

## First report of the mitrate *Lagynocystis* (Echinodermata: Stylophora) in the Ordovician of the Baltic paleobasin

SERGEY V. ROZHNOV<sup>1</sup>, GEORGY V. MIRANTSEV<sup>1</sup> & SERGEY S. TERENTIEV<sup>2</sup>

<sup>1</sup>Borissiak Paleontological Institute PAS, Profsoyuznaya str., 123, Moscow 117647, Russia

E-mail: Rozhnov@paleo.ru, gmirantsev@gmail.com

<sup>2</sup>St. Petersburg, Russia

E-mail: serge\_terentiev@yahoo.com

### Abstract

Three incomplete thecae of the stylophoran *Lagynocystis* cf. *pyramidalis* (Barrande, 1887) are described from the Upper Ordovician of the Baltic Paleobasin for the first time. These specimens of *Lagynocystis* are the first records of this genus from the Ordovician outside peri-Gondwana, thus significantly expanding its paleogeographical distribution of this genus. Due to the preservation of the specimens the microstructure of the stereom is studied for the first time in this genus.

**Keywords:** *Lagynocystis*, Stylophora, Mitrata, carpoids, echinoderms, Baltic Paleobasin, Ordovician, stereom

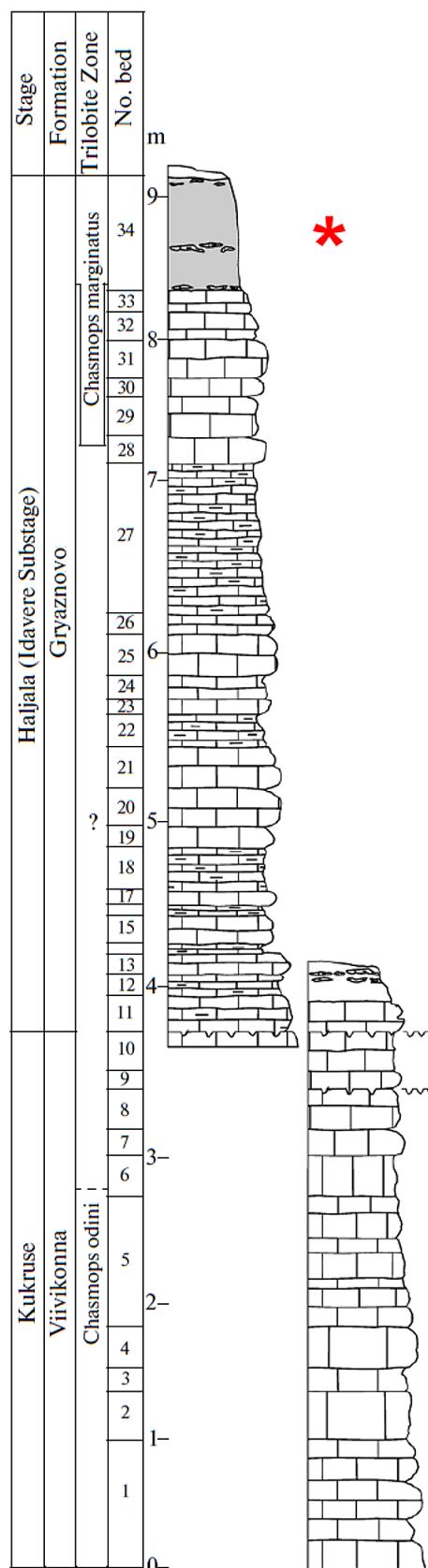
### Introduction

Stylophorans (cornutes and mitrates) are an unusual group of non-pentameral Paleozoic echinoderms. Because of its peculiar morphology, this group has long attracted the attention of paleontologists, and various, different interpretations have been proposed for their anatomy, systematic position and mode of life (Ubaghs 1961; Jefferies 1973, 1986; Philip 1979; Parsley 1988, 1998; Kolata *et al.* 1991; David *et al.* 2000; Lefebvre 2003; Clausen & Smith 2005). Here we describe the first discovery of the mitrate stylophoran *Lagynocystis* from the Ordovician of Baltiet *et al.*c Paleobasin. Although the three available specimens are represented by incomplete thecae, they can be confidently identified as *Lagynocystis* cf. *pyramidalis* (Barrande, 1887), because of their great similarity with that species. The three-dimensional preservation of the material made it possible to study the microstructure of the stereom on both the aulacophore apophyses and the lateral surfaces of marginals. The presence of this genus from the Baltic Paleobasin expands our knowledge about biogeographic relations between peri-Gondwana and the Baltic Paleobasin, and it also supports the remarkable adaptive possibilities of this long-ranging genus.

