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Reinterpretation of Baltic Ordovician *Heckerites multistellatus* Rozhnov, 1987 as a possible paracrinoid based on new material*

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Abstract

The monotypic genus *Heckerites* Rozhnov, 1987, that was found in the Upper Ordovician of Estonia, is redescribed on the basis of new findings. The morphology of the ambulacral system, peristome, the structure and the position of the hydropore, gonopore, and periproct are described in detail. In the morphology of this genus the features of eocrinoids and paracrinoids are unusually combined. Nevertheless, the analysis of these features points to a possible assignment of this genus, and hence the monotypic family Heckeritidae Rozhnov, 1987 based on this genus, to paracrinoids.

Key words: Eocrinoidea, Paracrinoidea, Heckeritidae, Early Echinoderms, Baltic Area, Palaeozoic

Introduction

The genus *Heckerites* was described on the basis of three specimens of different preservation from the Upper Ordovician of Estonia. It was assigned to eocrinoids with flat theca, and was placed in a new, independent family Heckeritidae due to its unusual morphology (Rozhnov 1987). New fragments of the skeleton, which allow identification and description of the structure of the hydropore, periproct, and peristome, were found after the publication of this work. New data cast doubt on the assignment of *Heckerites* to eocrinoids and allow us to bring together *Heckerites* with the North American paracrinoids. This article focuses on a more complete description of the morphology of this genus, its ecological features and the problem of its systematic position.

Location, taphonomic and ecological features

The material is represented by 5 fragmentary thecae and several separate marginal plates. They all come from one active quarry near the village Vasalemma (North-West Estonia, about 60 km south-west of Tallinn), from the Vasalemma Formation from the upper part of the Keila regional stage (Fig. 1). The Vasalemma Formation is represented by medium to thick layered coarse-grained or crystalline

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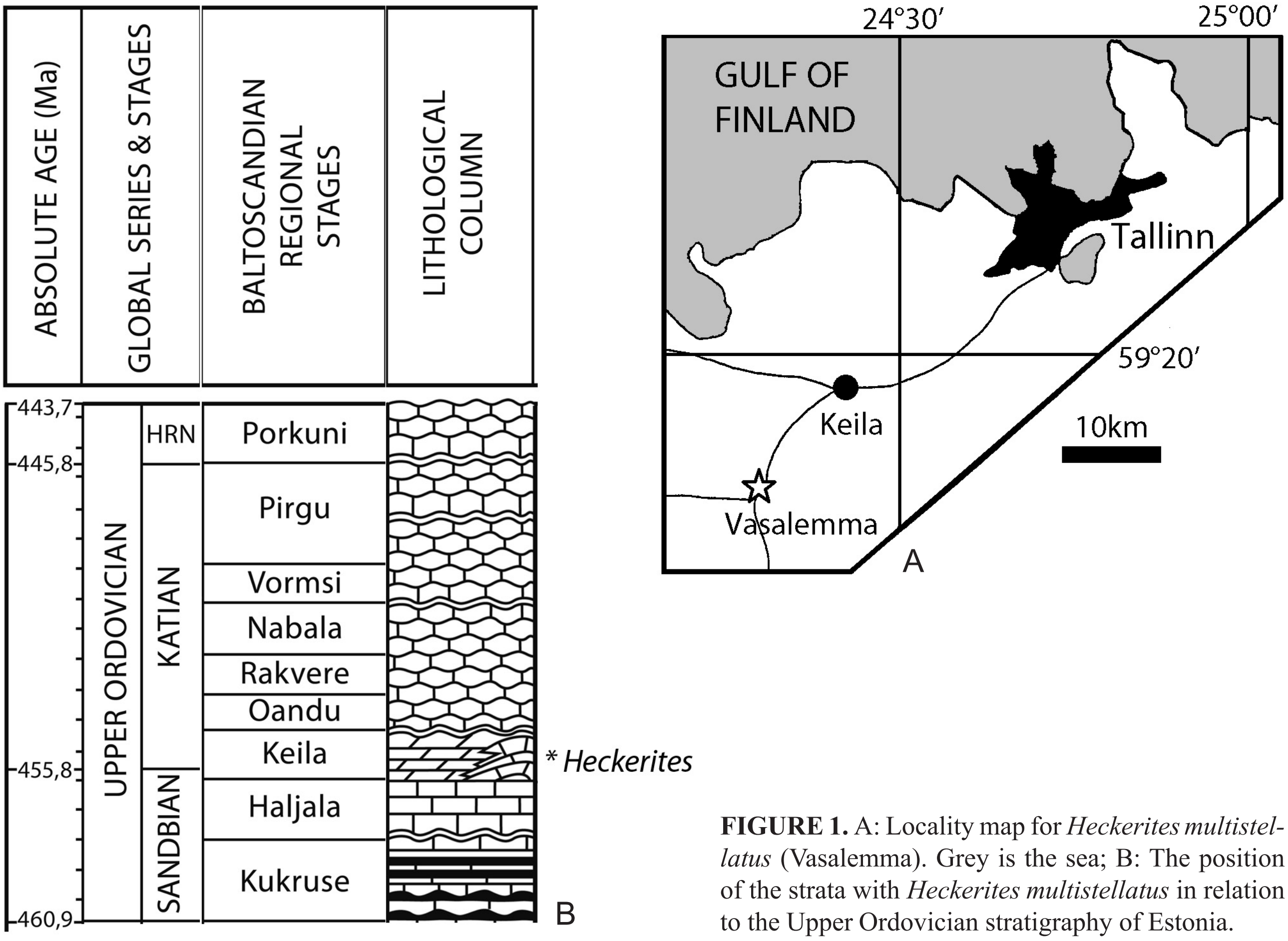

