äigu Beds)	
<i>Calliocrinus sedgwickianus</i> Angelin, 1878	
<i>Enalloocrinus</i> sp. in Ausich et al., 2012 (holdfasts and arms)	
<i>Eucalyptocrinites tumidus</i> Ausich et al., 2012	
<i>Eucalyptocrinites</i> sp. 1 in Ausich et al., 2012	
<i>Eucalyptocrinites</i> sp. 2 in Ausich et al., 2012	
<i>Methabocrinus laevigatus</i> (Ausich et al., 2012)	
<i>Protaxocrinus?</i> sp. herein	
<i>Saaremaocrinus estoniensis</i> Ausich et al., 2012	
<i>Velocrinus coniculus</i> new gen. and sp.	
Cladida indeterminate in Ausich et al., 2012	
Wenlock	
Jaagarahu	
<i>Pisocrinus (Pisocrinus) pilula</i> de Koninck, 1858	
<i>Pisocrinus (Pisocrinus) trialobus</i> Rozhnov and Männil in Rozhnov et al., 1989	
<i>Pisocrinus (Granulocrinus) lanceatus</i> Rozhnov, 1981	
Jaani Formation, Ninase Member	
<i>Calliocrinus</i> sp. in Ausich et al., 2012 and herein	
<i>Eucalyptocrinites regularis</i> (Hisinger, 1840a)	
<i>Eucalyptocrinites</i> sp. 1 in Ausich et al., 2012	
<i>Eucalyptocrinites</i> sp. in Ausich et al., 2012	
<i>Perichocrinus laevis?</i> Angelin, 1878	
<i>Protaxocrinus salteri?</i> in Ausich et al., 2012	
Jaani Formation, Mustjala Member	
<i>Eucalyptocrinites regularis</i> (Hisinger, 1840a)	
Jaani Formation, Member Unspecified	
<i>Periechocrinus longimanus?</i> (Angelin, 1878)	
<i>Pisocrinus (Pocillocrinus) rubeli</i> Rozhnov and Männil in Rozhnov et al., 1989	

Table 2. Systematic position of Pridoli crinoids from Saaremaa, Estonia.

Subclass Camerata	
Family Periechocrinidae	
<i>Saaremaocrinus estoniensis</i> Ausich et al., 2012	
Family Eucalyptocrinitidae	
<i>Calliocrinus sedgwickianus</i> Angelin, 1878	
<i>Eucalyptocrinites tumidus</i> Ausich et al., 2012	
<i>Eucalyptocrinites</i> sp. 1 in Ausich et al., 2012	
Family Carpocrinidae	
<i>Methabocrinus laevigatus</i> (Ausich et al., 2012)	
Subclass Cladida	
Family Crotalocrinidae	
<i>Enalloocrinus</i> sp. in Ausich et al., 2012	
<i>Velocrinus coniculus</i> n. gen and sp.	
Cladida indeterminate in Ausich et al. 2012	
Subclass Flexibilia	
Family Taxocrinidae	
<i>Protaxocrinus?</i> sp., herein	
Subclass Disparida	
Family Pisocrinidae	
<i>Cicerocrinus osiliensis</i> (Jaekel, 1900)	
<i>Cicerocrinus scanicus</i> (Jaekel, 1900)	
Family Myelodactylidae	
<i>Myelodactylus?</i> sp. in Ausich et al., 2012	

resolution in the Humevale Formation is insufficient to confidently recognize a Pridoli fauna (VandenBerg, personal communication, 2014).

Stratigraphy and paleoenvironments

The coastal cliffs and quarries of Saaremaa are the best natural exposures of Silurian strata in Estonia. Unlike the more thoroughly studied sections of Gotland, Sweden (which only include the latest Llandovery through Ludlow), Saaremaa geology includes Wenlock through Pridoli strata. Nestor and Einasto (1977), Raukas and Teedumäe (1997), Hints (2008), and Ausich et al. (2012) summarized the details of the Silurian

stratigraphy and depositional setting of Estonia. Figure 1 illustrates the Silurian stratigraphic units of Estonia. The crinoids reported here are from the Mustjala and Ninase members of the Jaani Formation and the Kaugatuma Formation, which are time slices Sh2 and Pr1, respectively, of Cramer et al. (2010).

During the Silurian, Baltica was located in equatorial latitudes (Melchin et al., 2004). The western part of modern Estonia, including the islands, was covered by the epicontinental Baltic paleobasin. This basin was characterized by diverse faunas and a wide range of tropical shelf environments (Hints, 2008). The sedimentary facies of the Silurian of Estonia can be divided laterally into five facies belts or sedimentary environments along the reconstructed bathymetric profile (Nestor and Einasto, 1977): tidal flat/lagoonal, shoal, open shelf, basin slope, and a basin depression. The first three environments formed a carbonate platform. The latter two formed a deeper basin with fine-clastic deposits. The flat/lagoonal, shoal, open shelf, and basin slope sediments are represented in outcrops of western Estonia, but crinoids (both articulated and disarticulated remains) occur only in rocks from shoal, open shelf, and basin slope origin.