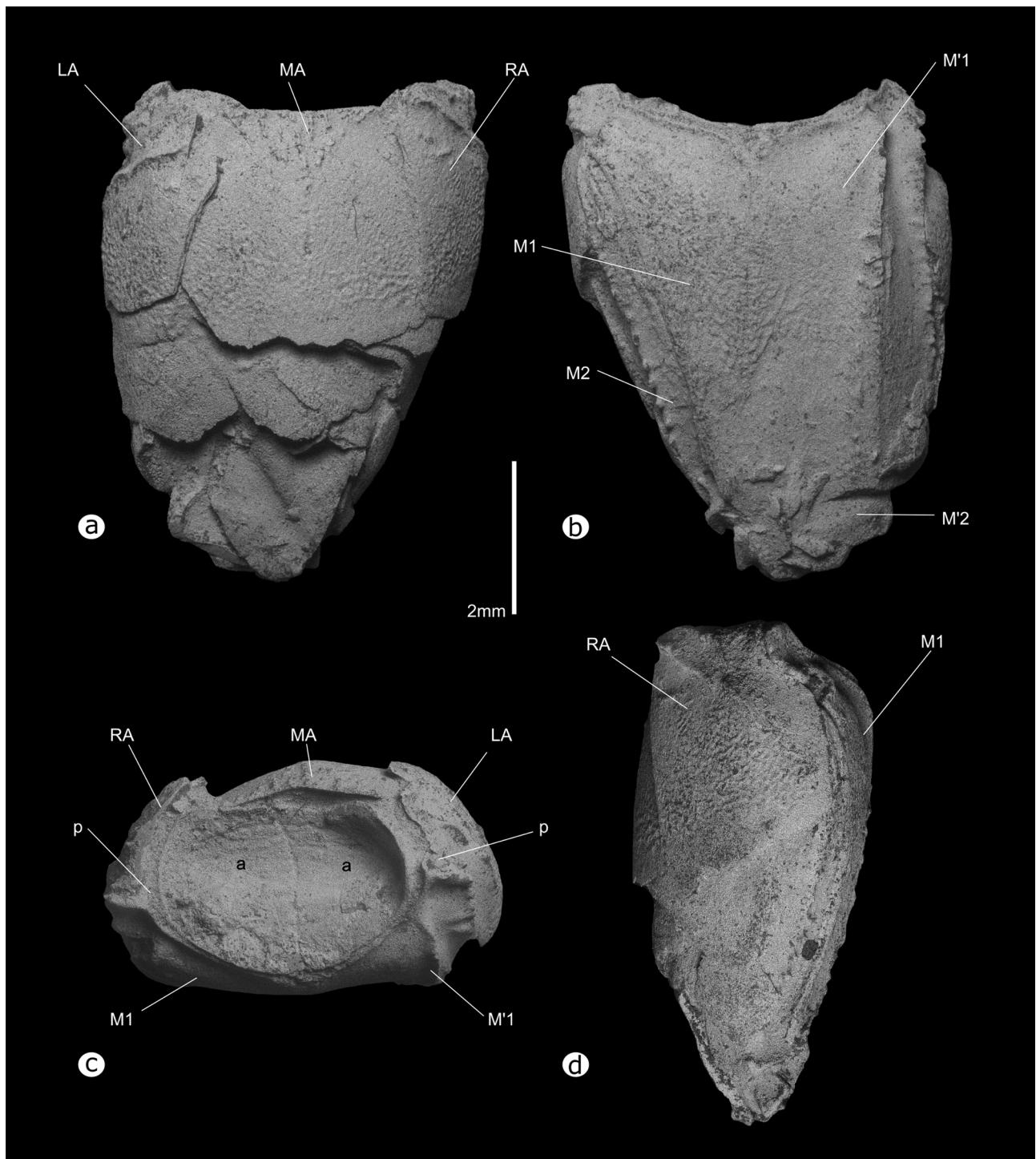
### Materials and methods

The specimens of *Lagynocystis* were collected in clays of the Upper part of Gryaznovo Formation (Upper Ordovician, Haljala regional stage, Upper Sandbian) in the west of the Leningrad Region in an old quarry near the village Klyasino (Fig. 1). This section was described by Dolgov & Meidla (2011). All specimens were found in the upper part of the section, in greenish-grey and bluish-grey clays with thin lenticular limestone interlayers (bed 34 according to Dolgov & Meidla, 2011). The thickness of the preserved part of this bed reaches 0.6 m. This layer contains a large number of well-preserved fossils (echinoderms, trilobites, brachiopods, bryozoans, ostracods, etc.). Echinoderms are represented mainly by isolated ossicles. Nevertheless, it was possible to determine at least 26 echinoderms species and 12 columnal-based taxa,

belonging to eight classes (homioosteleans, stylophorans, cyclocystoids (Mirantsev *et al.*, 2019), edrioasteroids, rhombiferans, diplopors, eocrinoids and crinoids).



**FIGURE 1.** Klyasino quarry section, the bed where specimens were collected is indicated by an asterisk (\*); modified from Dolgov and Meidla, 2011.



**FIGURE 2.** *Lagynocystis* cf. *pyramidalis* (Barrande, 1887); PIN No. 4125/943, a—superior face of the theca; b—inferior face of the theca; c—anterior end of the theca; d—lateral view of the right side of the theca. SEM photo. Abbreviations: LA, RA, MA—left, right and median adorals; M (right) and M' (left)—marginal plates; a—aulacophore apophysis; p—pore.

The first specimen (PIN No. 4125/942) was collected by one of the author (S.S.T.) in the 2000s, and its existence was only briefly reported (Rozhnov 2005; Lefebvre *et al.* 2010). The two specimens, including a more complete one, (PIN No. 4125/943, 4125/944), were collected during the expedition of the Borissiak Paleontological Institute RAS in the summer 2017.

The studied material is deposited at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN). The initial preparation of the specimens was made using 37% solution of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>).

Further preparation for cleaning the stereom was done using a weak solution of hydrochloric acid (HCl) and a hard brush. SEM images were taken using Tescan Vega XMU scanning electron microscope without coating.

