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Early Silurian crinoid diversification on Baltica: *Euspirocrinus varbolaensis* sp. nov.

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ABSTRACT

This article describes the crinoid *Euspirocrinus varbolaensis* sp. nov. from the early Silurian (Rhuddanian) of northern Estonia. Discovered within the lower Rhuddanian strata in the Reinu quarry, Rapla Parish, this is the second Rhuddanian species of *Euspirocrinus* from Estonia. Its discovery further documents the rapid faunal recovery of early Silurian crinoids following the Late Ordovician biotic crisis. This find supports the hypothesis that the early Silurian recovery of crinoids was primarily the result of the diversification and migration of Laurentian clades.

Introduction

The evolutionary history of crinoids was significantly altered by the Late Ordovician extinctions, the second-most severe biosphere collapse in Earth's history (e.g., Sepkoski 1996; Alroy 2008, 2010a, 2010b; Harper et al. 2014). Recent research has focused on understanding the tempo and mode of the extinction and recovery of crinoids during this period (e.g., Peters and Ausich 2008; Ausich and Deline 2012; Kozik et al. 2022). Understanding the Ordovician and Silurian crinoid faunas from the Baltica paleocontinent is important because paleogeography may be a key to unraveling this evolutionary history (Ausich and Wilson 2016; Wright and Toom 2017; Ausich et al. 2019a, 2019b). Hence, the discovery of a new, nearly complete crinoid from the basal Rhuddanian in the Reinu quarry, Rapla Parish, Estonia (Fig. 1), is particularly significant in deciphering the evolutionary history of crinoids. In this



study, we describe *Euspirocrinus varbolaensis* sp. nov. and discuss the evolutionary history of *Euspirocrinus* from the Late Ordovician to the early Silurian biotic crisis.

Geological setting and stratigraphy

Estonia formed part of the Baltica paleocontinent, which was located in equatorial latitudes in the Silurian and continued its northward drift (Cocks and Torsvik 2005; Torsvik and Cocks 2013). A shallow epicontinental sea covered central and western Estonia. The end-Ordovician was followed by major biotic and environmental changes in Estonia and adjacent areas (Cocks and Torsvik 2005; Dronov et al. 2011; Kaljo et al. 2011). The lower Rhuddanian strata (Juuru Regional Stage) crop out in the western islands and eastern mainland of Estonia. In central Estonia, the Rhuddanian includes two units: the fossil-rich limestone of the Varbola Formation and the coquina limestone of the Tamsalu Formation. Lower Rhuddanian fossil assemblages exhibit a “post-event syndrome”, characterized by low diversity, high abundance, and small body size (Kaljo 1996; Borths and Ausich 2011; Ausich and Wilson 2016).

The new crinoid described here comes from approximately the lower 1.7 meters of the lower Silurian Varbola Formation of the Reinu quarry (Fig. 2). In 2022, the Ordovician–Silurian boundary was exposed on a large scale in the quarry.

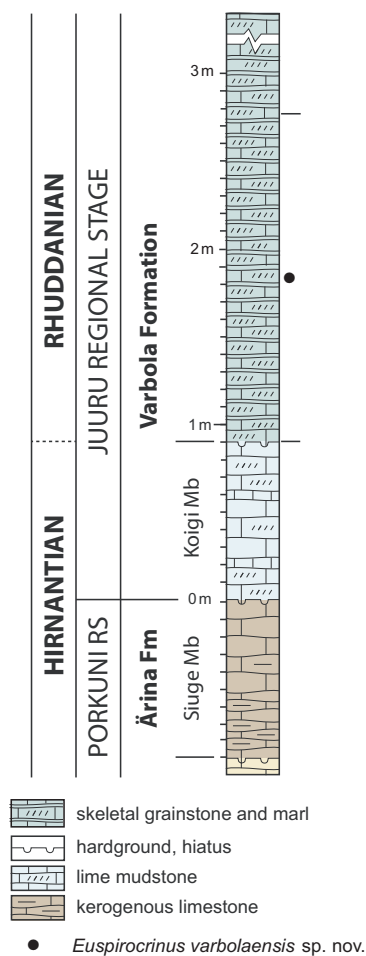


Fig. 2. Stratigraphic column of the Ordovician–Silurian boundary beds in the Reinu quarry, modified from Hints et al. (2023). Abbreviations: Fm – Formation, Mb – Member, RS – Regional Stage.