FIGURE 1. A: Locality map for *Heckerites multistellatus* (Vasalemma). Grey is the sea; B: The position of the strata with *Heckerites multistellatus* in relation to the Upper Ordovician stratigraphy of Estonia.

limestone, including bryozoan and algal bioherms (Männil 1960, 1966; Rõõmusoks 1970).

Bioherm deposits, near which were found interlayers with *Heckerites*, occur in a band 0.5–1 km wide that extends about 25 km from the village Myara on the west to the village Tula on the East.

Two types of bioherms were found in this area: algal and bryozoan. In bryozoan bioherms branching trepostomates, various members of the family Monticuliporidae, and encrusted cyclostomates, which are rare or absent in the normal facies, are the major reef-building biota. Algal limestones, composing the second type of bioherms, are cryptocrystalline, dense, yellowish-gray to bluish-gray with a greenish tinge, with irregular lenticular intercalations of marl and clay, with conchoidal fracture. Finely disseminated pyrite gives a bluish tint to this limestone. The content of terrigenous material in cystoid limestone is on average 1.9 % (0.6–2.8 %). In bioherm limestone the content of terrigenous material is on average 4–6 %. The pelitic fraction dominates in both cases (Põlma 1982). The form of the bioherms is often irregular, but there are some stock-like and conical bioherms with fairly regular shapes. The sizes of the bioherms fluctuate widely. Their diameter is usually 5–50 meters, but in rare cases it can reach up to 300 m. Their height varies from 1 to 10 m. The contact with the surrounding rocks is sharp.

The coarse-grained limestones lie between the bioherms. Among these limestones the most characteristic is the so-called cystoid limestone, composed mostly of fragments of the skeleton of the rhombiferan echinoderm *Hemicosmites*. Pyrite is present in small amounts in these limestones. There are thin layers of marl and clay marl on the bedding surfaces. All specimens of *Heckerites* come from these clay layers.