## Systematic paleontology

### Class STYLOPHORA Gill and Caster, 1960

#### Order MITRATA Jaekel, 1918

#### Family LAGYNOCYSTIDAE Jaekel, 1918

#### Genus LAGYNOCYSTIS Jaekel, 1918

##### *Lagynocystis cf. pyramidalis* (Barrande, 1887)

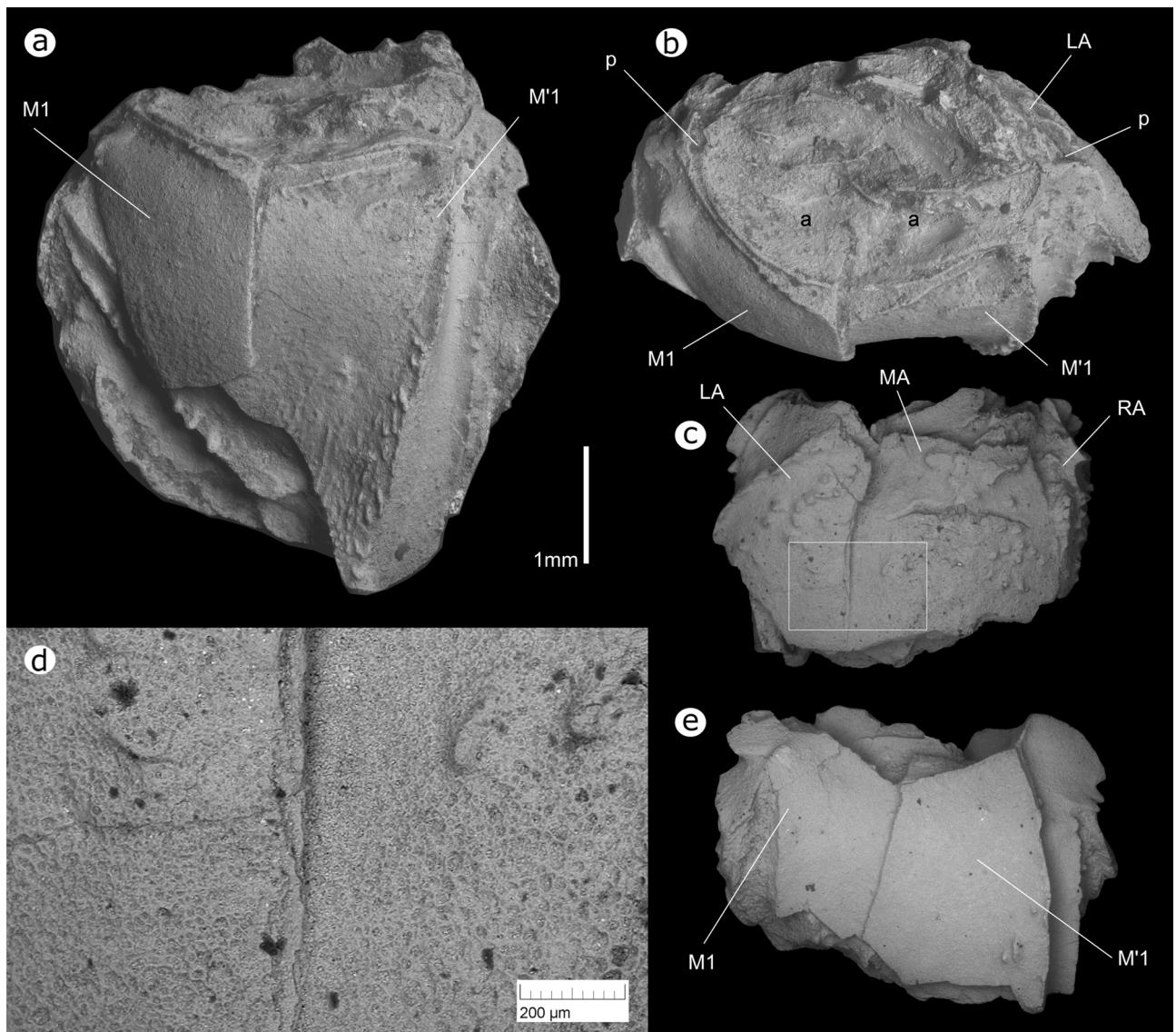
Description. The studied specimens of *Lagynocystis* are represented by three incomplete thecae without aulacophore (Figs 2–3). The left and right adoral plates (LA and RA) slightly overlap of the median adoral plate (MA) and together cover the upper anterior part of the theca. Distally the adoral plates overlap the partially preserved series of small imbricate plates that form the distal upper part of the theca. From the sides, the right and left adoral plates overlap marginal plates that form the lateral and anterior lower parts of the body. The anterior part of the left edge of the left adoral plate is connected tessellately with the anterior margin of the large first left marginal plate, and distally overlaps it imbricately. The right anterior part of the right adoral plate is connected by a short tessellate suture with the first right marginal plate, and distally overlaps the long second right marginal plate. The inward anterior processes of the right and left anterior marginals join together in the plane of symmetry with a vertical seam and together form a concave aulacophore apophysis, almost completely covering the theca at the attachment of the aulacophore.

The sculpture on the plates is represented by small spines and ridges on the marginal and adoral plates. These ridges are especially well marked on a median adoral plate, where they are represented by several rows diverging from the center to the top of the plate (figures 2, a). The thecal surface (on adoral and marginal plates) has alveolar microsculpture.

