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Carpozoan Echinoderms from the Middle Cambrian (Mayaktakh Formation) of Siberia (Lower Reaches of the Lena River)

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Abstract—Two new monotypic genera and a new monotypic family Rozanovicystidae of the class Cincta are described from the Middle Cambrian (Mayaktakh Formation) of the northeastern part of the Siberian Platform. Based on data obtained by morphofunctional analysis, there is a possibility that these animals could move by jet propulsion by ejecting water from the opercular aperture. Probable homologies of the main skeletal parts are discussed.

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Key words: echinoderms, Cincta, new taxa, Middle Cambrian, Siberia, Russia.

INTRODUCTION

Cincta is a small group of exclusively Middle Cambrian echinoderms with a small flattened theca with a rounded outline and posterior articulated stem (stele). The theca is bounded laterally by marginal plates forming a frame; and from above and below, by the upper and lower central plates, respectively. The mouth with two ambulacra going to the right and left is located at the right side of the anterior part of the body. In the center of the anterior side of the theca, near the mouth, there is a special aperture unknown in other echinoderms. It is covered by the opercular plate. On the upper surface of the theca, near to the mouth, there is a small aperture interpreted as a hydropore or gonopore. In the left anterior part of the theca there is an anus covered by a cone of extended plates. This is the general body plan of this group. Like other Carpozoa, cinctans lack fivefold symmetry and any other radial symmetry. Otherwise, the structural plan of cinctans is well expressed and clearly differs from all other animals. Hence, the group is considered to have class rank (Ubaghs, 1967; Friedrich, 1993) or to be a stem group of echinoderms (Jefferies, 1997) or hemichordates (Dominguez and Jefferies, 2005).

Up to now, 13 genera of cinctans are known, including two new genera from Siberia (Dominguez et al., 2002). Apart from Siberia (Rozhnov, 1990), they are known from the Czech Republic, France, Spain, Morocco, Germany, and Great Britain (Wales) (Gislen, 1927; Termier and Termier, 1973; Friedrich, 1993; Sdzuy, 1993; Fatka, 2001; Fatka and Kordule, 2001; Dominguez et al., 2002). The two new monotypic genera from Siberia described below considerably increase our knowledge of the morphology of these animals and their probable mode of life, which is very different from that of many others cinctans.

CHARACTERISTICS OF THE SIBERIAN MATERIAL AND THE LOCALITY

All Siberian cinctans have been found in the Mayaktakh Formation (Rozhnov, 1990) of the Middle Cambrian (Groshin and Korobov, 1975) and come from relatively closely spaced exposures of this Formation in the lower reaches of the Lena River, where it approaches the Tuora-Sis Range of the Kharaulakh Mountains of the northwestern part of the Verkhoyansk fold system. The largest exposure is located on the left bank of the Lena River, 4.5 km downstream from the Chekurovka settlement. Several exposures of the Mayaktakh Formation are located on the right bank of the Lena River along its right tributary, the Neleger River. From the geological point of view all sites are confined to the Chekurovka Anticline (Fig. 1).

Cinctans have been found in compact micritic, sometimes slightly clayey limestones of the Mayaktakh Formation. The age of this formation is thought to range from the upper Amgan Stage to the lower Mayan Stage. The fauna is rather rare in these limestones. Except for cinctans, carpoids are represented by a single skeletal fragment of a cornute *Ponticulocarpus* sp. (?) (Fig. 2, Pl. 5, fig. 17). Representatives of other echinoderms have not been found here.

Cinctans occur in limestones in small clusters, which are dominated by representatives of either of the two genera found here. In clusters, cinctan skeletons are rather numerous, although it is difficult to extract them from the rock due to the nearly identical density of their calcite skeletons and the host limestones. Therefore, despite the abundance of specimens, the preservation of skeletons does not allow all details of their morphology to be clearly revealed.

Limestones of the Mayaktakh Formation, which produce remains of cinctans, were deposited in rather deep-water conditions of standing water, probably at the boundary between the internal and external shelves. This is indicated by the fine-grained texture of limestone and the preservation mode of carpoid skeletons, which are usually intact or, if disintegrated, with their fragments and separate plates occurring close to each other and showing no size sorting (Fig. 2).

Paleogeographically, Siberian cinctans lived on the southern (in the Middle Cambrian) margin of the Siberian Platform, at a significant distance from the other known cinctans, which mainly occurred along the margin of Gondwana.

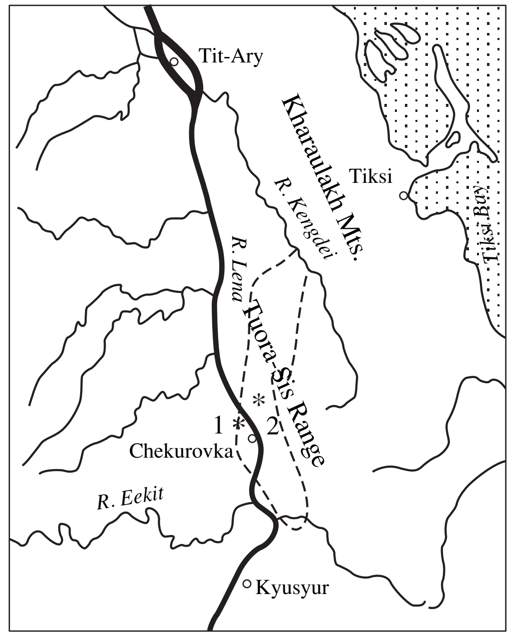


Fig. 1. Schematic position of localities in the lower reaches of the Lena River. Dotted line stands for the Chekurovka Anticline. The asterisk indicates sites: 1—left bank of the Lena Riva, 3 km downstream of the Chekurovka settlement; 2—group of sites on the right bank of the Lena, the Neleger River and its tributaries.