Since then, the lowermost beds of the Varbola Formation have been accessible. This formation is represented mainly by alternating packstones/grainstones and marl beds in a thickness of ~11 m (Hints et al. 2023). The lowermost part of the Varbola Formation (Koigi Member, Hirnantian) consists of lime mudstones. The formation contains abundant tabulate corals, stromatoporoids, rugosans, brachiopods, and other shelly fossils (Jeon et al. 2022). Additionally, benthic forms of microfossils such as scolecodonts are abundant (Hints and Tonarová 2023). The 1.7 meters of Rhuddanian sediments covering the Koigi Member are strongly bioturbated by the *Chondrites* tracemaker.

Taxonomy

The ordinal and superordinal classification of crinoids follows Cole (2017, 2018), Wright (2017a, 2017b), and Wright et al. (2017). The family-level classification of crinoids follows Moore and Teichert (1978). Morphological terminology for crinoids is from Webster (1974), Ubaghs (1978), Webster and Maples (2008), Kammer et al. (2013), Ausich et al. (2020), and Ausich and Donovan (2023). A, B, C, D, and E represent echinoderm rays following the Carpenter Ray system (see Ubaghs 1978, T63). Heteromorphic column patterns are indicated using the Webster (1974) system.

In specimen measurements, the following abbreviations are used: ACH – aboral cup height, ACW – aboral cup width, ASH – anal sac height, CrH – crown height, BH – basal plate height, BW – basal plate width, IBH – infrabasial plate height, IBW – infrabasial plate width, RH – radial plate height, and RW – radial plate width. All measurements are in mm, and an asterisk (*) after a measurement indicates that the feature is incompletely preserved.

The list of species within *Euspirocrinus* is taken uncritically from Webster (2014). The holotype of *Euspirocrinus varbolaensis* sp. nov. is housed in the Department of Geology, Tallinn University of Technology, Tallinn, Estonia (GIT). This new species is registered with ZooBank (urn:lsid:zoobank.org:act:9D872EC5-AEAB-4155-9A99-6B1618B007D7).

Class CRINOIDEA Miller, 1821
 Subclass PENTACRINOIDEA Jaekel, 1894
 Infraclass INADUNATA Wachsmuth and Springer, 1885
 Parvclass CLADIDA Moore and Laudon, 1943
 Magnaorder EUCLADIDA Wright, 2017a
 Superorder CYATHOFORMES Wright et al., 2017
 CYATHOFORMES INCERTAE SEDIS:
 ‘CYATHOCRINIDAE’ Bather, 1899
 Family Euspirocrinidae Bather, 1899
 Genus *Euspirocrinus* Angelin, 1878

Type species. *Euspirocrinus spiralis* Angelin, 1878, by monotypy.

Other species. *Euspirocrinus cirratus* Strimple, 1963; *E. gannoni* Ausich and Copper, 2010; *E. girvanensis* Donovan, 1992; *E. heliktos* Ausich, 1986; *E. hintsae* Ausich et al., 2019a; *E. varbolaensis* sp. nov.; and *E. wolcottense* Eckert and Brett, 2001.

Table 1. Temporal and paleogeographic distribution of *Euspirocrinus*

Period	Epoch	Age	Laurentia	Baltica
Silurian	Ludlow or Pridoli		<i>E. cirratus</i>	–
	Wenlock	Homerian	–	–
		Sheinwoodian	–	<i>E. spiralis</i>
	Llandovery	Telychian	<i>E. wolcottense</i>	–
		Aeronian	<i>E. heliktos</i>	–
Rhuddanian		<i>E.?</i> sp.	<i>E. hintsae</i> and <i>E. varbolaensis</i>	
Ordovician	Hirnantian	Hirnantian	<i>E. gagnoni</i>	–
	Katian	Katian	<i>E. girvanensis</i>	–

Occurrence. Ordovician: Katian, Scotland; Hirnantian, Canada. Silurian: Llandovery, Rhuddanian, Estonia, Canada; Aeronian, USA; Telychian, Canada; Wenlock, Sweden; Ludlow or Pridoli, USA (Table 1).

Remarks. Species-diagnostic characters for *Euspirocrinus* include the shape of the aboral cup, aboral plate sculpturing, occurrence and type of nodes on infrabasal plates, size of proximal anal sac plates, number of posterior plates in the aboral cup, number of primibrachials, arm branching, presence or absence of keels or nodes on brachial plates, columnal construction, column type, and relative column height (Table 2).

Euspirocrinus varbolaensis sp. nov.

Figs 3, 4

Holotype. GIT 405-349.