Systematic paleontology

Terminology follows Ubaghs (1978a) with modifications from Ausich et al. (1999), Sumrall and Waters (2012), and Kammer et al. (2013). Open nomenclature follows Matthews (1973) and Bengtson (1988). The scheme for defining relative proportions of the calyx follows Ubaghs (1978a, fig. 72). Geographic and stratigraphic details of Saaremaa Island localities are given in Ausich et al. (2012) and Appendix 1. All measurements are in millimeters, unless otherwise noted; and an asterisk indicates a crushed or broken specimen. Repositories are indicated as follows: TUG, University of Tartu; and TUT and TTÜGI, Institute of Geology, Tallinn University of Technology.

Class Crinoidea Miller, 1821

Subclass Camerata Wachsmuth and Springer, 1885

Order Monobathrida Moore and Laudon, 1943

Suborder Compsocrinina Ubaghs, 1978b

Superfamily Periechocrinoidea Bronn, 1849

Genus *Periechocrinus* Morris, 1843

Type species.—*Periechocrinus costatus* Austin and Austin, 1842.

Periechocrinus laevis? Angelin, 1878

Figure 2.3

- 1878 *Periechocrinus laevis* Angelin, p. 7, pl. 18, fig. 11.
 1881 *Periechocrinus minor* Wachsmuth and Springer, p. 132 (306).
 1943 *Periechocrinites laevis*; Bassler and Moodey, p. 599.
 1983 *Periechocrinus laevis*; Franzén, p. 6.
 2014 *Periechocrinus laevis*; Webster and Webster, p. 2056.

Remarks.—One poorly preserved crinoid calyx, assigned to *P. laevis?* Angelin, 1878, was collected from the Ninase Member of the Jaani Formation. The calyx has a high bowl shape and the fixed interrays have a biseries of interradsial plates (Fig. 2.3), which is consistent with *Periechocrinus*. Unfortunately, poorly preserved plating exists around approximately one third of the