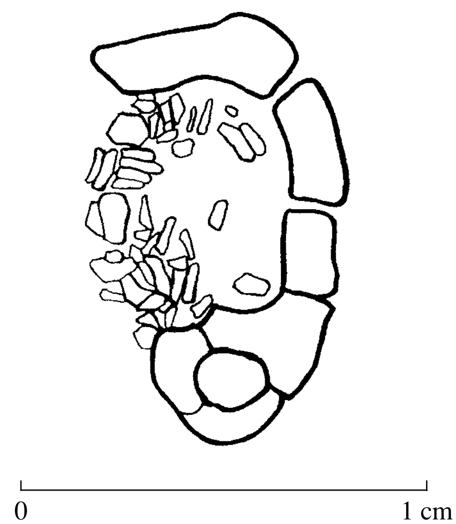


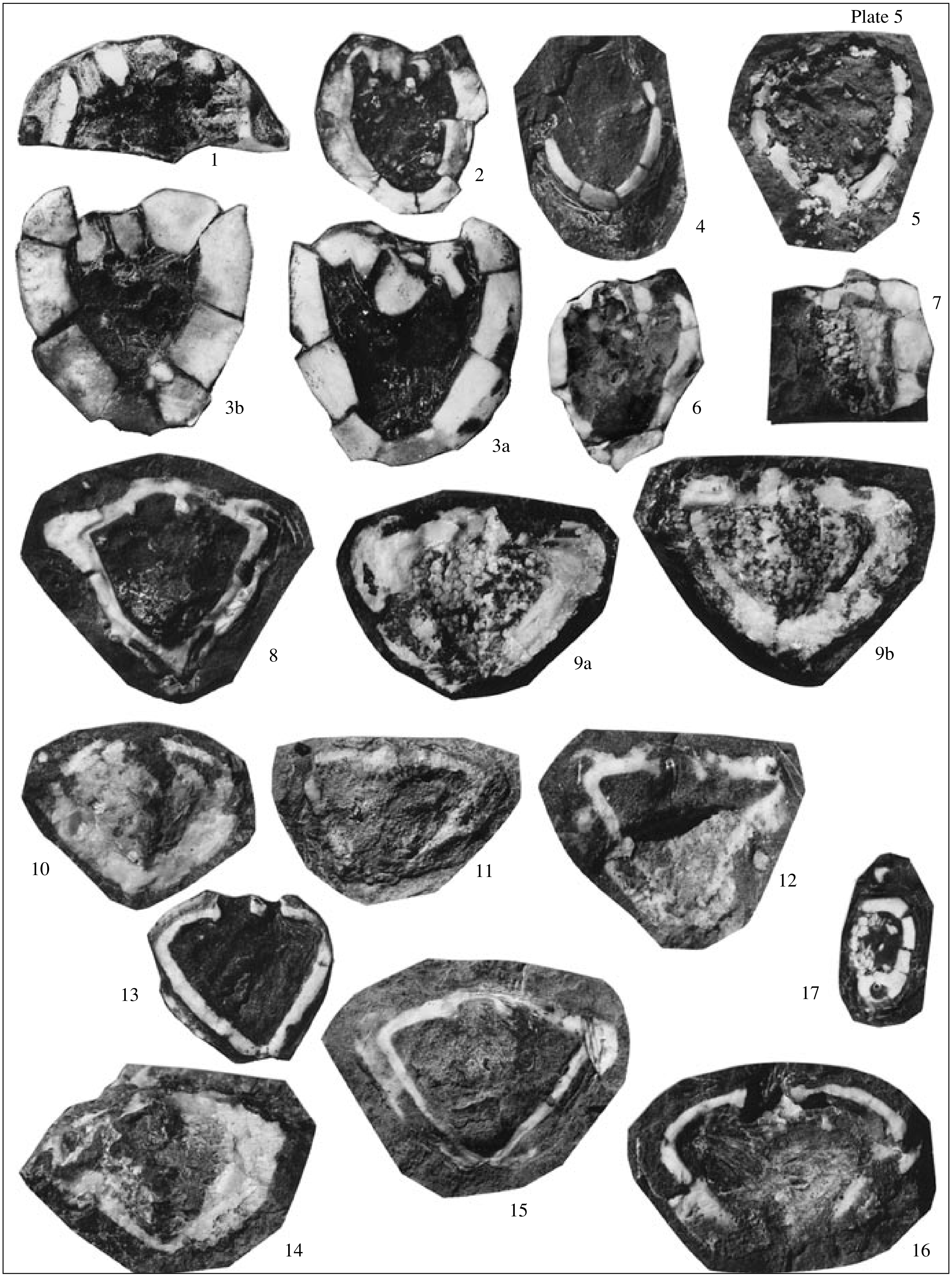
Fig. 2. Preservation of a fragmentary skeleton of cornute *Ponticulocarpos* sp. (?).

MORPHOLOGY AND TERMINOLOGY

All sparse representatives of Cincta are similar in skeletal morphology, which is thoroughly described by Ubaghs (1967) and in even more detail by Friedrich (1993). Thus, we will restrict our review to a brief description of the skeletal morphology and an explanation of the terms used.