Diagnosis. Aboral cup high bowl-shaped, various plate sculpturing with pustulose surface texture superimposed on various coarse nodes and depressions, proximal pointing nodes on infrabasal plates, large proximal anal sac plates, three posterior plates in the aboral cup, two or three primibrachials, isotomous arm branching (as known), keels or nodes on brachial plates absent, column holomeric, column type and height unknown.

Etymology. The species name *varbolaensis* recognizes the Varbola Stronghold, where the stratotype of the Varbola Formation is located.

Age/occurrence. Lower Silurian, Rhuddanian; collected from float that was a small slab with *Chondrites*, which is typical for the ~1.7 m above the base of the Ordovician–Silurian boundary in the Varbola Formation, Juuru Regional Stage, Reinu quarry, Rapla Parish, Estonia (latitude 59.087299 N, longitude 24.73768 E; Hints et al. 2023).

Description. Crown small in size. Aboral cup high bowl-shaped, plates convex, plate sutures slightly depressed (Fig. 3A). Basal and radial plates with various plate sculpturing with pustulose surface texture superimposed on various coarse nodes and depressions (Fig. 3B).

Infrabasal circlet ~18% of aboral cup height; infrabasal plates five, equal in size, visible in lateral view; each infrabasal plate with one large downward-pointing node (Figs 3C, 4C). Basal circlet ~42% of aboral cup height; basal plates five, as large as radial plates, ~1.3 times wider than high; AB, DE and AE basal plates hexagonal, CD and DE radial plates

heptagonal. Radial circlet ~40% of aboral cup height; radial plates five, pentagonal, ~1.7 times wider than high. Radial facets angustary, crescentic, declivate, details of articular facet unknown.

Three large posterior plates in the aboral cup (Fig. 3A); radianal plate beneath and to the left of the C radial plate, anal X plate above to the left of the radianal plate and between the D radial plate and the lower portion of the right sac plate, proximal part of the right sac plate in articulation with the C radial plate to the right and the radianal plate beneath, extends above the aboral cup; radianal, anal X and right sac plates all higher than wide. Above the aboral cup a robust series of plates along the CD portion of the anal sac, three to four plates across sac width, plates approximately as high as wide, convex, sutures between plates depressed; distal tip of the anal sac broken (Fig. 4A).

Five free arms, branched at least twice with isotomy (as known; Fig. 3D,E). Primibrachials ~4.6 times wider than high, primibrachial 2 or 3 axillary. Three secundibrachials, first secundibrachial ~2.0 times wider than high, other two secundibrachials also wider than high. At least one additional arm division in tertibrachials, other details unknown.

Proximal columnal circular, holomeric.

Oral surface and other features of the column unknown.

Remarks. *Euspirocrinus varbolaensis* sp. nov. has a unique combination of characters that differentiate it from congeners (Table 2). Two characters – a high bowl-shaped aboral cup and large downward-pointing nodes on the infrabasals – are unique among species within the genus *Euspirocrinus*. *Euspirocrinus hintsae*, the other Rhuddanian species from Estonia, has a low bowl-shaped aboral cup, fine pustulose aboral cup plate sculpturing, proximal-pointing nodes on infrabasal plates absent, size of proximal anal sacs unknown, number of plates in the posterior of the aboral cup unknown, two to three primibrachials, arm branching poor isotomy proximally and endotomous distally, column construction pentameric, and column heteromorphic. In contrast, *E. varbolaensis* has a high bowl-shaped aboral cup, basal and radial plates with various plate sculpturing with pustulose surface texture superimposed on various coarse nodes and depressions, proximal-pointing nodes on infrabasal plates, large proximal anal sac plates, three plates in the posterior of the aboral cup, two to three primibrachials, arm branching poor isotomy proximally and distally unknown, column construction holomeric, and column type unknown. *Euspirocrinus varbolaensis* differs from the Hirnantian *E. gagnoni* of Canada with the majority of known species-diagnostic characters (Table 2).