Stereom microstructure. On adoral plates of the largest specimen (PIN No. 4125/943), the stereom is differently sized, with a diameter from 1 to 10 microns (Fig. 4d–f). On the aulacophore apophyses of the same specimen, the stereom consists of nearly identical, evenly spaced cells with a diameter of about 10 microns (Fig. 4a–c). This well-ordered structure of the stereom on the aulacophore apophyses possibly indicates the presence of a movable joint of aulacophore with theca, due to the muscles or ligamentary tissues. On the adoral plates of the smallest specimen (PIN No. 4125/944), the stereom is represented by chaotically located large cells with a diameter of 10–25 microns (Fig. 3d). This small specimen does not display any evidence of the alveolar microsculpture, which is visible on a larger individual (Fig. 4,d). This difference in stereom structure may be due to different ontogenetic stages.

Discussion. The composition and the relative position of the adoral and marginal plates and the presence of distal imbricated plates make it possible to assign the Baltic specimens to *Lagynocystis* Jaekel, 1918; monotypic family Lagynocystidae Jaekel, 1918. *L. pyramidalis* was originally described from the Furongian of China (Zamora *et al.* 2013; Zhu *et al.* 2016), the late Tremadocian of Morocco (Lefebvre *et al.* 2016), the late Floian of Montagne Noire (Ubags 1991), the Dapingian of Wales (Jefferies 1987), the Darriwilian of the Prague Paleobasin (Barrande 1887; Jefferies 1973; Henry *et al.* 1997; Parsley 2000), the Armorican Massif (Chauvel & Nion, 1977; Henry *et al.* 1997) and the Ossa-Morena Zone of the Iberian Peninsula (Gutiérrez-Marco *et al.* 1999) and the Upper Ordovician of the South Armorican Domain (Lefebvre *et al.* 2010). Thus, the distribution of this monotypic genus was not limited to the western edge of Gondwana as previously suggested. The new discoveries of *Lagynocystis* in the Baltic Paleobasin significantly expand not only its geographical distribution, but also its adaptive possibilities. The occurrence of this stylophoran was usually associated with deep waters in high-latitude marginal basins with extreme conditions, where the hydrodynamic activity was minimal, the oxygen content was low, and the ground was muddy and soft, with a poor associated fauna (Henry *et al.* 1997; Lefebvre 2007; Lefebvre *et al.* 2010, 2016). In the Baltic Basin,

*Lagynocystis* lived in shallow-water conditions, with sufficiently high-oxygen waters, carbonate soft grounds with a high content of calcite detritus and rich diverse associated benthic fauna. However, the benthic fauna from this locality was characterized by dwarfism, since most specimens of echinoderms, trilobites and brachiopods from the locality were noticeably smaller than typical specimens from other locations.

