



ON THE PARACRINOID-LIKE ECHINODERMS *ACHRADOCYSTITES* VOLBORTH, 1870 AND *HECKERITES* ROZHNOV, 1987 FROM THE ORDOVICIAN OF BALTICA

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INTRODUCTION

Paracrinoids are a characteristic group of the Ordovician echinoderm fauna of Laurentia. Two endemic genera tentatively assigned to paracrinoids found in the Ordovician of Baltica are also found outside Laurentia. These are two very different genera, *Achradocystites* Volborth, 1870 and *Heckerites* Rozhnov, 1987 from the Upper Ordovician (Katian) of northern Estonia. Here, I do not discuss Baltic cryptocrinids, rhipidocystids, or similar North American taxa, which may be related to paracrinoids (Sprinkle, 1973), but are not very similar and need to be considered separately. Typical paracrinoids from Laurentia have uniserial exothecal, often recumbent "arms", with uniserial "pinnules". The Baltic *Achradocystites* and *Heckerites* have many features similar to North American paracrinoids, including the food-gathering system, but differ in the biserial "arms" and biserial "pinnules". A detailed study of their food gathering systems, evaluation of the possibility of biserial appendages becoming uniserial, and possible mechanisms for such transformations, are required to substantiate the unification or separation of the two Baltic genera from the North American paracrinoids. The food-gathering system of *Heckerites* has been studied in detail (Rozhnov, 2012). Until recently, the morphology of the brachioles of *Achradocystites* was only known from isolated brachials found separate from the theca (Hecker, 1958; Stukalina and Hints, 1989). New material, part of the theca with three "arms", two of them well preserved, allows detailed description of the "arm" morphology (Fig. 1). I use here the paracrinoid terminology although the "arms" with "pinnules" of *Achradocystites* are very similar with the "ambulacral trunks with brachioles" of some eocrinoids and other blastozoans (Sprinkle *et al.*, 2011). I suppose that paracrinoid and eocrinoid terminology can be combined in the future because the eocrinoid "biserial trunks with brachioles" could be ancestral for the paracrinoid "uniserial arms with pinnules". Both these exothecal structures appeared independently with true endothecal arms and pinnules of crinoids although the pattern of "pinnulation" is very similar in all these cases.

MORPHOLOGY OF BRACHIOLES OF *ACHRADOCYSTITES*

Each of three "arms" (A, C, and E) extends from a pair of large plates of the pre-oral field. The "arms" are long, ca. 50 mm, which is slightly shorter than the theca. The "arms" are biserial gradually decreasing distally. The "arm" width is 6 mm proximally and 4 mm distally. The height of the brachials is 3.5 mm proximally and 2.5 mm distally. Each segment had a semi-circular slightly depressed crested facet for "pinnular" attachment and is mounted on a