Table 2. Species diagnostic characters for *Euspirocrinus*

<i>Euspirocrinus</i> species	Aboral cup shape	Aboral cup sculpturing	Proximal pointing nodes on infrabasal plates	Proximal pointing anal sac plates	Number of plates in posterior	Number of primi-brachials	Arm branching	Keels or nodes on brachials	Columnal construction	Column type	Column height
<i>E. cirratus</i>	Low cone	Radial convex	Absent	Unknown	3	2	Unknown	Unknown	Unknown	Unknown	Unknown
<i>E. gagnoni</i>	Medium bowl	Smooth	Absent	Small	3	2-3	Imperfect endotomy	Absent	Holomeric	Heteromorphic	Long
<i>E. girvanensis</i>	Medium bowl	Unknown	Unknown	Small	3	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>E. heliktos</i>	Medium bowl or cone	Various coarse sculpturing	Absent	Large	4	2 (rarely 3)	Weak endotomy	Present	Poor pentameric	Heteromorphic	Long
<i>E. hintsae</i>	Low bowl	Fine pustulose	Absent	Unknown	Unknown	2-3	Poor isotomy proximally and endotomous distally	Absent	Pentameric	Heteromorphic	Unknown
<i>E. spiralis</i>	Medium cone	Smooth	Absent	Large	3	2	Weak endotomy	Absent	Pentameric	Heteromorphic	Short
<i>E. wolcottense</i>	Medium bowl	Ridges and pustules	Absent	Small	3 (rarely 4)	2-3	Weak endotomy	Absent	Pentameric distally	Xenomorph	Short
<i>E. varbotaensis</i> sp. nov.	High bowl	Pustulose surface texture superimposed on various coarse nodes and depressions	Present	Large	3	2-3	Isotomy (as known)	Absent	Holomeric	Unknown	Unknown