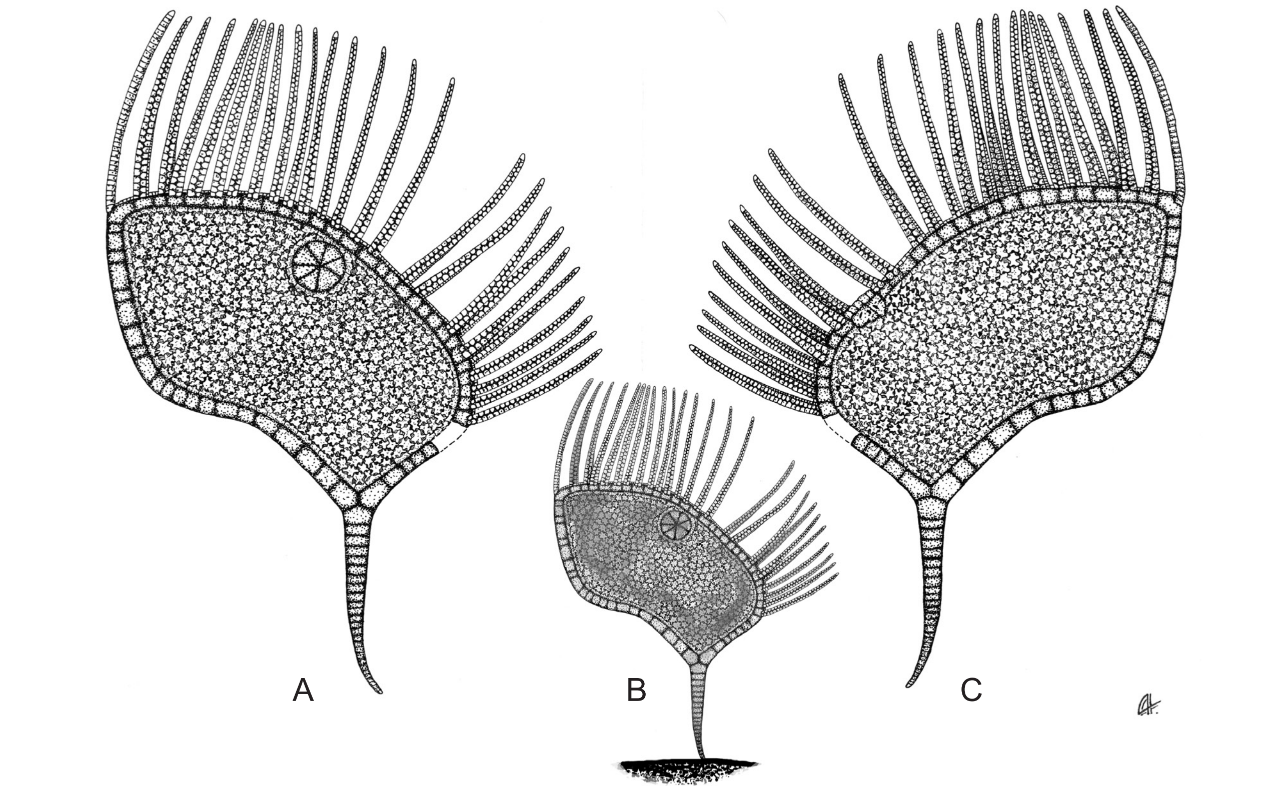

FIGURE 2. Reconstruction of *Heckerites multistellatus* in anterior (A) and posterior (B) aspects, and mode of life (C).

There were different hydrodynamic conditions, rapidly changing particularly after heavy storms, in the area of these bioherms. *Heckerites* lived in conditions where they were sheltered by the surrounding bioherms from strong wave action, on a thin, slightly silty substrate, around which is usually located a more or less dense layer of coarse calcite detritus. The distal end of the stem of *Heckerites*, which is present in one of the specimens in its life position, was slightly immersed in this detritus. The animal was located in the water column, leaned on its slightly anchored stem, and its brachioles extended above the bottom about 10–15 cm. *Heckerites* could not lie on the bottom at one of its flat sides, as in one case this would cause clogging of the hydropore by sediment, and in the other clogging of the periproct. The disproportionately large periproct probably could pulsate and may have served for respiration in addition to its direct function (Fig. 2). The marked flatness of the theca is not adapted to high hydrodynamics with an unstable flow direction, as it implies a strictly parallel position in the flow. During strong flow, the theca would require too much effort to maintain its position or lies on the bottom, herewith the animal could dies.

Therefore, especially combined with a well-developed pore system, as in *Heckerites*, or with thin central plates, as in *Rhipidocystis*, the flatness of the theca may have been improved oxygen uptake from the sea water and distribution to the internal organs.

Systematic Paleontology

All specimens are conserved in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, under the collection number PIN4125.

Family Heckeritidae Rozhnov, 1987

Diagnosis. Theca, flattened anterior-posteriorly, with two basals and two rows of marginals that frame thin anterior and posterior integuments of numerous small stellate plates with numerous sutural pores; two recumbent ambulacra with biserial flooring plates form a portion of the thecal wall; some flooring plates bear biserial brachioles; right recumbent ambulacrum continues in an erect biserial brachiole located on the special marginal plate ending the recumbent part of the ambulacrum; peristome is formed of two posterior plates and one anterior plate, and is covered by additional external rows of large cover plates; peristome and right ambulacrum are sloped to the anterior side of the theca, and left ambulacrum is sloped in the opposite direction to the posterior side of the theca; large periproct located on the anterior side of the theca, opposite of the side where the hydropore and gonopore are situated; the hydropore and gonopore are located on the posterior lip of the peristome; the stem is formed by triangular-rounded columnals with a thin central lumen.

Stratigraphic and geographic distribution. Upper Ordovician (Sandbian and Katian) of Baltica.