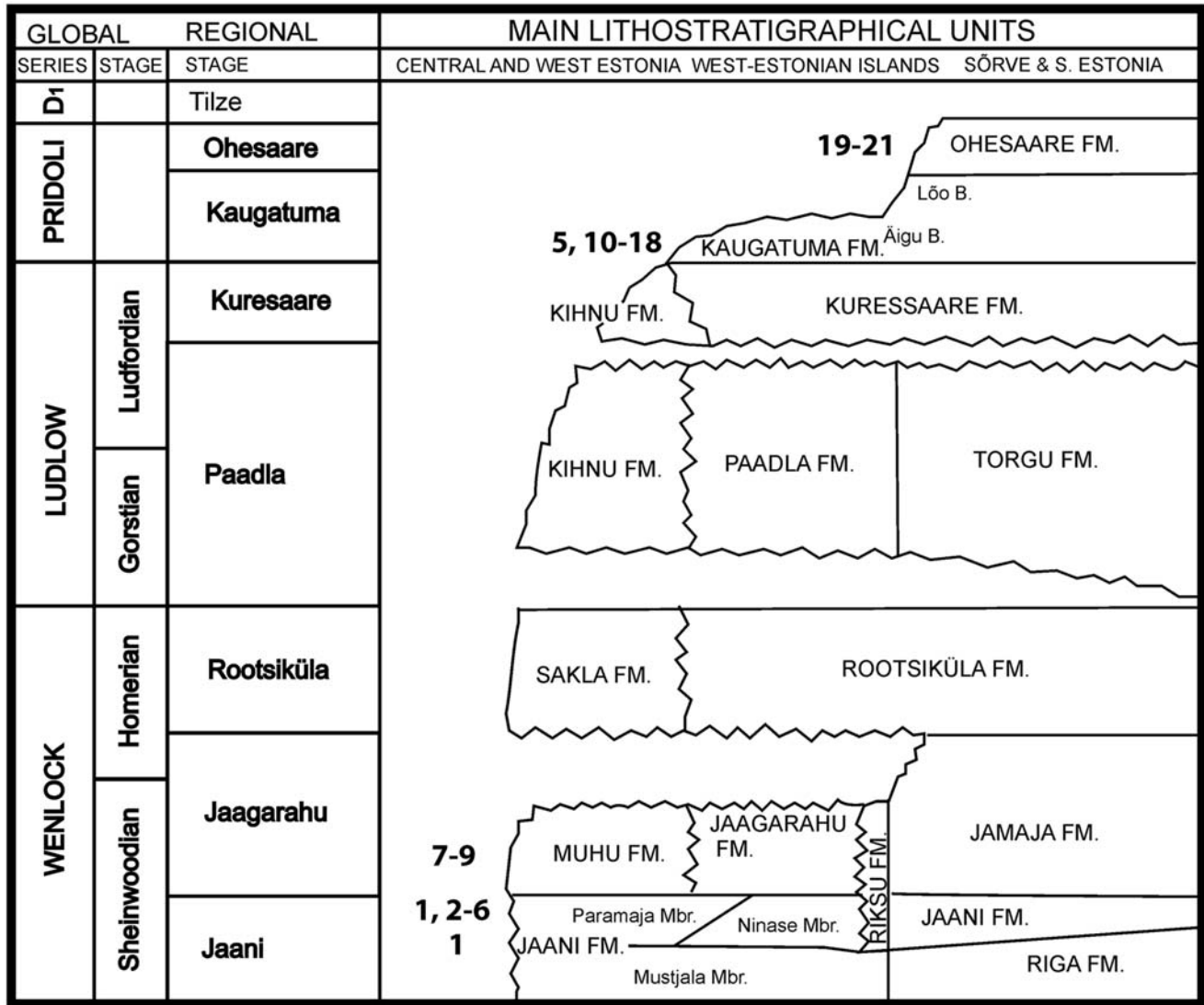


Figure 1. Silurian stratigraphy of Estonia. New fossil specimens are from the West-Estonian islands, the middle column of the chart of lithostratigraphic units (based on Hints, 2008). D1, Lower Devonian; O, Ordovician, O3, Upper Ordovician.

specimen, and the remainder of the calyx is preserved as an internal mold.

This new specimen is larger (25 mm high, 20 mm wide) than the specimens reported as *P. longimanus* (Angelin, 1878) by Ausich et al. (2012), and they also differ because the new specimen has median ray ridges, which at present is regarded a reliable species-level character among *Periechocrinus* species from Gotland. Franzén (1983) reported four Gotland specimens of *Periechocrinus* that have smooth plate sculpturing and median ray ridges (like the new specimen). Of these, *P. annulatus* (Angelin, 1878) and *P. lindstromi* Wachsmuth and Springer, 1881 have lower calyces than TUG 1395-61. *Periechocrinus scanicus* Angelin, 1878 has more fixed brachials than the new specimen is interpreted to have, but the new Saaremaa specimen is very similar to *P. laevis*. Because TUG 1395-61 is so poorly preserved, a tentative identification is appropriate; thus, we recognize this taxon as *P. laevis*?. Franzén (1983) was unable to determine the location of this species on Gotland, so its probable occurrence in the Wenlock of Estonia helps to define the stratigraphic range of this species.

Material.—TUG 1395-61.

Occurrence.—Ninase Member, Jaani Formation at Undva Cliff, Saaremaa Island, Estonia.

Suborder Glyptocrinina Moore, 1952
 Superfamily Eucalyptocrinitoidea Roemer, 1855
 Family Eucalyptocrinitidea Roemer, 1855
 Genus *Eucalyptocrinites* Goldfuss, 1831

Eucalyptocrinites regularis (Hisinger, 1840a)
 Figure 2.9

- 1840a *Actinocrinites regularis* Hisinger, p. 6, pl. 39, fig. 6.
- 1840b *Actinocrinites regularis*; Hisinger, p. 45.
- 1848 *Eucalyptocrinus regularis*; Bronn, p. 474.
- 1851 *Eucalyptocrinus regularis*; Roemer in Bronn and Roemer, p. 260.
- 1852–1854 *Eucalyptocrinus regularis*; Roemer in Bronn, p. 260.