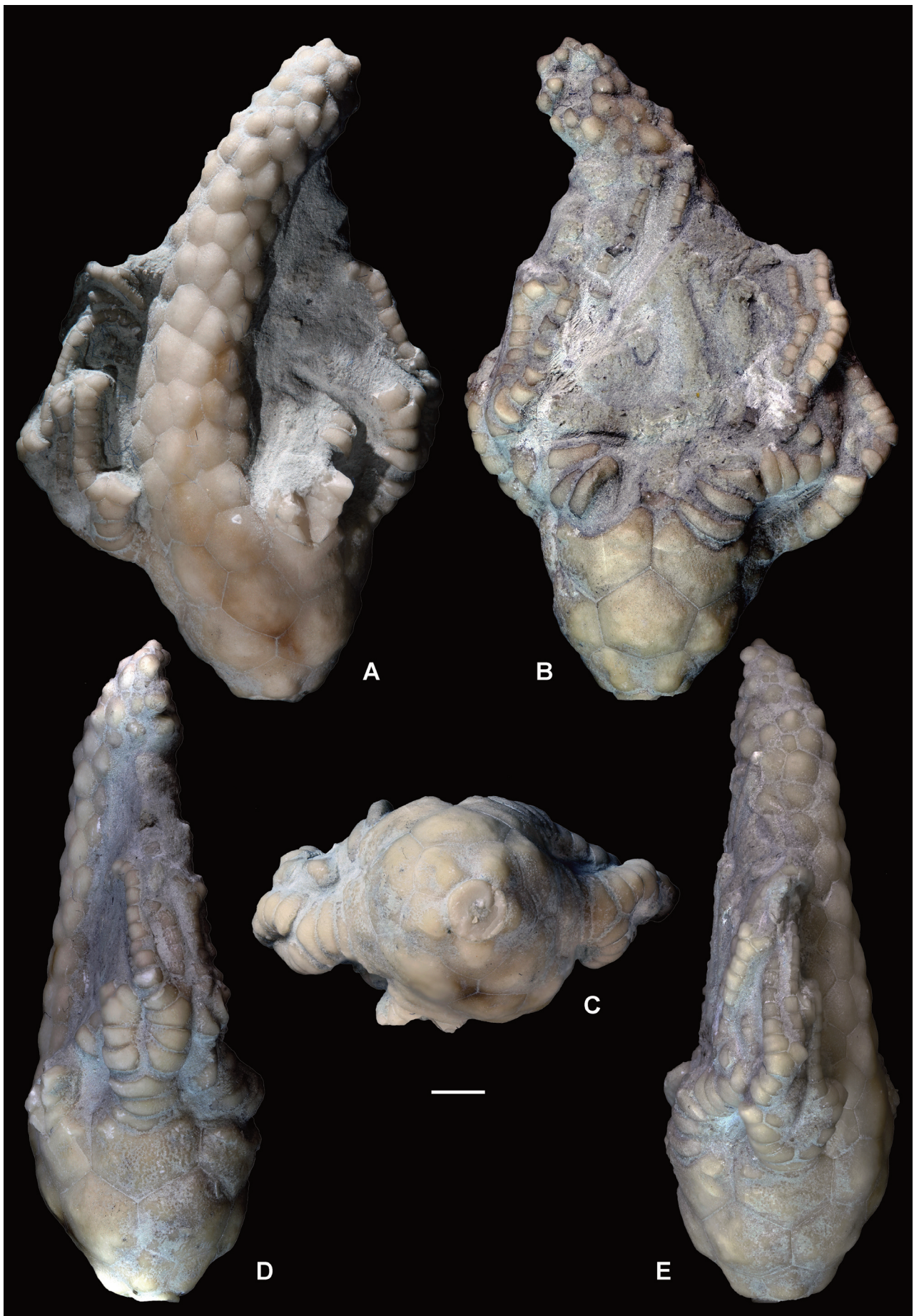


Fig. 3. Crown of *Euspirocrinus varbolaensis* sp. nov. A – CD-interray lateral view of the crown (note the large plates of the anal sac), B – AE-interray lateral view of the calyx (note the three primibrachials on E-ray), C – basal view of the slightly compacted crown (note the circular proximal columnal and the relatively small axial canal), D – B-ray lateral view of the crown (note arm branching and granular aboral cup plating), E – D-ray lateral view of the crown (note the contrasting number of primibrachials in E-ray vs D-ray). Scale bar 2.5 mm.

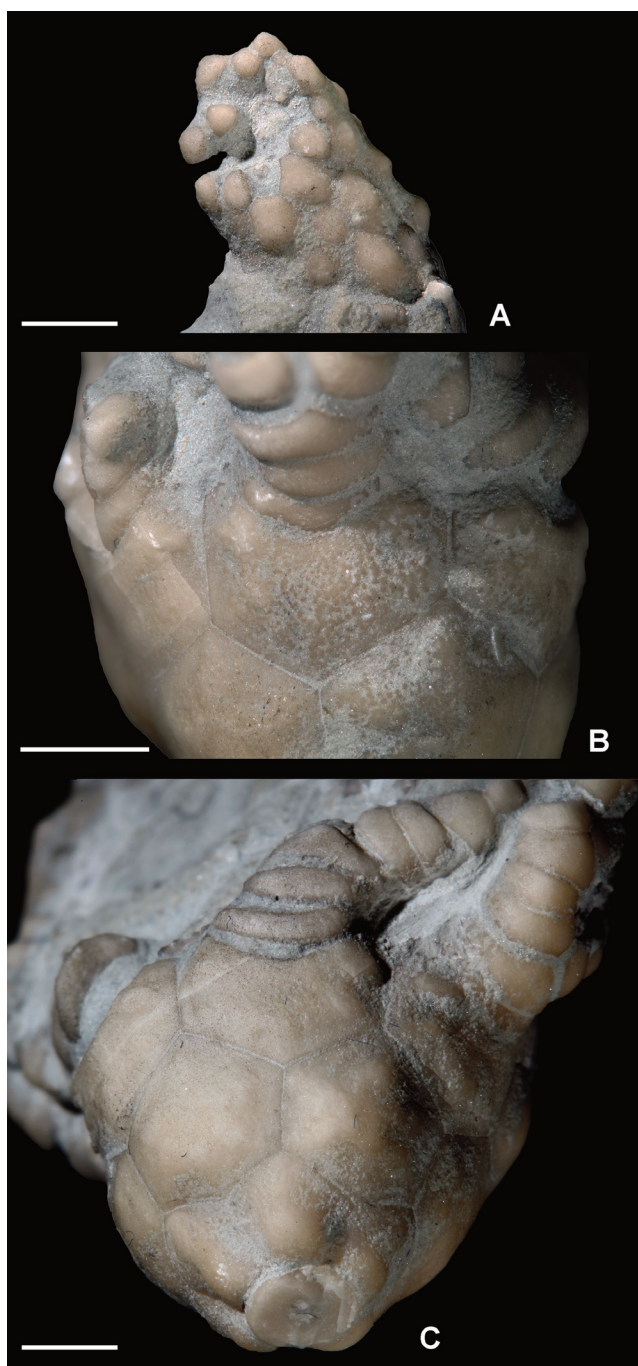


Fig. 4. *Euspirocrinus varbolaensis* sp. nov. **A** – broken distal tip of the anal sac, **B** – D-ray lateral view of the aboral cup (note plate sculpturing), **C** – oblique lateral view of E-ray (note large downward-pointing nodes on the infrabasals plates). All scale bars 2.5 mm.

Measurements. GIT 405-349: CrH – 34.8*, ACH – 9.7, ACW – 10.4, IBH – 2.5, IBW – 3.1, BH – 4.6, BW – 5.2, RH – 3.2, RW – 4.5, ASH – 25.1.