Genus *Heckerites* Rozhnov, 1987

Type species. *Heckerites multistellatus* Rozhnov, 1987

Diagnosis. As for the family.

Distribution. North-West Estonia, Vasalemma formation, Upper Keila, Lower Katian, Upper Ordovician; West of St. Petersburg region, Grjazno formation, Haljala regional stage, Sandbian, Upper Ordovician (S. Terentiev, pers. comm.); Norway, Asker near Oslo, regional stage 5a, Upper Katian, Upper Ordovician (F. Bockelie, pers. comm., 3 Dec. 1987)

***Heckerites multistellatus* Rozhnov, 1987**
Figures 2–5

Holotype. PIN 4125/62b: adoral part of theca with brachioles. Upper Ordovician, Keila regional stage, lower part of the Vasalemma Formation, quarry near the village Vasalemma (North-West Estonia, about 60 km south-west of Tallinn, near the small town of Keila). The material is represented by 5 fragmentary thecae and several separate marginal plates.

Additional material studied. PIN 4125/891, peristomal part of theca with adjacent ambulacral parts, periproct, gonopore and hydropore; PIN 4125/892, peristomal part of theca with adjacent parts of ambulacra, brachioles, gonopore and hydropore.

Description (Figs. 3, 4, 5). The theca is flat, triangular, covered with small stellate plates and is bordered by two rows of marginal plates, located on the extension of the two basal plates. The stem branches off from the basal plates, joined at right angles, and quickly narrows and ends with a pointed distal end. The oral side of the theca is bordered by the external parts of the ambulacral flooring plates and peristomal plates. Two ambulacra tilted in opposite directions stretch out to the right and left of the peristome. Biserial brachioles branch off from some of the ambulacral plates. The theca is about 4–5 cm in height, with a width of 2.5–3.5 cm and a thickness of 5–7 mm. On one side of the theca near the peristome is a large anal pyramid, and on the opposite side are the gonopore and the hydropore. The flat side with the hydropore here is adopted as the posterior side, and the opposite side, despite the fact that there is the anus in this side, here is adopted as the anterior side. The marginal and ambula-