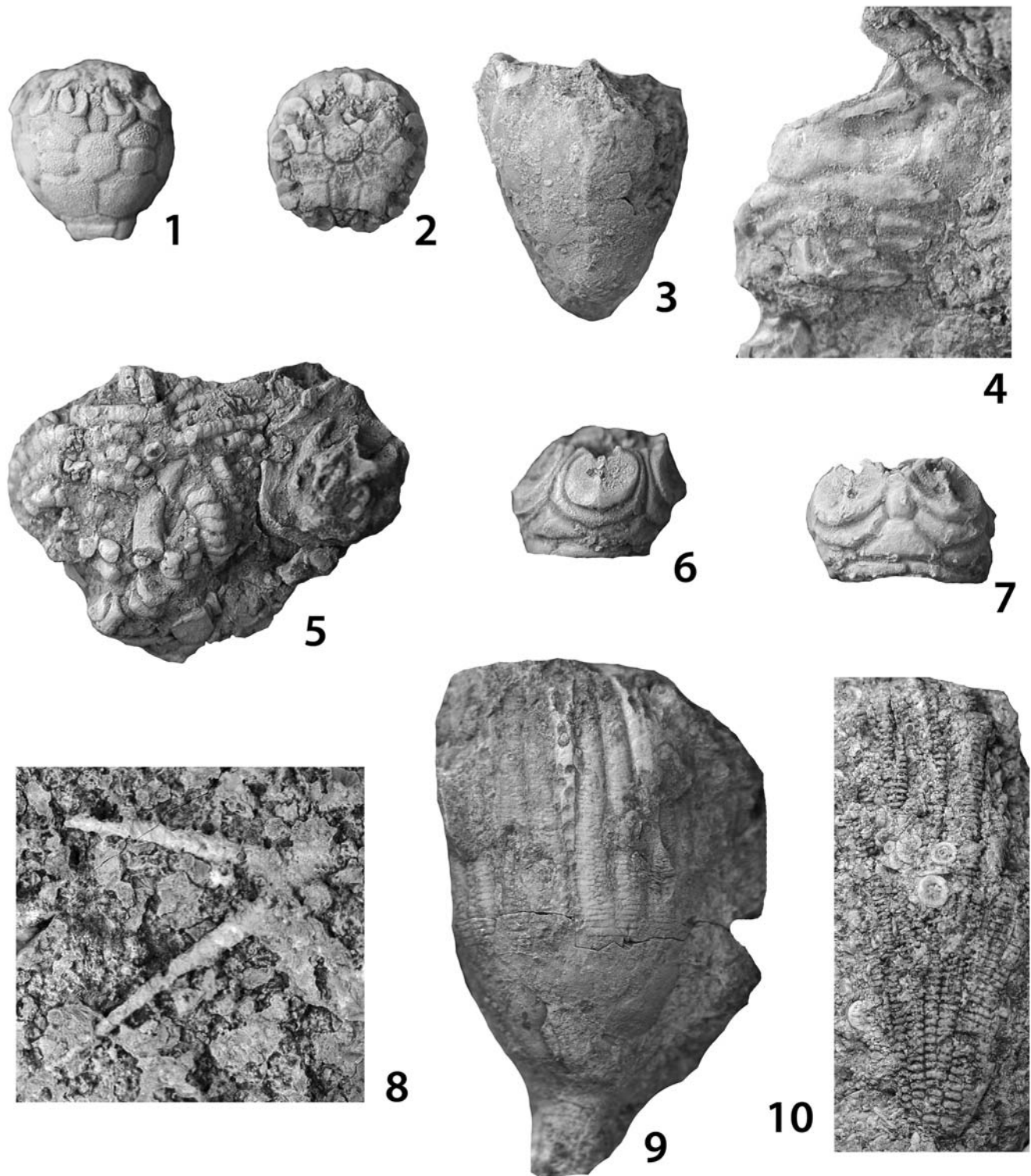


Figure 2. Estonian Silurian Crinoids. (1, 2) *Methabocrinus laevigatus* (Ausich, Wilson, and Vinn, 2012) TUG 1395-40, X2.5; 1, CD-interray view; (2) tegmen view. (3) *Periechocrinus laevis?* Angelin, 1878, lateral view, TUG 1395-61, X1.75. (4) *Enallocrinus?* sp., lateral view of a partial aboral cup, TUG 1395-44, X2.5. (5) *Protaxocrinus?* sp., oral view of a crown with infolded arms, TUG 1395-60, X2.5. (6, 7) *Velocrinus coniculus*, TUG 1395-42, X2.5; (6) E-ray lateral view; (7) CD-interray lateral view. (8) *Calliocrinus* sp., tegmen spine, TUG 1395-43, X1.5. (9) *Eucalyptocrinites regularis* (Hisinger, 1840), lateral view of crown, note *Sedilichnus* along partition plates, TUG 1395-46, X1.0. (10) *Enallocrinus* sp., aboral view of one isolated arm, TUG 1395-45, X1.0.

1862 *Eucalyptocrinus regularis*; Dujardin and Hupé, p. 116.
 1868 *Actinocrinus regularis*; Bigsby, p. 196.
 1876 *Actinocrinus regularis*; Quenstedt, p. 636, pl. 112, figs. 57, 58.

1878 *Hypanocrinus regularis*; Angelin, p. 17, pl. 6, figs. 2–3c, pl. 24, figs. 11–11f, 20; pl. 29, figs. 35–64, 71.
 1880 *Hypanocrinus regularis*; Zittel, p. 380, fig. 266.
 1895 *Hypanocrinus regularis*; Zittel, p. 133, fig. 253.

- 1900 *Eucalyptocrinus regularis*; Wachsmuth in Zittel, p. 148, fig. 251.
 1943 *Eucalyptocrinites regularis*; Bassler and Moodey, p. 466.
 1983 *Eucalyptocrinites regularis*; Franzén, p. 8.
 2014 *Eucalyptocrinites regularis*; Webster and Webster, p. 1448.

Diagnosis.—Medium cone-shaped tegmen, smooth calyx plate sculpturing, base of calyx relatively narrow, basal plates not visible in side view, partition plates conspicuously widen distally.

Description.—Calyx medium size for genus; low cone. Calyx plate sculpturing smooth; median ray ridges.

Basal circling covered. Radial circling approximately 20% of calyx height; presumably five radial plates, pentagonal. Normal interrays in contact with tegmen partition plates; first interradial decagonal, higher than wide, larger than radial plate, much larger than first primibrachial. Second range with two plates that are sutured to the interradial tegmen partition plates. Posterior interray not exposed or indistinguishable from normal interrays (as in other species).

First primibrachials tetragonal, approximately as wide as high, approximately same size as primaxil. Second secundibrachial axillary in all rays, yielding four arms per ray. One fixed intrabrachial sutured distally with partition plate, approximately two times higher than wide.