The skeleton of cinctans consists of a small, flattened theca of oval or, occasionally, triangular outline and a tail-like process, the stele. The theca consists of marginal plates that form its frame and bound the cinctan body laterally, and of the lower and upper central plates limiting the body from below (infracentrals) and from above (supracentrals). Several apertures perforate the theca. The oral aperture is situated between marginal plates in the anterior part of the theca, with right and left ambulacra branching off, confined to a special groove on the marginal plates. To the left of the oral orifice, there is a large aperture covered by a special plate. Ubaghs (1967) considered it to be the anus, whereas Friedrich (1993) has shown that the anal aperture is actually located in the left anterior part of the upper side of the theca and is covered with the anal cone consisting of small slightly extended plates. The aperture near the oral one is an entrance into a distinct cavity, the homology and functional significance of which is unclear. The fourth small aperture is located behind and to the right of the mouth, close to the marginal plates of the frame. The marginal plates number from eight up to twelve. They are located almost symmetrically to the right and left of the opercular aperture. Friedrich (1993) proposed that the marginal plate occurring below the opercular one be denoted as the marginal zero (M_0), and those to the right and to the left of it, as first marginal plates right (M_1r) and left (M_1l), and so on up to the junction of the right and left rows at the point of the stele attachment. In my view, there is no need to designate a zero marginal plate because topologically it is the first one on the left. Nevertheless, in order to avoid confusion in this paper I follow the terminology proposed by Friedrich (1993). From above, the opercular aperture is covered by a large opercular plate bordered from behind by supraopercular plates contacting supracentrals. The oral aperture is located above the first right marginal plate and is covered from

Plate 5



above by the supraoral plate. The last marginal plates form walls of the central canal that continues into the stele. This is the skeletal morphology of this compact group in outline. The structural patterns of these basic elements of the skeleton allow subdivision of cinctans into families, genera, and species.

SYSTEMATICS OF CINCTA AND THE TAXONOMIC POSITION OF SIBERIAN FORMS

I follow Ubaghs (1967) and Friedrich (1993) in considering this group as a class in the subphylum of carpoid echinoderms. I think that this class would be better called Cincta Jaekel, as in Friedrich (1993), rather than Homostelea Gill et Caster with the single order Cincta, as in Ubaghs (1967). Dominges and Jefferies (2005) demonstrated some similarities of this group with hemichordates.

The genus *Rozanovicystis* gen. nov. is significantly different from all hitherto known representatives of cinctans. First of all, it has a triangular theca, strongly convex lower surface, very long ambulacra running along almost the entire edge of the theca, and reduced stele. These characters place this genus into a separate family. In the length of ambulacra the new family closely approaches Trochocystitidae, which includes some forms with rounded-triangular theca, but differs from them in the much longer ambulacra, smaller number of marginals, the convex lower side of the theca, and the reduced stele. In the length of the ambulacra the new family differs still further from Sucocystidae and Gyrocystidae. The shape of the theca, the convexity of its lower side, and the small height of the marginal plates emphasize this distinction. A certain similarity can be seen in the presence of a collar in some representatives of these two families, but in the new family it is much stronger, and its internal edge has a well expressed groove that hosted the ambulacra. The morphology of the genus *Nelegerocystis* gen. nov. fits well with that of the family Trochocystitidae.

SYSTEMATIC PALEONTOLOGY

Phylum Echinodermata

Subphylum Carpozoa

CLASS CINCTA

Family Trochocystitidae Jaekel, 1900

Genus *Nelegerocystis* Rozhnov, gen. nov.

Etymology. From the Neleger River.

Type species. *N. ivantzovi* sp. nov.

Diagnosis. Rounded theca with flat upper and lower sides, with ten marginal plates, numerous fine upper central plates and larger lower ones. Marginals flat from below, slightly oblique upwards and inside. Ambulacra do not reach point of greatest theca width, with right ambulacrum much shorter than left one. Well expressed notch in front of anal cone affects first left marginal plate. Opercular plate bordered from behind and right by several large plates. Stele short and narrow.

Species composition. Type species.

Comparison. From the closest genus *Sotocinctus* Sdzuy, 1993 the new genus differs in a different arrangement of plates behind the opercular plate, the presence of a well-expressed notch anterior to the anal cone. From *Trochocystites* Barrande, 1859 it differs in the flat upper and lower sides of the theca, shorter ambulacra, and tightly contacting upper marginal plates. From *Trochocystoides* Jaekel, 1918 it differs in more elongated theca, shorter ambulacra, larger lower central plates and flat rather than convex upper side of the theca.

Nelegerocystis ivantzovi Rozhnov sp. nov.

Plate 5, figs. 1–7

Etymology. In honor of A.Yu. Ivantsov who discovered the locality of echinoderms on the Lena River.

Explanation of Plate 5

All specimens come from the Mayaktakh Formation, Middle Cambrian. Magnification is ×5 (fig. 1) and ×3 (all other figures).

Figs. 1–7. *Nelegerocystis ivantzovi* sp. nov., (1) specimen PIN, no. 4326/8, anterior part viewed from above; (2) holotype PIN, no. 4326/9, theca viewed from above; right bank of the left unnamed tributary of the Daldyn-Eznike River; (3) specimen PIN, no. 4326/1, (3a) theca viewed from above, (3b) theca viewed from below; The Neleger River (the right tributary of the Lena River); (4) specimen PIN, no. 4326/10, fragment of the posterior part of theca viewed from above with proximal plates of stele; (5) specimen PIN, no. 4326/5, theca viewed from above; the left bank of the Lena River, 4.5–5 km downstream from the Chekurovka settlement; (6) specimen PIN, no. 4326/11, theca viewed from above; the right bank of the Neleger River; (7) specimen PIN, no. 4326/12, fragment of the anterior right part of theca with preserved supracentrals; the right bank of the left unnamed tributary of the Daldyn-Eznike River.