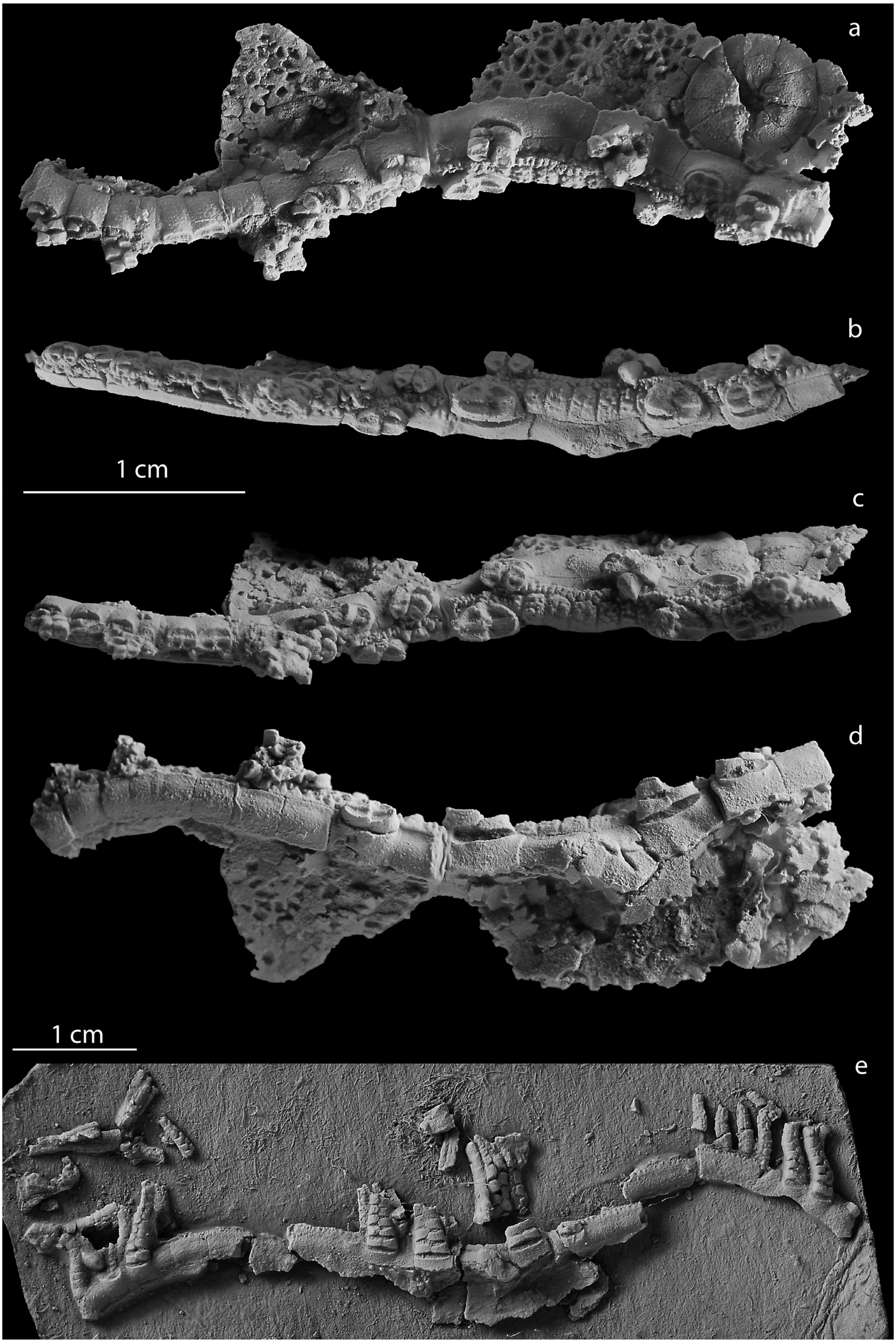

FIGURE 3. *Heckerites multistellatus* Rozhnov, 1987. a–d: PIN 4125/891, peristomal part of theca with adjacent ambulacral parts: a: anterior aspect with periproct; b: upper aspect; c: upper anterior aspect; d: posterior aspect with gonopore and hydropore; e: PIN 4125/892 , peristomal part of theca with adjacent parts of ambulacra and brachioles in posterior aspect with gonopore and hydropore.