Tegmen comprised of ten partition plates that extend to base of the anal tube and rise to full height of arms. Partition plates widen distally to three times proximal width; broad, deep centrally positioned groove along distal one third of partition plate (Fig. 1.9). Short anal tube extends above arms.

Free arms 20, atomous, probably pinnulate, first few tertibrachials fixed, cuneate uniserial through the first five tertibrachials, thereafter biserial. Arms reach to the distal extent of the partition plates.

Column unknown.

Material.—GIT 405-238, 1395-46 to #1395-55, TUG 860-136, TUG 860-137, TUG 1395-10, TUG 1395-12 to TUG 1395-16.

Occurrence.—*Eucalyptocrinites regularis* was originally described from Gotland, Sweden, where it is currently recognized from the Höglint Formation (Wenlock) (Franzén, 1983). As listed above, this species is now recognized from Saaremaa, Estonia, from the Mustjala and Ninase Members of the Jaani Formation at Liiva Cliff, Suuriku Cliff, and Undva Cliff, Saaremaa Island, Estonia.

Remarks.—As discussed in Ausich et al. (2012), Franzén (1983) listed three species of *Eucalyptocrinites* from Gotland with smooth calyx plating, basal plates not visible, and partition plates that conspicuously widen distally, including *E. plebejus* (Angelin, 1878), *E. regularis* (Hisinger, 1840), and *E. rigens* (Angelin, 1878). These three species are distinguished by the following (based both on specimens and on figures from Angelin, 1878): both *E. plebejus* and *E. rigens* have broadly truncate calyx bases from which a basal concavity begins,

whereas *E. regularis* has a much narrower calyx base. The latter is consistent with specimen 1395-46, our only complete crown, and with numerous calyxes that are preserved in isolation from the tegmen and arms. Therefore, we identify *E. regularis* from the Ninase Member, Jaani Formation (Wenlock) from Undva Cliff (TUG 1395-47 to TUG 1395-54). Further, we identify the following specimens that have less complete preservation as *E. regularis*: Mustjala Member, Jaani Formation, from Suuriku Cliff (TUG 1395-12); Ninase Member, Jaani Formation, from Suuriku Cliff (TUG 1395-14 and TUG 1395-55); Ninase Member, Jaani Formation, from Undva Cliff (TUG 1395-15, TUG 1395-16); and Ninase Member, Jaani Formation, from Panga Cliff (TUG 1395-13).

An interesting aspect of this species is that specimens have been heavily drilled. The trace fossil *Sedilichnus* Müller, 1977 occurs along the partition plates of *E. regularis* (Fig. 2.9).

Measurements.—TUG 1395-47: Crown height, 40 mm; aboral cup height, 15 mm; aboral cup maximum width, 21 mm.

Genus *Calliocrinus* d'Orbigny, 1850

Type species.—*Eugeniocrinites? costus* Hisinger, 1837.

Calliocrinus sp.
Figure 2.8

Material.—TUG 1395-5 and TUG 1395-6 from Suuriku Cliff; new material is from Undva Cliff: TUG 1395-43.

Occurrence.—*Calliocrinus* sp. is recognized from the Ninase Member, Jaani Formation at Suuriku Cliff and Undva Cliff, Saaremaa Island, Estonia.

Remarks.—Ausich et al. (2012) reported large, isolated, bifurcating spine plates from the Ninase Member of the Jaani Formation at Suuriku Cliff and identified them as belonging to *Calliocrinus* sp. An additional specimen TUG 1395-43 is reported, herein, from the Ninase Member at Undva Cliff. This spine is approximately 40 mm long and approximately 30 mm wide at its widest breadth (Fig. 2.8).

Superfamily Carpocrinoidea de Koninck and Le Hon, 1854
 Family Carpocrinidae de Koninck and Le Hon, 1854
 Genus *Methabocrinus* Jaekel, 1918

Type species.—*Methabocrinus erraticus* Jaekel, 1918.

Occurrence.—It is unlikely that the original stratigraphic and geographic location of the type species will ever be known. Thus, the occurrence of *M. laevigatus* must represent this genus, which is Pridoli, Silurian; Estonia.

Remarks.—Ausich et al. (2012) described *Desmidocrinus laevigatus* from two calyxes (one significantly weathered), but neither specimen had a preserved tegmen. Placed in *Desmidocrinus*, this material was a somewhat unusual species for the genus with a reduced number of arms and reduced plating in the regular and CD interrays. However, with the newly discovered

specimen TUG 1395-43, which preserves a nearly complete tegmen diagnostic of *Methabocrinus*, this species is transferred to *Methabocrinus*. It is a species with more plates in the regular and CD interrays than the type species, *M. erraticus*.

This is an especially significant discovery because *Methabocrinus* was previously known from a single specimen collected from glacial drift in Germany (Jaekel, 1918; Ubaghs, 1958, 1978b), thus its age and provenance was speculative. Although the age of the type species may never be known, the genus can now be recognized with certainty from the Pridoli of Estonia.

Methabocrinus laevigatus (Ausich, Wilson, and Vinn, 2012)
Figure 2.1, 2.2

2012 *Desmidocrinus laevigatus* Ausich, Wilson, and Vinn,
p. 622, fig. 5G, 5H.