Conclusions

Euspirocrinus varbolaensis sp. nov. represents the second species of *Euspirocrinus* known from the Varbola Formation in the Reinu quarry in Estonia. Ausich et al. (2019a, 2019b) described *E. hintsae*, which was collected from younger Rhuddanian strata of the Varbola Formation, Juuru Regional Stage, Reinu quarry. The discovery of *Euspirocrinus varbo-*

laensis sp. nov. within the lower ~1.7 m of the Varbola Formation, near the base of the Rhuddanian portion, further confirms the rapid recovery of *Euspirocrinus*, along with migration to Baltica, during the earliest Rhuddanian.

The oldest known species of *Euspirocrinus* is from the Katian Lady Burn Starfish beds of Scotland, which was part of Laurentia during the Ordovician (Donovan 1992). *Euspirocrinus* persisted on Laurentia, with the occurrence of *E. gagnoni* (Ausich and Copper 2010) from the Hirnantian of Anticosti Island, Quebec, Canada. *Euspirocrinus* was one of a handful of crinoid genera to cross the Ordovician–Silurian boundary (Ausich and Deline 2012), and it occurred in Rhuddanian strata on both Laurentia and Baltica. *Euspirocrinus* persisted into the upper Silurian of Laurentia and the Wenlock (Sheinwoodian) of Baltica before becoming extinct (Table 2).

These results are consistent with those of Ausich and Deline (2012), who concluded that the post-extinction Silurian recovery of crinoids was largely the result of the diversification and migration of Laurentian clades. Rhuddanian crinoids from Estonia establish the fact that the post-extinction diversification and migration to Baltica was very rapid.

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References

- Alroy, J. 2008. Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences*, **105**(S1), 11536–11542. <https://doi.org/10.1073/pnas.0802597105>
- Alroy, J. 2010a. Geographic, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, **53**(6), 1211–1235. <https://doi.org/10.1111/j.1475-4983.2010.01011.x>
- Alroy, J. 2010b. The shifting balance of diversity among major marine animal groups. *Science*, **329**(5996), 1191–1194. <https://doi.org/10.1126/science.1189910>
- Angelin, N. P. 1878. *Iconographia Crinoideorum in Stratis Sueciae Siluricis Fossilium*. Samson & Wallin, Stockholm.
- Ausich, W. I. 1986. Early Silurian inadunate crinoids (Brassfield Formation, Ohio). *Journal of Paleontology*, **60**(3), 719–735. <https://doi.org/10.1017/S0022336000022241>
- Ausich, W. I. and Copper, P. 2010. The Crinoidea of Anticosti Island, Québec (Late Ordovician to early Silurian). *Palaeontographica Canadiana*, **29**, 1–157.
- Ausich, W. I. and Deline, B. 2012. Macroevolutionary transitions in crinoids following the Late Ordovician extinction event (Ordovician to early Silurian). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **361–362**, 38–48. <https://doi.org/10.1016/j.palaeo.2012.07.022>
- Ausich, W. I. and Donovan, S. K. 2023. Chapter 7: Glossary of morphological terms. In *Treatise on Invertebrate Paleontology, Pt. T, Revised, Vol. 1* (Ausich, W. I., ed.). University of Kansas Press, Lawrence, Kansas, 1–26.
- Ausich, W. I. and Wilson, M. A. 2016. Llandovery (early Silurian) crinoids from Hiiumaa Island, western Estonia. *Journal of Paleontology*, **90**(6), 1139–1147. <https://doi.org/10.1017/jpa.2016.120>