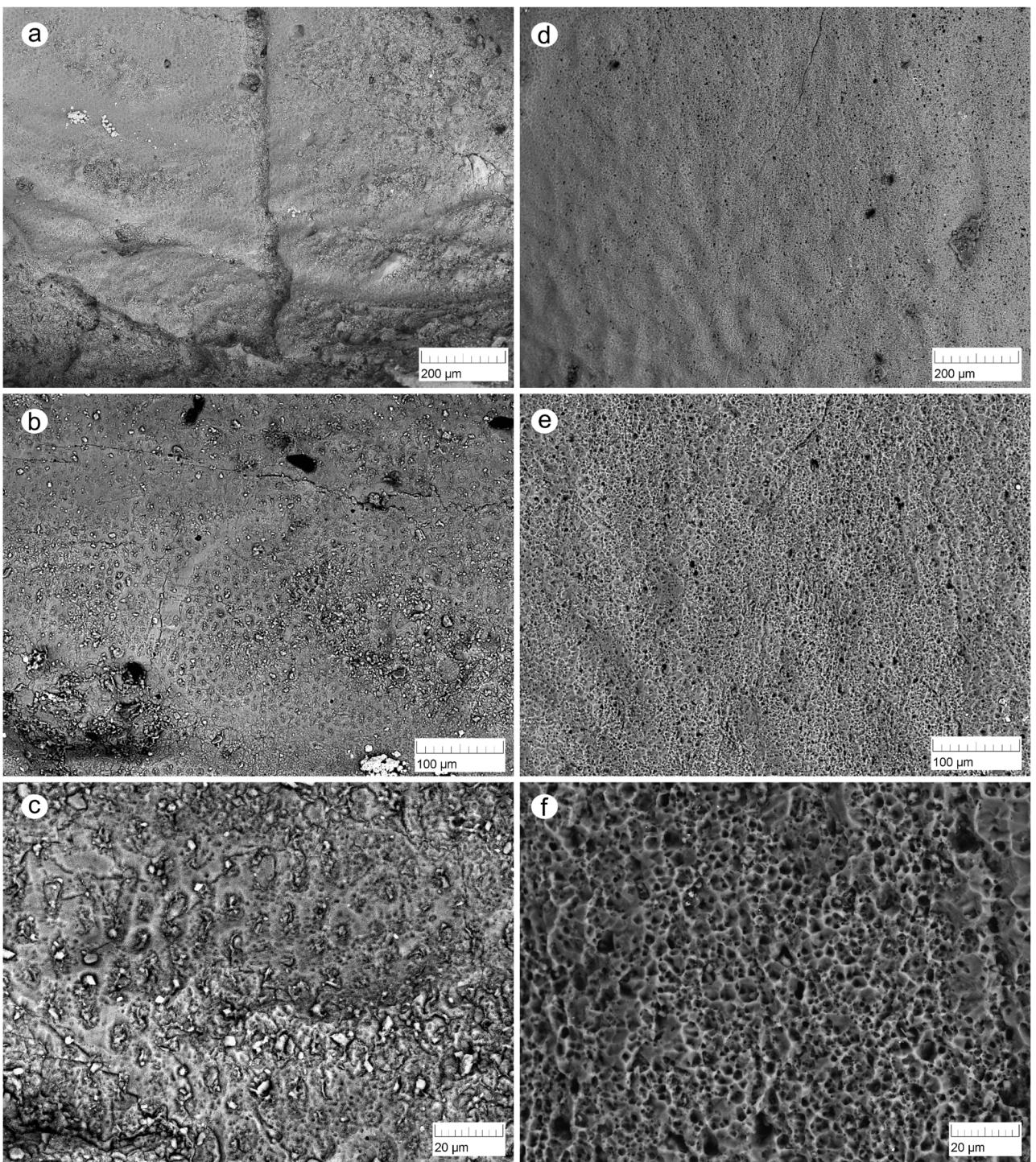


**FIGURE 3.** *Lagynocystis* cf. *pyramidalis* (Barrande, 1887); a–b: PIN No. 4125/942, a—inferior face of the theca; b—anterior end of the theca; c–e: PIN No. 4125/944, c—superior face of the theca, d—close-up of the previous photo, showing the surface, e—inferior face of the theca. SEM photo. The abbreviations are the same as on the previous figure.

The microstructure of the stereom of the Early Paleozoic stylophorans has been studied previously (e.g. Ubaghs 1968; Clausen & Smith 2005). However, in previous works, the microstructure of the stereom in *Lagynocystis* was not explored, because specimens are mostly preserved as external molds. The three-dimensional preservation of the Baltic material made it possible to study the microstructure of the stereom in details.

**TABLE 1.** Size, in mm (\*-indicates incompleteness of plates).

Specimen, No.	aulacophore apophysis Ø	Adoral length (MA)	Marginal length (M'1)
4125/942	3.0	3.1	4.5
4125/943	3.2	3.3	5.2
4125/944	2.0	1.9*	2.3*



**FIGURE 4.** Stereom structure in *Lagynocystis* cf. *pyramidalis* (Barrande, 1887). PIN No. 4125/943; a–c: photos with different magnification showing the surface of aulacophore apophysis, d–f: same scaled photos showing the surface of median adoral plate. SEM photo.