Figs. 8–16. *Rozanovicystis triangularis* sp. nov., (8) specimen PIN, no. 4326/20, theca viewed from above; the left bank of the Lena River, 4.5–5 km downstream from the Chekurovka settlement; (9) holotype PIN, no. 4326/17, (9a) theca viewed from above, (9b) theca viewed from below; (10) specimen PIN, no. 4326/16, theca from above; the right bank of the left unnamed tributary of the Daldyn-Eznike River; (11) specimen PIN, no. 4326/26, theca viewed from above, Khoz-Nelege River; (12) specimen PIN, no. 4326/25, theca viewed from above; the left bank of the Lena River, 4.5–5 km downstream from the Chekurovka settlement; (13) specimen PIN, no. 4326/19, theca viewed from above; Khoz-Nelege River; (14) specimen PIN, no. 4326/15, theca viewed from above; (15) specimen PIN, no. 4326/23, theca viewed from above; the left bank of the Lena River, 4.5–5 km downstream from the Chekurovka settlement; (16) specimen PIN, no. 4326/26, theca viewed from above; the right bank of the Neleger River.

Fig. 17. *Ponticulocarpus* (?) sp., specimen PIN, no. 4326/27, a fragment of the theca; Khoz-Nelege River.

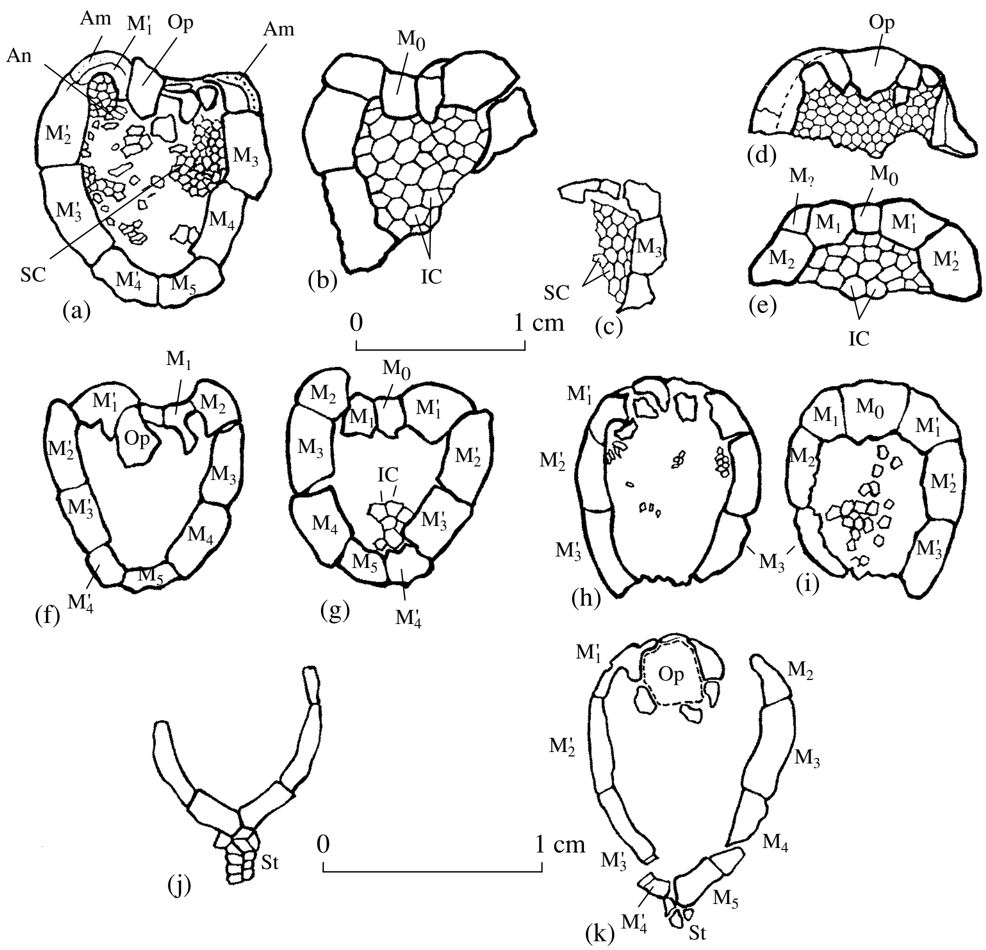


Fig. 3. *Nelegerocystis ivantzovi* sp. nov., figures of fragments of the skeleton traced from photographs, holotype PIN, no. 4326/9, (a) theca from above, (b) theca from below; (c) specimen PIN, no. 4326/12, a fragment of the anterior right part of theca with preserved supracentrals; (d, e) specimen PIN, no. 4326/8, anterior part of theca, (d) dorsal view, (e) ventral view; (f, g) specimen PIN, no. 4326/1, theca, (f) dorsal view, (g) ventral view; (h, i) specimen PIN, no. 4326/10, theca, (h) dorsal view, (i) ventral view; (j) specimen PIN, no. 4326/10, dorsal view of a fragment of posterior part of theca with proximal plates of stele; (k) specimen PIN, no. 4326/2, dorsally viewed theca with proximal plates of stele. Designations: (M_1–M_5) right marginal plates, (M'_1 – M'_5) left marginal plates, (M_0) marginal plate located under opercular aperture, (Op) opercular plate, (Or) oral aperture, (IC) lower central plates (infracentrals), (SC) top central plates (supracentrals), (An) anus, (S) stele, and (Am) ambulacra.