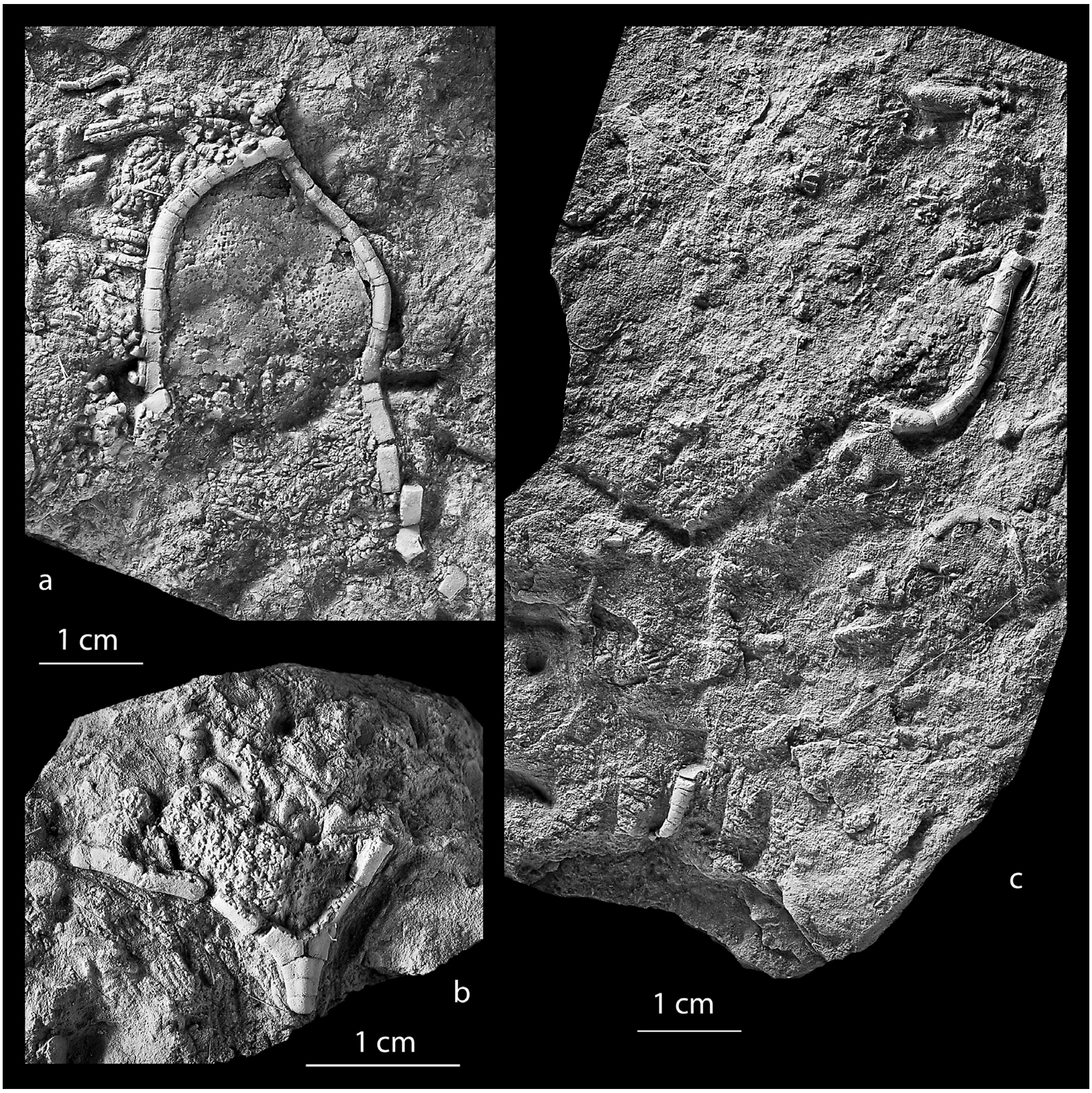

FIGURE 4. *Heckerites multistellatus* Rozhnov, 1987. a: holotype PIN 4125/62 , adoral part of theca in posterior aspect; b: PIN 4125/122 , basal part of theca and proximal part of stem; c: PIN 4125/123, imprint of theca and stem with some calcite parts of skeleton in posterior aspect.

cral plate series will be called right and left in accordance with this orientation.

Two rows of marginal plates branch off at a right angle from the right and left basals, forming the frame on the edges of the theca. The length of the marginal plates is from 2 to 5 mm and the diameter is about 2 mm. The external edge of the marginal plates is convex, and the internal edge is slightly concave with serrated edges on both sides of the groove. The rays of the stellate plates, covering both sides of the thecal integument between the marginal plates, join to the denticles. The stellate plates are usually small, mostly six-rayed, with a diameter of about 1 mm, and are connected to each other at the tips of the rays. Between the connected rays there are pores, evenly covering both sides of the theca.

Two basal plates are joined by their proximal ends at a right angle. Each of them continues distally by the row of the marginal plates. The facet for the attachment of the stem, a rounded triangle shape is located at the junction of the basals. The facet, as the stem, is penetrated by a narrow central channel.