Diagnosis.—*Methabocrinus* with a more globe-shaped calyx in adults, basal plates equal in size, regular interray plating 1-1, concave; primary peristomial cover plates, broadly convex radially positioned tegmen plates.

Description.—Calyx medium in size for genus, low bowl to globe shape (Fig. 2.1); arms not grouped; calyx plates convex, finely and irregularly granulose sculpturing, plate sutures broadly impressed (Fig. 2.1).

Basal circlet visible in side view (Fig. 2.1), projects downward altering convex profile of remainder of calyx, approximately 18 % of calyx height, shallow basal concavity; basal plates three, equal in size. Radial circlet averages 32 % of calyx height, interrupted in posterior; radial plates five, hexagonal, approximately 1.4 times wider than high. Normal interrays in contact with tegmen, first interradial octagonal, approximately 1.1 times wider than high, smaller than radials and much larger than first primibrachials, extends from shoulders of radial plates to the lower part of the first secundibrachial; only one other interradial plate fixed in calyx resulting in 1-1 plating, although this series of plates articulated to one or two proximal plates of tegmen. Primanal hexagonal, approximately equal in height and width, same size as radial plates, and interrupts the radial circlet; plating in CD interray P-3-3-4; anitaxis of plates, anitaxial ridge absent; CD interray in contact with tegmen.

First primibrachial tetragonal, approximately 1.5 times wider than high, much smaller than radial plates and somewhat smaller than primaxil; second primibrachial axillary, pentagonal to heptagonal. First secundibrachial fixed, distal-most fixed brachial with narrow crenularium around margin of facet, adjacent first secundibrachials within a ray in contact medially. A single intrabrachial plate in center of ray sutured on upper shoulder of first secundibrachials and extending onto tegmen.

Tegmen with mouth subtegmenal, five large primary peristomial cover plates with CD peristomial cover plate the largest occupying a central position and extending abaxially to the periproct (Fig. 2.2). Primary peristomial cover plates in regular interrays concave, extend to the arm openings, articulated to two smaller plates that are either articulated with the distal-most interradial plate or articulated with a second range of two small plates that in turn articulate with the distal-

most interradial plate. A single, large, roughly diamond-shaped, broadly convex, radially positioned tegmen plate in each ray forms admedial frame around arm opening and articulates to a single intrabrachial plate.

Free arms 10, branch, brachials biserial; aborally very convex; arms branch on approximately ninth free brachial; pinnules and other aspects of free arms unknown.

Most proximal columnal circular, holomeric; lumen pentalobate. Narrow crenularium (30 % of columnal radius), areola wide (48 % of columnal radius), and lumen 22 % of columnal radius. Other aspects of column unknown.

Material.—TUG 1395-1 (holotype), TUG 1395-2 (paratype), and the following additional specimens: TUG 1395-40 and TUG 1395-41.

Occurrence.—All specimens of this species are from the Middle Äigu Beds, Kaugatuma Formation (Pridoli), at Kaugatuma Cliff, Saaremaa Island, Estonia.

Remarks.—The two new specimens (TUG 1395-40 and TUG 1395-41) are both smaller than the previously known specimens, with TUG 1395-40 having a complete calyx and nearly complete tegmen. TUG 1395-40 is not weathered, so plate sculpturing is well preserved. *M. laevigatus* differs from *M. erraticus* with more interradial plates fixed into the calyx in regular interrays, the CD interray, and in a medial intrabrachial position. Further, the topography of the tegmen differs. *Methabocrinus erraticus* has a prominent ridge on both the primary peristomial cover plates and the large radially positioned tegmen plates that together form concave niches into which the ten free arms were presumably placed. In contrast, these niches do not exist in *M. laevigatus*, with the primary peristomial cover plates concave and large radially positioned tegmen plates only broadly convex.

Subclass Cladida Moore and Laudon, 1943
Order Cyathocrinida Bather, 1899
Superfamily Gasterocomoidea Roemer, 1854
Family Crotalocrinitidae Bassler, 1938
Genus *Enallocrinus* d'Orbigny, 1850

Type species.—*Apiocrinites scriptus* Hisinger, 1828.

Enallocrinus sp.
Figure 2.4, 2.10

Occurrence.—*Enallocrinus* holdfasts are recognized from Gotland, Sweden, in the Hemse Beds (Gorstian, lower Ludlow; Franzén 1977) and the lower Klinteberg Formation (Homerian, Wenlock; Donovan et al., 2007). In Estonia, *Enallocrinus* holdfasts are from the Middle Äigu Beds, Kaugatuma Formation (Pridoli), at Kaugatuma Cliff, Saaremaa Island, Estonia.