H o l o t y p e. PIN, no. 4326/9, theca; right bank of the Lena River, western slope of the Tuora-Sis Range, right bank of the left unnamed tributary of the Daldyn-Eznike River (the first one upstream from the Khoz-Nelege River mouth); Middle Cambrian, Mayaktakh Formation (the upper Amgan Stage–lower Mayan stages).

D e s c r i p t i o n (Figs. 3, 4). The theca is bilaterally symmetrical and oval in outline. The anterior edge of the theca is straighter and wider than the rounded posterior side. The theca is widest at one-quarter to one-third of the theca length from the anterior side. The theca is bordered by ten marginal plates, with five plates to the right from the zero marginal below the opercular aperture, and four to the left from it. Marginal plates are flat basally; their lateral sides are high and slightly oblique toward the theca. The fifth right and the fourth left marginals contact along the axis of symmetry, and their junction point bears a small facet for the attachment of the stele. The third and the second left marginals are nearly equal in size and symmetrical with the third and the fourth right marginals. The second right marginal is slightly shorter than its symmetrical counterpart, the first left marginal. The anterior part of the second right marginal forms the right side of the oral aperture. The first right marginal borders the lower part of the oral aperture, and the anterior part of its large left lateral process limits the left part of the narrow oral aperture. The oral aperture is covered from above by a special supraoral plate. The left first marginal has a more complex shape because its anterior end is strongly posteriorly extended and forms the left wall of the opercular aperture. To the left of the posterior end of this process there is a large anal cone with a strongly extended notch anterior to it, which runs into the first

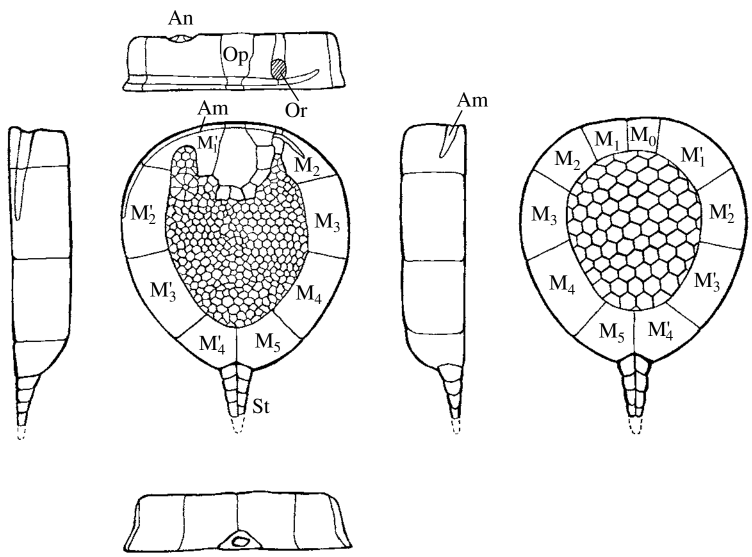


Fig. 4. Reconstruction of theca of *Nelegerocystis ivantzovi* sp. nov. in six projections. For designations, see Fig. 3.

left marginal. The zero marginal, located below the opercular aperture, is the shortest. The opercular plate is large, tapering in the anterior part, and framed from behind and from the right by large plates.

The ambulacra are poorly preserved. They run to the center of the second marginal plates. The left ambulacrum is much longer than the right. Its posterior end just slightly misses the widest point of the theca. The right ambulacrum passes from the anterior part of the theca to its lateral face only slightly. The stele is small, narrow, and consists of two rows of alternating plates.

M e a s u r e m e n t s, mm:

Specimen PIN, no.	Length of theca	Width of theca	Position of maximal width from the stele facet	Width of marginal plates
4326/9, holotype	11.5	11.5	7.0	3.0
4326/11	12.0	10.0	8.0	2.0
4326/10	–	8.0	–	2.0
4326/7	12.0	8.0	8.0	1.5
4326/6	11.0	9.0	7.5	2

Specimen no. 4326/10 has a stele about 4 mm long with its width at the base being about 2 mm. Thus, the length of a stele is about half of the theca width, or, recalculated for its length, about two-thirds to half of the length. The thickness of the theca of the holotype is about a quarter of its length.

V a r i a b i l i t y. The width/length ratio of theca changes from 1.0 to 1.5, and the greatest width is located approximately at one-third of the theca's length from its anterior side. The width of marginal plates on both sides changes from 0.26 to 0.19 of the theca's width. Specimen no. 4326/8 in the anterior part of the theca has an additional triangular marginal plate that intercalates from the anterior between the second and the first right marginals. The upper part of this additional marginal forms the right wall of the oral aperture.

O c c u r r e n c e. The lower Lena River basin; Middle Cambrian, Mayaktakh Formation (upper Amgan Stage–lower Mayan stages).

M a t e r i a l. More than 15 incompletely preserved thecae and various fragments. The left bank of the Lena River, 4.5–5 km downstream of the Chekurovka settlement; the right bank of the Neleger River (the right-bank tributary of the Lena River); the right bank of the left unnamed tributary of the Daldyn-Eznike River (upstream of the Khoz-Nelege River).

Family Rosanovicystidae Rozhnov, fam. nov.

T y p e g e n u s. *Rozanovicystis* gen. nov., Middle Cambrian of Siberia.