- Ausich, W. I., Wilson, M. A. and Toom, O. 2019a. Early Silurian recovery of Baltica crinoids following the end-Ordovician extinctions (Llandovery, Estonia). *Journal of Paleontology*, **94**(3), 521–530. <https://doi.org/10.1017/jpa.2019.89>
- Ausich, W. I., Wilson, M. A. and Tinn, O. 2019b. Kalana Lagerstätte crinoids: Early Silurian (Llandovery) of central Estonia. *Journal of Paleontology*, **94**(1), 121–144. <https://doi.org/10.1017/jpa.2019.27>
- Ausich, W. I., Wright, D. F., Cole, S. R. and Sevastopulo, G. D. 2020. Homology of posterior interarray plates in crinoids: a review and new perspectives from phylogenetics, the fossil record and development. *Palaeontology*, **63**(4), 525–545. <http://doi.org/10.1111/pala.12475>
- Bather, F. A. 1899. A phylogenetic classification of the Pelmatozoa. *Report of the British Association for the Advancement of Science (1898)*, 916–923.
- Borths, M. R. and Ausich, W. I. 2011. Ordovician–Silurian Lilliput crinoids during the end-Ordovician biotic crisis. *Swiss Journal of Paleontology*, **130**(1), 7–18. <http://doi.org/10.1007/s13358-010-0003-2>
- Cocks, L. R. M. and Torsvik, T. H. 2005. Baltica from the late Precambrian to mid-Palaeozoic times: The gain and loss of a terrane's identity. *Earth-Science Reviews*, **72**(1–2), 39–66. <https://doi.org/10.1016/j.earscirev.2005.04.001>
- Cole, S. R. 2017. Phylogeny and morphologic evolution of the Ordovician Camerata (Class Crinoidea, Phylum Echinodermata). *Journal of Paleontology*, **91**(4), 815–828. <https://doi.org/10.1017/jpa.2016.137>
- Cole, S. R. 2018. Phylogeny and evolutionary history of diplobathrid crinoids (Echinodermata). *Palaeontology*, **62**(3), 357–373. <https://doi.org/10.1111/pala.12401>
- Donovan, S. K. 1992. New cladid crinoids from the Late Ordovician of Girvan, Scotland. *Palaeontology*, **35**(1), 149–158.
- Dronov, A. V., Ainsaar, L., Kaljo, D., Meidla, T., Saadre, T. and Einasto, R. 2011. Ordovician of Baltoscandia: Facies, sequences and sea-level changes. In *Ordovician of the World* (Gutierrez-Marco, J. C., Rabano, I. and Garcia-Bellido, D., eds). *Cuadernos del Museo Geominero*, **14**, 143–150.
- Eckert, J. D. and Brett, C. E. 2001. Early Silurian (Llandovery) crinoids from the Lower Clinton Group, western New York State. *Bulletins of American Paleontology*, **360**, 1–88.
- Harper, D. A. T., Hammarlund, E. U. and Rasmussen, C. M. Ø. 2014. End Ordovician extinctions: A coincidence of causes. *Gondwana Research*, **25**(4), 1294–1307. <https://doi.org/10.1016/j.gr.2012.12.021>
- Hints, O. and Tonařová, P. 2023. A diverse Hirnantian scolecodont assemblage from northern Estonia and resilience of polychaetes to the end-Ordovician mass extinction. *Estonian Journal of Earth Sciences*, **72**(1), 46–49. <https://doi.org/10.3176/earth.2023.20>
- Hints, O., Ainsaar, L., Meidla, T., Nõlvak, J. and Toom, U. 2023. Stop 8: Reinu quarry. In *ISOS-14 Field Guide: The Ordovician of Estonia* (Hints, O. and Toom, U., eds). TalTech Department of Geology, Tallinn.
- Jaekel, O. 1894. Über die Morphogenie und Phylogenie der Crinoiden (On the Morphology and Phylogeny of Crinoids). *Sitzungsberichten der Gesellschaft Naturforschender Freunde*, **4**, 101–121.
- Jeon, J., Vinn, O., Liang, K., Zapalski, M. K., Toom, U. and Kershaw, S. 2022. Stromatoporoid-coral/tubeworm intergrowths in the lowermost Silurian Varbola Formation of Estonia: First evidence of competitive interaction. *Lethaia*, **55**(2), 1–13. <https://doi.org/10.18261/let.55.2.4>
- Kaljo, D. 1996. Diachronous recovery patterns in Early Silurian corals, graptolites and acritarchs. In *Biotic Recovery from Mass Extinction Events* (Hart, M. B., ed.). *Geological Society, London, Special Publications*, **102**(1), 127–133. <https://doi.org/10.1144/GSL.SP.1996.001.01.10>
- Kaljo, D., Hints, L., Hints, O., Männik, P., Martma, T. and Nõlvak, J. 2011. Katian prelude to the Hirnantian (Late Ordovician) mass extinction: A Baltic perspective. *Geological Journal*, **46**(5), 464–477. <https://doi.org/10.1002/gj.1301>
- Kammer, T. W., Sumrall, C. D., Zamora, S., Ausich, W. I. and Deline, B. 2013. Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms. *PLOS ONE*, **8**(11). <http://dx.plos.org/10.1371/journal.pone.0077989>