### Acknowledgments

The authors are grateful to the Guest Editor Tatsuo Oji (Nagoya University Museum, Nagoya University) and Bertrand Lefebvre (Lyon 1 University) for their helpful and valuable comments on an earlier draft of the manuscript. The authors thank Roman A. Rakitov and Elena A. Zhegallo (PIN RAS) for their assistance in SEM studies. The study was supported by the Russian Foundation for Basic Research (RFBR), research

project No. 18-04-01046 and the Basic Research Program of the Presidium of the Russian Academy of Sciences” Biodiversity of natural systems. Biological resources of Russia: assessment of the state and fundamental bases of monitoring”. This paper is a contribution to the International Geoscience Programme (IGCP) Project 653—The onset of the Great Ordovician Biodiversification Event.

## References

- Barrande, J. (1887) Classe des Echinodermes. Ordre des Cystidées. In: Jaroslav, P., Felip, P. & Heinrich, W.W. (Eds.), *Système Silurien du centre de la Bohème*, 7. Riva (Prague) and Gerhard (Leipzig), pp. 1–233
- Chauvel, J. & Nion, J. (1977) Echinodermes (Homalozoa: Cornuta et Mitrata) nouveaux pour l'Ordovicien du Massif armoricain et conséquences paléogéographiques. *Geobios*, 10 (1), 35–49.  
[https://doi.org/10.1016/S0016-6995\(77\)80053-3](https://doi.org/10.1016/S0016-6995(77)80053-3)
- Clausen, S. & Smith, A.B. (2005) Palaeoanatomy and biological affinities of a Cambrian deuterostome (Stylophora). *Nature*, 438 (7066), 351.  
<https://doi.org/10.1038/nature04109>
- David, B., Lefebvre, B., Mooi, R. & Parsley, R.L. (2000) Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology*, 26 (4), 529–555.  
[https://doi.org/10.1666/0094-8373\(2000\)026<0529:AHEAAF>2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)026<0529:AHEAAF>2.0.CO;2)
- Dolgov, O. & Meidla, T. (2011) Trilobite biostratigraphy in the Middle and Upper Ordovician of western Leningrad Region. *Stratigraphy and Geological Correlation*, 19 (6), 618–630.  
<https://doi.org/10.1134/S0869593811060025>
- Gill, E. & Caster K.E. (1960) Carpoid echinoderms from the Silurian and Devonian of Australia. *Bulletins of American Paleontology*, 41, 5–71.
- Gutiérrez Marco, J.C., Rabano, I., Sarmiento, G.N., Aceñolaza, G.F., San José, M.A., Pierren, A.P., Herranz, P., Couto, H.M. & Piçarra, J.M. (1999) Faunal dynamics between Iberia and Bohemia during the Oretanian and Dobrotivian (late Middleearliest Upper Ordovician), and biogeographic relations with Avalonia and Baltica. *Acta Universitatis Carolinae, Geologica*, 43, 487–490.
- Henry, J.L., Lefebvre, B. & Chauvin, D. (1997) Stratification thermique probable des eaux marines sur la marge gondwanienne (Massif Armorican) pendant l'Ordovicien (Llanvirn): implications paléogéographiques. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 205, 373–392.  
<https://doi.org/10.1127/njgpa/205/1997/373>
- Jaekel, O. (1918) Phylogenie und system der Pelmatozoen. *Palaontologische Zeitschrift*, 3, 1–128.  
<https://doi.org/10.1007/BF03190413>
- Jefferies, R.P.S. (1973) The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of amphioxus. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences*, 265, 409–469.  
<https://doi.org/10.1098/rstb.1973.0032>
- Jefferies, R.P.S. (1986) *The Ancestry of the Vertebrates*. British Museum (Natural History), London, 396 pp.
- Jefferies, R.P.S. (1987) The chordates—a preliminary note. *Bulletin of the British Museum (Natural History), Geology*, 41, 285–290.
- Kolata, D.R., Frest, T.J. & Mapes, R.H. (1991) The youngest carpoid: occurrence, affinities, and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. *Journal of Paleontology*, 65 (5), 844–855.  
<https://doi.org/10.1017/S0022336000037811>
- Lefebvre, B. (2003) Functional morphology of stylophoran echinoderms. *Palaeontology*, 46 (3), 511–555.  
<https://doi.org/10.1111/1475-4983.00309>
- Lefebvre, B. (2007) Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 245, 156–199.  
<https://doi.org/10.1016/j.palaeo.2006.02.021>
- Lefebvre, B., Régnault, S., Lardeux, H., Kundura, J.P. & Roussel, P. (2010) New Ordovician mitrates (Echinodermata, Stylophora) from the Ancenis Basin (South Armorican Domain, France): palaeogeographic and palaeoenvironmental implications. In: Harris, L.G., Bottger, S.A., Walker, C.W. & Lesser, M.P. (Eds.), *Echinoderms: Durham*. Balkema, Rotterdam, pp. 37–44.  
<https://doi.org/10.1201/9780203869543-c6>
- Lefebvre, B., Allaire, N., Guensburg, T.E., Hunter, A.W., Kouraïss, K., Martin E.L.O., Nardin, E., Noailles, F., Pittet, B., Sumrall, C.D. & Zamora, S. (2016) Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 460, 97–121.