D i a g n o s i s. Theca triangular in outline with eight marginal plates, strongly convex carinate central part of lower side composed of numerous hexagonal central plates. Ambulacra long, encircling entire or significant part of wide theca collar.

C o m p a r i s o n. The new family differs from the three other families in clear triangular shape of the theca, convex carinate central part of the lower surface, in short or missing stele, a wide collar around the entire theca and ambulacra stretching along the collar and covering nearly the whole lateral part of the theca.

S p e c i e s c o m p o s i t i o n. Type species.

Genus *Rozanovicystis* Rozhnov, gen. nov.

E t y m o l o g y. In honor of A.Yu. Rozanov, the well-known researcher of the Cambrian in Siberia.

T y p e s p e c i e s. *R. triangularis* sp. nov.

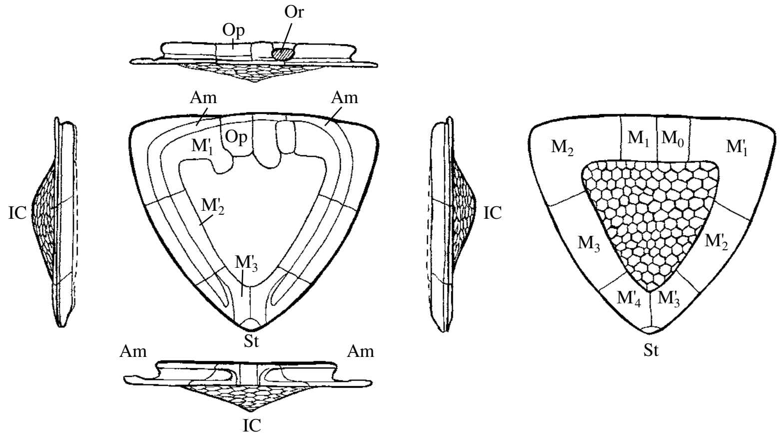


Fig. 5. Reconstruction of theca of *Rozanovicystis triangularis* sp. nov. in six projections. For designations, see Fig. 3.

D i a g n o s i s. Theca triangular in outline with strongly convex lower side and low upper surface. Eight marginal plates with well expressed wide collar along entire theca border towering ridgelike part of marginal plates. Ambulacra located between collar and ridge and stretch along entire length of marginals. Stele reduced to single plate within theca, or very short.

S p e c i e s c o m p o s i t i o n. Type species.

Rozanovicystis triangularis **Rozhnov sp. nov.**

Plate 5, figs. 8–16

E t y m o l o g y. From the Latin *triangularis* (triangular).

H o l o t y p e. PIN, no. 4326/17, theca; lower reaches of the Lena River, western slope the Tuora-Sis Range, the right bank of the left unnamed tributary of the Daldyn-Eznike River (the first one upstream from the Khoz-Nelege River mouth); Middle Cambrian, lower parts of the Mayaktakh Formation.

D e s c r i p t i o n (Fig. 5). The theca is triangular in outline, slightly rounded at the corners, with approximately equally long straight lateral faces and a usually slightly longer anterior side. It is bordered by eight marginal plates. The lower side of the theca is strongly convex in the central part, with a well expressed, particularly at the anterior part of the theca, ridgelike flexure stretching along the median part of the theca. The entire central part of the lower side of the theca, bordered by the marginal plates, is covered by small hexagonal infracentral plates. The upper side is covered with poorly preserved small irregularly shaped plates. Marginal plates are wide with flat bases and more complex upper sides. Their internal parts tower to form a ridge, and the external parts are bordered by a wide collar. This collar passes along the entire edge of theca, except the posterior sector, and it is narrower along the anterior side. The ambulacral groove passes at the boundary between the ridge and the collar nearly reaching the stele plate. Thus, ambulacra start at the oral orifice and pass along nearly the entire length of the marginal plates. The anterior part of a theca bears two apertures. The wide central aperture is covered from above by the opercular plate, which is supported by faceted processes of two marginal plates. Near to it and slightly to the right, a narrower oral aperture covered by a narrow supraoral plate is located. The posterior sector of the theca opposite to its anterior side with oral and opercular apertures contains a small triangular plate perforated by the central channel passing from the theca cavity. This plate represents the proximal plate of the stele; however, whether there were other stele plates or they were completely absent in the described species remains unknown because of the state of preservation of the material. The fact that this plate lacks a facet and sometimes has a pointed shape indicates the absence of other stele plates and the lack of a morphologically manifested stele in this species.

M e a s u r e m e n t s, mm:

Specimen PIN, no.	Width of theca along its anterior side	Length of theca	Height of theca, maximal	Width of marginal plates	Width of collar of marginal plates
4326/17, holotype	16.0	13.0	2.0	3.0	2.0
4326/14	14.0	11.0	2.0	2.0	–
4326/15	14.0	11.0	2.5	2.5	–
4326/19	13.0	10.0	–	3.5	2.0
4326/20	15.5	13.5	–	3.0	2.0
4326/21	17.0	13.0	–	3.0	2.0
4326/22	15.5	12.0	–	3.0	2.0
4326/23	16.0	12.0	–	2.5	1.5

V a r i a b i l i t y. The width of the theca is usually 1.3 times its length (range, 1.15 to 1.36). The theca is about 2 mm thick, i.e., from 0.12 to 0.17 of the greatest width of the theca. The width of marginal plates on each side of the theca is about 0.19 of the greatest width of the theca (0.14 up to 0.27). The width of the collar of marginal plates is about two-thirds of their width.