- Kozik, N. P., Young, S. A., Newby, S. M., Liu, M., Chen, D., Hammarlund, E. U. et al. 2022. Rapid marine oxygen variability: Driver of the Late Ordovician mass extinction. *Science Advances*, **8**(46). <https://doi.org/10.1126/sciadv.abn8345>
- Miller, J. S. 1821. *A Natural History of the Crinoidea, or Lily-shaped Animals; with Observations on the Genera Asteria, Euryale, Comatula and Marsupites*. C. Frost, Bristol.
- Moore, R. C. and Laudon, L. R. 1943. Evolution and classification of Paleozoic crinoids. *Geological Society of America Special Papers*, **46**, 1–154. <https://doi.org/10.1130/SPE46-p1>
- Moore, R. C. and Teichert, C. (eds) 1978. *Treatise on Invertebrate Paleontology. Pt. T. Echinodermata 2*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- Peters, S. E. and Ausich, W. I. 2008. A sampling-adjusted macro-evolutionary history for Ordovician–Early Silurian crinoids. *Paleobiology*, **3**, 104–116. <https://doi.org/10.1666/07035.1>
- Sepkoski, J. J., Jr. 1996. Patterns of Phanerozoic extinction: A perspective from global data bases. In *Global Events and Event Stratigraphy in the Phanerozoic* (Walliser, O. H., ed.). Springer-Verlag, Berlin, 31–51. https://doi.org/10.1007/978-3-642-79634-0_4
- Strimple, H. L. 1963. Crinoids of the Hunton Group (Devonian–Silurian) of Oklahoma. *Oklahoma Geological Survey Bulletin*, **100**, 1–169.
- Torsvik, T. H. and Cocks, L. R. M. 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In *Early Palaeozoic Biogeography and Palaeogeography* (Harper, D. A. T. and Servais, T., eds). *Geological Society, London, Memoirs*, **38**, 5–24. <https://doi.org/10.1144/M38.2>
- Ubahgs, G. 1978. General morphology. In *Treatise on Invertebrate Paleontology. Pt. T. Echinodermata 2* (Moore, R. C. and Teichert, C., eds). Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, T58–T216.
- Wachsmuth, C. and Springer, F. 1880–1886. Revision of the Palaeocrinoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia, Pt. III, Sec. 1. Discussion of the classification and relations of the brachiote crinoids, and conclusion of the generic descriptions (1885)*, 225–364 (separate repaged, 1–138).
- Webster, G. D. 1974. Crinoid pluricolumnal noditaxis patterns. *Journal of Paleontology*, **48**(6), 1283–1288.
- Webster, G. D. 2014. *Bibliography and Index of Paleozoic Crinoids, Coronates, and Hemistreptocrinoids*. <http://crinoids.azureweb sites.net/> (accessed 2023-02-06).
- Webster, G. D. and Maples, C. G. 2008. Cladid crinoid radial facets, brachials, and arm appendages: A terminology solution for studies of lineage, classification, and paleoenvironment. In *Echinoderm Paleobiology* (Ausich, W. I. and Webster, G. D., eds). Indiana University Press, Bloomington, Indiana, 196–226.
- Wright, D. F. 2017a. Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata). *Journal of Paleontology*, **91**(4), 799–814. <https://doi.org/10.1017/jpa.2016.141>
- Wright, D. F. 2017b. Phenotypic innovation and adaptive constraints in the evolutionary radiation of Palaeozoic crinoids. *Scientific Reports*, **7**, 13745. <https://doi.org/10.1038/s41598-017-13979-9>
- Wright, D. F. and Toom, U. 2017. New crinoids from the Baltic region (Estonia): Fossil tip-dating phylogenetics constrains the origin and Ordovician–Silurian diversification of the Flexibilia (Echinodermata). *Palaeontology*, **60**(6), 893–910. <https://doi.org/10.1111/pala.12324>
- Wright, D. F., Ausich, W. I., Cole, S. R., Peter, M. E. and Rhenberg, E. C. 2017. Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata). *Journal of Paleontology*, **91**(4), 829–846. <https://doi.org/10.1017/jpa.2016.142>

Vara-Siluri krinoidide mitmekesistumine Baltica paleokontinendil: *Euspirocrinus varbolaensis* sp. nov.

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Artiklis kirjeldatakse uut krinoidi liiki *Euspirocrinus varbolaensis* sp. nov., mis avastati Eesti Vara-Siluri ladestust, Rhuddani lademest. Liik leiti Rapla maakonnas asuvast Reinu karjäärast, Rhuddani lademe alumisest, umbes 1,7 meetri paksusest kihist. See on teine *Euspirocrinus*'e liik Eesti Rhuddani lademest ning näitab krinoidifauna kiiret taastumist Vara-Siluris pärast väljasuremist Hiliis-Ordoviitsiumis. Uus liik toetab hüpoteesi, et krinoidide varajane taastumine Siluris oli peamiselt Laurentia paleokontinendi monofüleetiliste rühmade mitmekesistumise ja rände tagajärg.