Remarks.—Ausich et al. (2012) concluded that the abundant, large rhizoid holdfasts that characterize the Kaugatuma Cliff locality belonged to *Enallocrinus* sp. based on comparison to Gotland specimens discussed in Donovan et al. (2007). Herein, this assignment is corroborated further by new material from Kaugatuma Cliff. The calcite of the Saaremaa *Enallocrinus*

holdfasts varies in color from dark gray to white. On one limestone slab a dark gray holdfast occurred adjacent a light to dark gray partial set of articulated arms approximately 80 cm long (TUG 1395-45) (Fig. 2.10). This partial arm set begins proximally with three, laterally fused arms, which divide into five laterally fused arms. The fused brachials have a normal shape (unlike *Crotalocrinites* Austin and Austin, 1843). The brachials are uniserial, and each brachial has a prominent, elongate node (Fig. 2.10). They are much wider than high and vary from tetragonal to hexagonal in shape. The arms bifurcate irregularly a few additional times and remain laterally fused for a total of approximately 50 mm, after which they become free with uniserial brachials that may divide further. Although not identical, this partial arm set is quite similar to *Enallocrinus* arms illustrated in Angelin (1878, e.g., pl. 15, figs. 1, 1a, 3).

More speculative but supporting the occurrence of *Enallocrinus* is a small fragment of a crinoid calyx (GUT 1395-44) that is tentatively identified as *Enallocrinus* sp. This fragment is interpreted to be primarily the most proximal fixed brachials of an *Enallocrinus* calyx (Fig. 2.4). Some species of *Enallocrinus* have very elongate, very nodose fixed primibrachials and secundibrachials, similar to this specimen. However, the exact interpretation of this specimen must be tentative because it is such a small fragment.

In summary, the *Enallocrinus* interpretation by Donovan et al. (2007) of the distinctive Gotland rhizoid holdfasts is supported by new material from the Kaugatuma Formation of Saaremaa.

Material.—TUG 1395-38 and TUG 1395-39 were previously deposited by Ausich et al. (2012). Additional specimens include TUG 1395-45 and TUG 1395-44 (which is questionably assigned to this taxon).

Genus *Velocrinus* new genus

Type species.—*Velocrinus coniculus* n. gen. and sp., by monotypy.

Diagnosis.—Crotalocrinitid with a calyx cone shaped, lacking stereomic overgrowths, comprised of relatively large plates; infrabasals not fused, visible in lateral view; two anal plates; primaxil minute, not visible in lateral view; fixed brachials present; free arms not laterally linked; anus on tegmen; (nature of tegmen plating unknown).

Etymology.—From *velo* (L., n.; cover), which refers to the diminutive primibrachials not visible in lateral view.

Occurrence.—Pridoli, Late Silurian, Estonia.

Remarks.—*Velocrinus* n. gen. is recognized as belonging to the Crotalocrinitidae because of the plating in the CD interray, fixed brachial plates, and axial canal within radial plates and brachial plates. However, this crinoid differs from other crotalocrinitids with a combination of having fixed brachials, fixed arms not sutured or linked, primaxial minute and not visible in lateral view, five infrabasal plates that are visible in lateral view, and two anal plates in the cup. With a cone-shaped calyx, *Velocrinus*

is most similar to *Enallocrinus*, *Pleuroptyx*, and *Syndetocrinus*. The latter three genera have fixed brachials through the tertribrachials, the primaxil visible in lateral view, and one anal plate in the cup. *Enallocrinus* has a minute primaxil, whereas *Syndetocrinus* has a large primaxil. In contrast, *Velocrinus* has only fixed primibrachials, a minute primaxil that is not visible in lateral view, and two anal plates in the cup.

Velocrinus coniculus new genus and species

Figure 2.6, 2.7

Diagnosis.—Velocrinid with a calyx cone-shaped, lacking stereomic overgrowths, comprised of relatively large plates; infrabasals not fused, visible in lateral view; primaxil minute, not visible in lateral view; fixed brachials present; free arms not laterally linked; anus on tegmen (nature of tegmen plating unknown).

Etymology.—From *coniculus* (L.; cone-like, conical), which refers to the cone-shaped calyx.

Description.—Aboral cup small, low globe shape, width to height ratio approximately 1.75, plates very gently convex, irregular sculpturing, sutures deeply impressed. Infrabasals probably five and equal in size, 5.6 times wider than high, infrabasal circlet approximately 10 % of aboral cup height, base truncate (Fig. 2.6). Basals five, triangular, 2.1 times wider than high, smaller than radials; basal circlet approximately 30 % of aboral cup height. Radials five, broadly pentagonal except C and D radials that articulate with small CD interray plates, approximately 1.1 times wider than as high; radial circlet approximately 60 % of aboral cup height (Fig. 3). Radial facets large, angustary, horseshoe shape, declivate, occupy approximately 87 % of distal radial plate width (Fig. 2.6). Dumbbell-shaped axial canal; ovate adoral groove partially enclosed distally by distal extensions of the radial plate curving adaxially and partially divided by primaxil that divides the axial canal; radial facet topography unknown.

Two anal plates in cup; arranged 1-1, interpreted as anal X and right tube plate (Fig. 2.7). Anal X in contact with CD basal beneath, hexagonal, nodose, extends distally to middle height of radial facet. Right tube plate pentagonal, directly above anal X in contact distally with small plates that form margin of periproct. Anal opening at margin of tegmen; other details of tegmen unknown.