Material. About 20 thecae of varying preservation and fragments; left bank of the Lena River, 4.5–5 km downstream of the Chekurovka settlement; right bank of the Neleger River (the right-bank tributary of the Lena River); right slope of the left unnamed tributary of the Daldyn-Eznike River (upstream of the Khoz-Nelege River).

Occurrence. The Lower Lena River basin; Middle Cambrian, Mayaktakh Formation (upper Amgan Stage–lower Mayan stages).

LIFE MODE OF CINCTA

Friedrich (1993) has shown that cinctans rested on the sea floor with the theca side bearing the anus and the opercular plate upwards. This side is normally flat or slightly convex. The theca was anchored into the soft sediment at a slight angle to the surface due to the action of water ejected from the opercular aperture, which is always strictly in line with the stele. By energetic ejection of water from the opercular aperture forward and slightly upward the animal drove the distal part of the stele into the sediment at a low angle. Bottom currents influenced the stele and orientated the animal along the current. The anterior part of theca with ambulacra usually points along the current (Friedrich, 1993; Gil Gid et al., 1998). This gave a hydrodynamic advantage in the feeding process because of a higher concentration of food particles near the ambulacra by water turbulence at the anterior part of the theca. Similar alimentary position is characteristic for crinoids with their crowns oriented along the current and food particles are caught from eddies formed at the ambulacral arms (Meyer, 1979). For this reason, according to Jefferies (1997), in cinctans the ambulacra never reach beyond the theca's bend, into the zone impoverished in food particles under this feeding model. This interpretation of the cinctan mode of life is quite convincing, particularly for forms with a high theca and a well expressed stele, more so if there is evidence of their occurrence in conditions of significant currents. When currents are weak this mechanism of food enrichment is less efficient. This can be illustrated by the environment and morphology of Siberian forms. These forms lived in conditions of still water. Firstly, it is indicated by sedimentary conditions. Micritic limestone that contains thecae of Siberian cinctans is composed of very fine calcite particles, often with a small addition of clay particles. The second evidence is in the way of preservation of fossils. Skeletons of cinctans are not usually disintegrated into separate plates and when they are, these plates are not far apart.

Conditions of stagnant water in which Siberian cinctans lived, suggest a somewhat different life mode from other cinctans. First of all, it is hardly probable that weak currents could influence the orientation of an oval theca with short stele of *Nelegerocystis*. Likewise, the flattened upper surface and the low theca could not provide a significant enrichment of food particles at the anterior part of the theca. Even less such a life model fits *Rozanovicystis* gen. nov. The theca of this animal has an outline which is almost an equilateral triangle. With the lack of a stele or its small size currents could well orient such a theca in three directions with any side facing along the current. A small theca height and a weak water current resulted in almost no turbulence or, even if it took place, the theca orientation played no important role in feeding efficiency because the ambulacra girdled the entire perimeter of the theca. This suggests that Siberian cinctans had a different mode of life, with marked importance of the opercular aperture through which water could be ejected creating jet propulsion.

The feeding system of all cinctans is actually situated at the boundary of two media, i.e., seawater and substrate. This boundary sustains a thin half-liquid layer of sediment with abundant organic particles and bacteria living on them. This layer is continuously enriched by organic particles from the uppermost layer of water, first of all as pellets from pelagic filter feeders. Even small water movements result in the moving and mixing of particles in this layer. Therefore, water movement produced by rhythmic pulsations of the opercular aperture and the opercular covering plate refresh the half-liquid layer near the ambulacra. Additionally, the ejecting of water from the opercular aperture created a jet that moved the animal in the opposite steleward direction. Friedrich (1993) believed that this jet force resulted in the imbedding of the stele into the sediment at a low angle and thus to the anchoring of the animal. This fastening could only be realized with certain morphological features of an animal: the presence of a long stele and the movement of water directed downwards from the opercular aperture. The morphology of Siberian cinctans does not fit these requirements. Therefore, it is supposed that they could move by the jet force of the water ejected from the opercular aperture. This mode of life is particularly likely for *Rozanovicystis* gen. nov., and is clearly indicated by the skeletal morphology. The lower side of the central part of the theca of this animal was slightly immersed into the upper layer of the sediment (Fig. 6). The preservation of the skeleton well supports this: the convex part of the theca embedded into the sediment is always well preserved, whereas the upper side is always destroyed and pressed into the theca. These features confirm the above suggested life orientation of cinctans on the sea floor. Wide and basally flat marginal plates prevented the animal from excessive penetration into the deposits. The central part of its lower surface was convex with a well expressed longitudinal bend which, when slightly embedded into the deposit, and could obviously serve as a good keel in the movements of this animal. The upper surface of the central part of the theca in *Rozanovicystis* is unknown, but judging from the structure