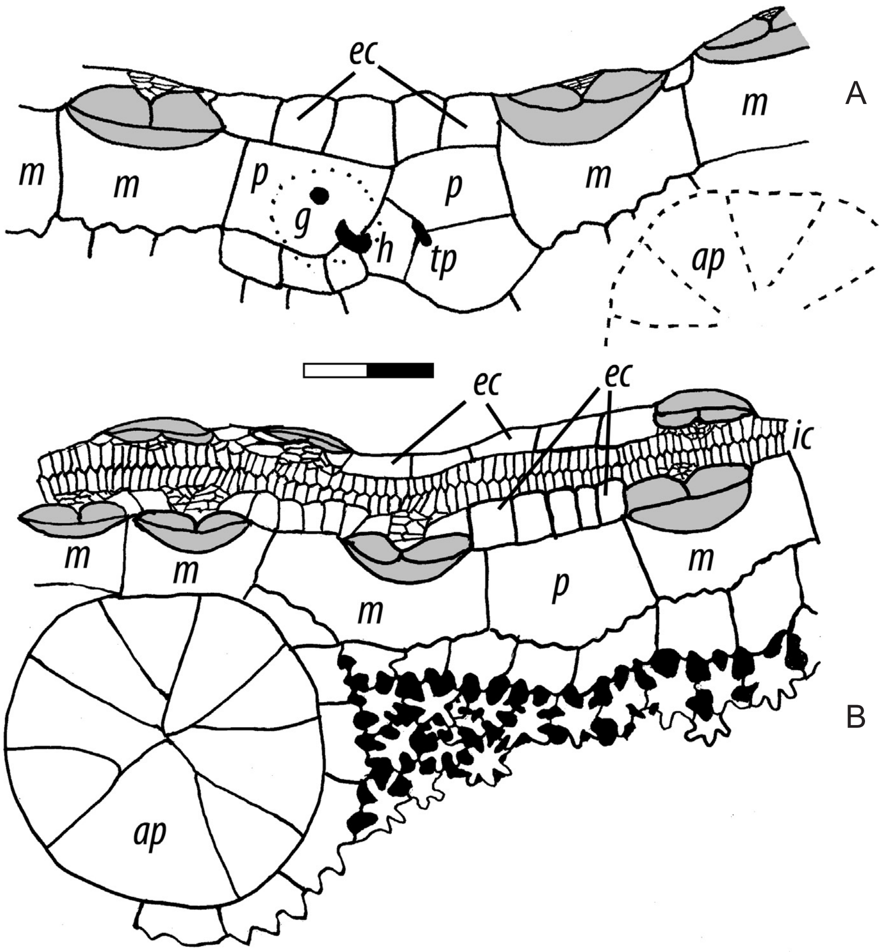

FIGURE 5. *Heckerites multistellatus* Rozhnov, 1987. Details of the posterior (a) and anterior (b) peristomal area. Drawing is based on specimen PIN 4125/891: facets for brachiole attachment are gray, pores are black, *g*—gonopore, *h*—hydropore, *tp*—third pore, *ap*—anal pyramid, *p*—peristomal plates, *m*—marginal plates, *ic*—internal row of biserial cover plates, *ec*—external rows of cover plates. Scale bar equals 2 mm.

The stem in its proximal part is constructed with large rounded triangular segments (the diameter is 3–4 mm and their height is about 1.5–2 mm) with a very narrow lumen. The stem, consisting of small columnals, quickly narrows and ends distally in a point without a special holdfast. The length of the stem is somewhat less than the height of the theca.

The right row of marginal plates is preserved in two specimens mostly as the imprint and partly as the skeleton. Only the proximal part is known for the left row. The location and nature of its connection with the ambulacral part of the theca are unknown.

The right row of the marginal plates ends by an angular plate, with the distal end of which a row of biserial ambulacral flooring plates is connected. The angle plate boards the recumbent part of the right ambulacrum. However, it has a facet for the attachment of a biserial brachiole, which is located perpendicular to the ambulacrum. This brachiole is actually an extension of the right recumbent ambulacra outside the theca. The angular plate is connected with a neighboring marginal plate by a flat suture and is connected with a series of biserial alternated ambulacral flooring plates by a stepped suture at the opposite side. The ambulacral groove, slightly tilted to the anterior (with the anus) side of the theca begins with these plates. Flooring plates form a portion of the thecal wall. The length of the flooring plates are usually 2–2.5 mm with a height of about 3 mm, but some are longer in two times. The facets for the attachment of the biserial brachioles are located on some of the flooring plates. There are not less than 6–8 plates with brachioles on the anterior side of the right ambulacrum. On the posterior side of the right ambulacrum there are four plates with brachioles, two of which are located directly one after the other, after the peristomal plates, and two others are consecutive before the locked angular plate. Each facet for the attachment of brachioles has a well developed sculpture: a deep semilunar depression along the entire width of the facet; on the external side it is separated from the two pits by two longitudinal ridges, which are separated by a transverse ridge that is located on the inner part of the facet. The length of the facet is about 2 mm and its width is about 1mm. The brachioles, quickly narrowed distally, are about 10–15 mm long; the width of their proximal part is about 2 mm. They are constructed by biserial brachioles, the proximal parts of which are almost opposite one another, and distal parts are alternating.

There are two peristomal plates on the posterior side and one on the anterior side. They are located on the extension of flooring plates and delineate the peristomal opening. Like the right ambulacrum, the peristome is tilted to the anterior side of the theca. The left ambulacrum is tilted to the opposite (posterior) side of the theca. The peristomal part of the theca is covered by additional external rows of large cover plates. Therefore, there are four rows of cover plates: an internal biserial row of small alternated plates with a zigzag suture between them is bordered by external rows of large cover plates. The external cover plates from the posterior side are larger than those from the anterior side. The additional external rows of large cover plates extend slightly outside the peristomal area in the ambulacra, but quickly disappear distally, so a series of small biserial cover plates covers the main part of the ambulacra.

The anal pyramid is large, 7 mm in diameter, and consists of nine plates, most of which are in the shape of a sector, reaching the center of the circle, and are slightly convex. It located near the marginal plates on the anterior side of the theca, opposite the side with the hydropore, near the right end of the peristome.

The gonopore is round and situated on the centre of a tubercle, in which two peristomal plate and a third thecal plate connect. A slit-like hydropore is located in the place of contact of these three plates, and possibly a third, slit-like pore is also located near the tubercle.