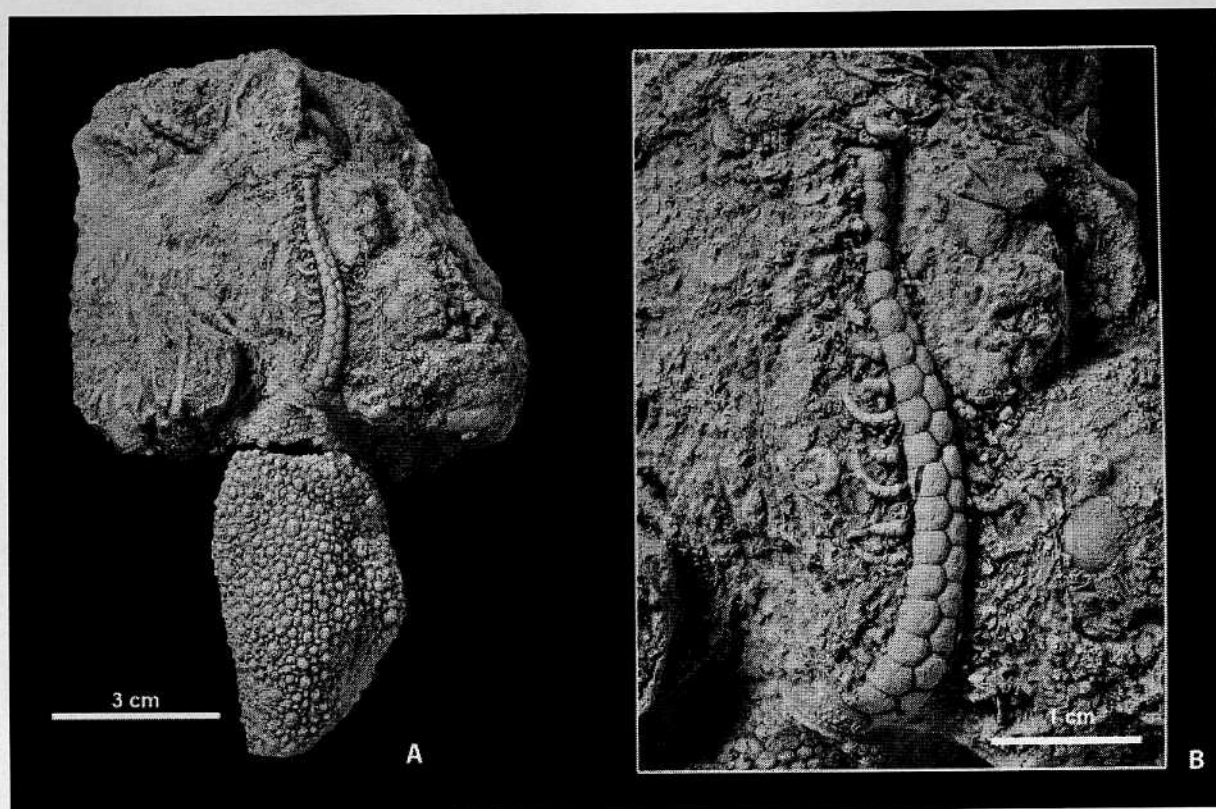


Figure 1. Theca of *Achradocystites* sp. with biserial "arms" and "pinnules", PIN 4125/909, general view (A) and detail of the "arm" (B). Vasalemma Formation, Keila regional stage, Katian. Upper Ordovician, quarry near Vasalemma, North Estonia.

small pedestal. The ambulacral canal is deep, V-shaped, branching in the middle of each brachial, approaching the facet and running further, into the "pinnule". Biserial "pinnules" arise from each plate beginning from the proximal; they are 10-12 mm long, each composed of 8-10 pairs of plates, rapidly narrowing and forming a dense meshwork on the right and left of the ambulacrum. The gradual narrowing and lowering of the plates of the main branch and "pinnules" shows that the new plates were added terminally.

DISCUSSION

The complex morphology of "pinnule"-bearing "arms" of *Achradocystites* suggests that the ambulacral groove included, apart from the ambulacral canal and ciliated epithelium, other organ systems necessary for the function and growth of the food-gathering system, i.e., mesoderm for formation and growth of the calcite skeleton, neural system for coordination of the movements of the ambulacral appendages, and blood circulatory system and/or coelomic canal system necessary for feeding this food-gathering system. Therefore, despite the exothecal characters of biserial "arms" in *Achradocystites* and uniserial arms in typical paracrinoids, coeloms and their derivatives continued into the ambulacral canals (at least the left coelom). The biserial terminal growth model of the flooring plate series and the cover plates is strikingly similar to that of the development and growth of radial ambulacral canals of extant crinoids and other echinoderms. This model can be characterized as a terminal growth with serial branching on the right and left alternating ambulacral appendages. Therefore the hydrocoel and its derivatives, primarily radial ambulacral canals, can be considered as inductors of successive events, including skeleton development. This is analogous to the dorsal blastopore lip and its derivatives, the chord and prechordal mesoderm in vertebrates. Growth and branching of radial ambulacral canals can be considered as a model inducing a similar model first in the development of the axial skeleton, and later in some parts of the extraxial skeleton (in the terminology of David and Mooi, 1998). As the autonomy of

the skeleton of the food-gathering appendages increased, the model of alternating biserial terminal growth could apparently be simplified to uniserial, terminal growth. This process could have followed a pattern, which can be reconstructed by comparing brachiolar morphology in different rhipidocystids. Initially, the brachiolars of adjacent series were shifted to the same level to form paired plates. This corresponds to a change in growth from alternating terminal biserial to simultaneous biserial. Later, the fusion of paired plates resulted in uniserial terminal growth. In paracrinooids with arms arising from the theca, the transition from uniserial to biserial growth could have followed this rhipidocystid pattern. In genera with recumbent arms, the transition from biserial to uniserial brachiolar plates was probably more complex. This can be inferred from the morphology of the ambulacra in *Heckerites*. Biserial flooring plates in this genus are at the same time thecal plates covering the thecal interior, similar to edrioasteroids. However, in contrast to the ambulacra of edrioasteroids, at least one of the two ambulacra of *Heckerites* terminates with a terminal plate. This terminal plate is probably equivalent to the ocular plate in echinoids and the terminal plate in starfish, which limits the terminal growth of an ambulacrum to the theca. In comparison, in the North American paracrinooid genus *Platycystites*, only the most proximal plates of the uniserial recumbent arm directly cover the thecal interior, and later the plates of the theca become fused, so a lumen expanded proximally and decreasing distally is developed between the arm ossicle and thecal callus (Parsley and Mintz, 1975). There is no terminal plate, and the ambulacrum growth is not limited to the theca and sometime continues much further down to the stem.

CONCLUSIONS

The biserial skeleton of the food-gathering appendages of the Baltic genera *Achradocystites* and *Heckerites* could transform into uniserial arms and pinnules characteristic of the North American paracrinooids, following the rhipidocystid pattern. Therefore the biserial pattern in the Baltic genera does not contradict their placement within paracrinooids but suggests that they separated from the main stalk of paracrinooids of Laurentia at the early stages of its development, probably beyond the realms of both Laurentia and Baltica.

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