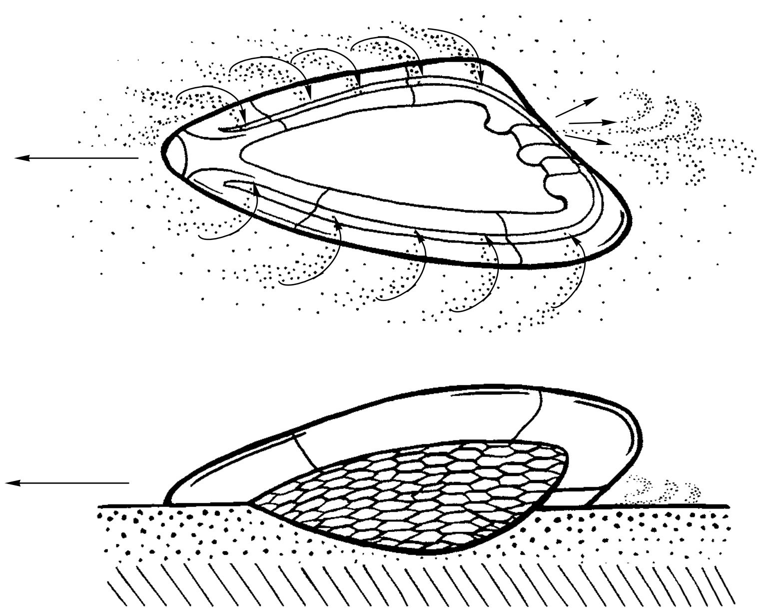


Fig. 6. Probable life mode of *Rozanovicystis triangularis* sp. nov. The arrow indicates the animal's movement direction after ejecting water from the opercular aperture. Dots show a thin boundary layer between seawater and compacted sediment.

and shape of the marginals, it was flat or slightly convex. Therefore, it did not restrict the movement of the animal. During the movement of an animal, its morphologically posterior pointed end turned into a functionally anterior one. This efficiently cut through the half-liquid bottom layer that thus contacted the ambulacra and always provided feeding access to the new, undepleted parts of the bottom layer. Thus, the theca of *Rozanovicystis* gen. nov. morphologically represented an ideal jet device, comparable in shape with some modern jet plane engines.

The theca of *Nelegerocystis* gen. nov. was less adapted to jet propulsion. The theca of this genus is rounded with the flat lower and upper sides. The small stele streamlined the posterior side of the animal, improving backward jet propulsion. The theca morphology of many other cinctans also allowed jet propulsion by ejecting water from the opercular aperture, but with lower efficiency. In some cinctans, for example in *Trochocystites* and *Davidocinctus*, these movements were prevented by ledges in the anterior part of the lower surface. It is these forms that could anchor in currents as assumed by Friedrich (1993).

Thus, cinctans within the general "snowshoe" strategy (Fatka et al., 2006) had different modes of life ranging from backward movement in still waters while collecting organic particles from the sediment/water boundary layer, anchoring in currents with the stele and ledges of the lower part of the body feeding from emerging turbulence of the bottom layer of water, and a combination of both these feeding strategies.

HOMOLOGIES OF THE MAIN BODY PARTS

The structural plan of cinctans is clearly outlined and differs markedly from other classes of echinoderms. It is possible to assume that the alimentary canal passed posterior to the mouth, turned to the left side to end in an anus located in the left anterior part of the upper side of the theca. It is possible that this loop of the alimentary tract reflects an early reorganization stage of the initial metamerism in the ancestral forms of echinoderms into the cyclomery typical for the majority of echinoderms. Ambulacral grooves are important elements of the body plan of echinoderms. Jefferies (1997) homologized these ambulacra with non-ramified parts of ambulacra BC and DE of pentaradiate forms. Based on the order of emergence of ambulacra in sea lilies and eocrinoideans, we have assumed (Rozhnov, 2002) that the ambulacra of cinctans are homologous to ambulacra C and D of pentaradiate echinoderms. The calcite stereom skeleton of cinctans is also one of the prominent features of the body plan of echinoderms. Thus, the phylogenetic relationship of these animals with echinoderms is doubtless. The referral of this class to the phylum Echinodermata produces questions on the homology of the opercular aperture and stele, which are difficult to homologize with any structures of pentaradiate echinoderms. The opercular aperture is located directly to the left of the oral aperture. Therefore, Jefferies (1997) has assumed that this aperture is the left branchial slit, homologous to the gill slits of cornutes and solutans, and, hence, one of the left branchial slits of hemichordates. In my view, it is more probable that the opercular plate covers not a gill slit itself but rather an atrial cavity where the branchial slits open. Such an atrial cavity could have emerged during the outgrowth of the left body part of ancestral cinctans associated with the posterior looping of the gut and moving of the anal aperture to the left anterior part of the body. If the assumption of the outgrowth of the left part of the body of ancestral cinctans is correct, then the homology of the posterior articulated stem of cinctans to the postanal part, i.e., the tail of hemichordates and chordates (Rozhnov, 1990) is obvious.

If the cinctan stele is actually homologous with the tail of chordates, it should be homologous to the tail of solutans too. But the comparison with solutans reveals contradictions. In the solutan *Maennilia estonica* from the Upper Ordovician of Estonia, the animal's body was oriented upon the substratum in a way that the mouth appeared at the left part of the anterior side; and the anus, at the left side of the posterior side (Rozhnov and Jefferies, 1996), i.e., growth of the left part of this animal and the moving of the anus to the anterior part could result in the cinctan body plan during the formation of the second ambulacrum. However, Jefferies (1997) believes that the majority of solutans, for example, *Dendrocystoides* and *Girvanicystis* (Jefferies, 1990; Daley, 1992), rested on the bottom with the opposite side down, and that *Maennilia estonica* was an exception. If Jefferies' reconstruction of the solutan mode of life is correct, and if it reflects promorphological and morphogenetic features of solutans, it could indicate mirror symmetry in the arrangement of basic body parts of solutans and cinctans. In my view, it seems more probable that cinctans and solutans had morphogenetically and promorphologically comparable orientation of the body. Despite a slightly different interpretation of promorphology of solutans and cinctans, Jefferies' (1997) theory of the possible descent of cinctans from solutans, or more precisely, from their direct soft-bodied ancestors seems to me correct, although our views on the mode of reorganization of one body plan into another are considerably different.

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