Discussion

A flattened theca is considered the feature which originally united eocrinoids with a similar structure into one clade (Broadhead 1982; Dean & Smith 1998). Therefore *Heckerites* was assigned to eocrinoids (Rozhnov 1987) as a monotypic family Heckeritidae. Sumrall *et al.* (2001) described a new eocrinoid with a flattened theca, *Haimacystis*, from the Early Ordovician of Utah. Comparing *Haimacystis* with other eocrinoids with a flattened theca, these authors showed that the differences between the rhipidocystids, a *Haimacystis* and two other families, lingulocystids and cardiocystitids, are very great. In particular, rhipidocystids are flattened laterally, whereas the others are flattened in the anteroposterior direction. Therefore, the flatness of the theca, in their opinion, cannot combine them into a single clade, and to determine relationship each of these groups should be compared not only among themselves but also with the other eocrinoids having the usual rounded theca. Sumrall *et al.* (2001) did not take into account the structure of *Heckerites*. Morphological features of *Heckerites* support the view of these authors. New data on the morphology of the adambulacral part of the theca, the position of the gonopore, hydropore, and anus allow us to compare *Heckerites* not only with eocrinoids, but also with paracrinoids. The main characteristics of *Heckerites* include:

1. the anterior-posteriorly flattened theca;
2. two rows of marginal plates above the basal circlet;
3. only two basals are present;
4. the marginals articulate to a thin integument of numerous small stellate plates;
5. numerous sutural pores are located between rays of stellate plates and are distributed evenly on both the anterior and posterior sides of the theca;
6. two recumbent ambulacra are extended from the peristome in opposite directions;
7. ambulacral flooring plates are biserial and form a portion of the thecal wall;
8. the right recumbent ambulacrum is continued in an erect biserial brachiole located on the special marginal plate locking the recumbent part of the ambulacrum (the end of the left ambulacrum is unknown);
9. some flooring plates bear biserial brachioles;
10. the peristome is formed by one anterior and two posterior plates, and it is covered by additional external rows of large cover plates;
11. the peristome and right ambulacrum are sloped to the anterior side of the theca, and the left ambulacrum is sloped in the opposite direction (to the posterior side of the theca);
12. the large periproct is located on the anterior side of the theca (opposite of the side where the hydropore and gonopore are situated); the hydropore and gonopore are located on the posterior lip of the peristome;
13. the stem is formed by triangular-rounded columnals with a thin central lumen.

The combination of these features is highly unusual. Among them are features that are typical for different clades of eocrinoids and paracrinoids. For eocrinoids, first of all, biserial brachioles are typical (Sprinkle 1973); however, their location on the flooring plate of the recumbent arm is similar to the morphology of paracrinoid recumbent arms (Parsley & Mintz 1975). Despite such a similarity between the structure of the food-gathering system of *Heckerites* and paracrinoids, there is one more significant difference except the arm seriality: flooring plates of *Heckerites* form a portion of the thecal wall, unlike paracrinoids. A great similarity in the location and structure of the gonopore and hydropore in *Heckerites* and typical paracrinoids is significant. At the same time, the location of the anus on the opposite side of the theca from the hydropore in *Heckerites* distinguishes it from paracrinoids. This difference can be explained by paedomorphosis: the development of the gut in *Heckerites*, growing, like in most other echinoderms, in a clockwise direction, stopped at an unusually early stage, which has not led to the location of the anus in the CD interray. Such a shift of the periproct from the typical position is known in other echinoderms as well (*e.g.*, *Cryptocrinites,* Rozhnov 1994). By the way, the absence of the hydropore in *Haimacystis* near the periproct may not be explained by poor preservation of this side of the theca (judging from the illustrations, it is good enough), but by the fact that the hydropore of this genus is like in *Heckerites*, on the opposite side of the theca from the anus, which is not seen in the studied specimens. *Heckerites* is similar to lingulocystids in the presence of marginals and small integumental plates (Ubaghs 1960).

The pore system of *Heckerites*, however, is similar to that of some paracrinoids by being evenly distributed on both sides of the theca. Finally, *Heckerites* and paracrinoids are united by the flatness of the theca in the anteroposterior view: strong flatness of theca in *Heckerites* and weak or moderate in many paracrinoids.

Thus, the morphology of *Heckerites*, despite the unusual combination of many features, allows to associate it with paracrinoids. Therefore, in this paper this genus and the family based on it are placed among paracrinoids, but with a certain degree of caution.

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