<https://doi.org/10.1016/j.palaeo.2016.02.039>

- Mirantsev, G.V., Anekeeva G.A., Terentiev S.S. & Semenov N.K. (2019) First finds of cyclocystoids in the Middle–Upper Ordovician of the St. Petersburg Region. In *Paleostrat-2019. Annual meeting (scientific conference) of the Paleontological group of the Moscow Society of Naturalists and the Moscow branch of the Paleontological Society under the Russian Academy of Sciences, Moscow*. 28–30 January 2019, Paleontol. Inst. Russ. Acad. Scien., Moscow, p. 43.
- Parsley, R.L. (1988) Feeding and respiratory strategies in Stylophora. In: Paul, C.R.C. & Smith, A.B. (Eds.), *Echinoderm phylogeny and evolutionary biology*. Clarendon Press, Oxford, pp. 347–361.
- Parsley, R.L. (1998) Taxonomic revision of the Stylophora. In: Mooi, R. & Telford, M. (Eds.), *Echinoderms: San Francisco*. Balkema, Rotterdam, pp. 111–117.
- Parsley, R.L. (2000) Morphological and paleoecological analysis of the Ordovician ankyroid *Lagynocystis* (Stylophora: Echinodermata). *Journal of Paleontology*, 74 (2), 254–262.  
<https://doi.org/10.1017/S0022336000031474>
- Philip, G.M. (1979) Carpoids–echinoderms or chordates? *Biological Reviews*, 54 (4), 439–471.  
<https://doi.org/10.1111/j.1469-185X.1979.tb00845.x>
- Rozhnov, S.V. (2005) Echinoderms. In: Dronov, A., Tolmacheva, T., Raevskaya, E. & Nestell, M. (Eds.), *Cambrian and Ordovician of St. Petersburg region. Guidebook of the pre-conference field trip. 6th Baltic Stratigraphical Conference, St. Petersburg*, 23–25 August 2005. Saint Petersburg: St. Petersburg State University & A.P. Karpinsky All-Russian Research Geological Institute, pp. 23–26.
- Ubags, G. (1961) Sur la nature de l'organe appelé tige ou pédoncule chez les carpoïdes Cornuta et Mitrata. *Comptes Rendus de l'Académie des Sciences, Paris*, 253, 2738–2740.
- Ubags, G. (1968) Stylophora. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Pt. S, Echinodermata, Volume 2*. Geological Society of America and University of Kansas Press, Lawrence, pp. S495–S565.
- Ubags, G. (1991) Deux Stylophora (Homalozoa, Echinodermata) nouveaux pour l'Ordovicien inférieur de la Montagne Noire (France méridionale). *Paläontologische Zeitschrift*, 65 (1–2), 157–171.  
<https://doi.org/10.1007/BF02985781>
- Zamora, S., Zhu, X. & Lefebvre, B. (2013) A new Furongian (Cambrian) Echinoderm-Lagerstätte from the Sandu Formation (South China). *Cahiers de Biologie Marine*, 54, 565–569.
- Zhu, X., Peng, S., Zamora, S., Lefebvre, B. & Chen, G. (2016) Furongian (upper Cambrian) Guole Konservat-Lagerstätte from South China. *Acta Geologica Sinica*, 90, 801–808.  
<https://doi.org/10.1111/1755-6724.12640>