Arms known only from first and second (axillary) primibrachials. First primibrachial facet large, horseshoe-shaped, 1.3 times wider than high. Primaxil diminutive, hexagonal, 2.1 times wider than high, not visible on aboral side of arm, forms a narrow partition plate dividing the dumbbell-shaped axial canal on the radial facet. Facet onto which the first secundibrachials articulate is primarily that of the first primibrachial (only articulating medially with the diminutive primaxil). First primibrachial facet topography a series of concentrically aligned nodes from the facet margin toward the axial canal.

Column unknown.

Holotype.—TUG 1395-42.

Occurrence.—Middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island, Estonia.

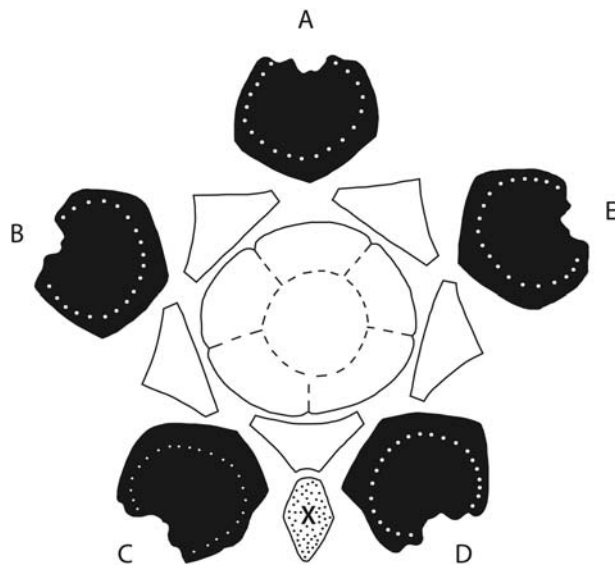


Figure 3. Plate diagram of *Velocrinus coniculus* n. gen. and sp. Black, radial plates; stippled pattern, anal X; and dotted line, limits of radial facet; dashed line, poorly visible or inferred plate sutures.

Measurements.—Infrabasal plate height, 2.0; width, 11.2. Basal plate height, 6.1; width 12.8. Radial plate height, 12.4; width 14.1. First primibrachial facet height, 8.4, width, 10.8.

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? sp.
 Figure 2.5

Material.—TUG 1395-60.

Occurrence.—Middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island, Estonia.

Remarks.—An incomplete and partially disarticulated crown (mostly arms) is assigned to *Protaxocrinus?* sp. It is small (less than 20 mm in diameter) and may represent a juvenile. Both the abaxially incurved arms and patelloid processes on some proximal brachials indicated that this specimen is a flexible and potentially a taxocrinid (Fig. 2.5). What is known of its morphology is consistent with other Silurian examples of *Protaxocrinus*.

Crinoidea incertae sedis

Remarks.—Several (TUG 1395-64 to TUG 1395-70) terminal holdfasts with branching pseudocirri occur in the Middle Äigu Beds, Kaugatuma Formation (Pridoli) at Kaugatuma Cliff, Saaremaa Island, Estonia.

Acknowledgments

We thank A. Bancroft, R. Ekka, J. Novak, M. Peter, J. Thompson, and I. Vinn for help with field work. The reviews by D.L. Meyer and G.D. Sevastopulo significantly improved an earlier draft of this manuscript. Support for this research was from the National Geographic Society (NGS 60031112), The College of Wooster, The Ohio State University, and the University of Tartu. O.V. acknowledges Estonian Science Foundation grant ETF9064, Estonian Research Council grant IUT20-34 and the target-financed project (from the Estonian Ministry of Education and Science) SF0180051s08 for financial support.

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Appendix 1. Locality details.

Saaremaa Island

Kaugatuma cliff (2.5 m high) is situated on the western coast of the Sörve 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).

Kuriku cliff (58° 30' 10.1514" 22° 0' 46.224") is located on the western shore of Tagalaht Bay a few hundred meters east of the Suuriku cliff. The outcrop is a 2-3 meters high section of Ninase Member of Jaani Formation. The upper part of the section is characterized by dolomitic boundstones with marlstone interbeds and cavernous dolomites (Hints, 2008). Small bioherms occur in the middle part of the section containing numerous bryozoans (O.V. personal communication.). Dolomitized crinoidal limestones and coarse-grained skeletal grainstones occur in the lower part of the section (Hints, 2008). The

crinoid fossils are more common in the lower part of the section (O.V. personal communication). Most common fossils at the Kuriku cliff are tabulate corals, rugose corals and bryozoans (Hints, 2008).

Suuriku cliff is 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 grainstones with interlayers of marlstones 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 (Olev Vinn personal communication) The lower part of the Suuriku section consists of marlstones of the Mustjala Member (Hints, 2008).

The Undva cliff is 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 grainstones with interlayers of marlstone (Hints, 2008). Fragments of crinoid calyxes are common in the grainstones of the Ninase Member.

Accepted 2 April 2014