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Revision of *Scoliocystis* (Rhombifera: Echinoencrinitidae) and Related Cystoid Genera

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Abstract—Species attributed to *Scoliocystis* Jaekel, 1899, including the type species *S. pumila* (Eichwald, 1860) and *S. thersites* Jaekel, 1899 from the Ordovician of the Leningrad Region, are reviewed. *Scoliocystis* sp. from the Upper Ordovician of Estonia, figured by Hecker (1964), is redescribed as *Maennilocystis heckeri* gen. et sp. nov. and it is attributed to the family Callocystitidae Bernard, 1895. The genus *Scoliocystis* is intermediate between the families Cheirocrinidae and Echinoencrinitidae in having five periproct border plates (as in cheirocrinids), but lacking plate R5 and having a reduced oral area, as in echinoencrinitids, but is retained in the Echinoencrinitidae. The similarity of *Scoliocystis* to the unusual North American cheirocrinid genus *Sprinkleocystis* is convergent. The genus *Gonocrinites* Eichwald, 1840, with two species, is restored among echinoencrinitids, as having four periproct border plates, whereas *Echinoencrinites* sensu stricto has three. The families Echinoencrinitidae and Callocystitidae arose from cheirocrinids with closed plate circlets by the loss of plate R5 and substitution of radial:lateral for radial:radial pectinirhombs. In addition, echinoencrinitids are characterized by a reduced oral area, whereas in callocystitids, the recumbent ambulacra are extensive. *Scoliocystis* is a stem-group genus to Echinoencrinitidae plus Callocystitidae. Several glyptocystitoid genera independently developed advanced pectinirhombs.

Keywords: *Scoliocystis*, *Maennilocystis heckeri* gen. et sp. nov., *Sprinkleocystis*, Echinoencrinitidae, Callocystitidae, Cheirocrinidae, pectinirhombs

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INTRODUCTION

Jaekel (1899, p. 257) introduced the genus *Scoliocystis* based on two species from the Ordovician of Russia, *"Caryocystites" pumilus* Eichwald, 1860 and *Scoliocystis thersites* Jaekel, 1899, with the former as the type species. There are some discrepancies between Jaekel's plate diagrams, especially of the type species (Jaekel, 1899, p. 196, text-fig. 36E, p. 258, text-fig. 51) and his illustrations of actual specimens (Jaekel, 1899, pl. 11, figs. 11, 12), which led to uncertainties about the precise characters of *S. pumila* and, hence, of the genus *Scoliocystis*. Paul and Donovan (2011, pp. 438–439) discussed the problems at length. This matters, among other things, because Jaekel (1899, p. 235) also made *Scoliocystis* type genus of his new family Scoliocystidae. Although, the name Scoliocystidae has usually been considered a junior synonym of the Echinoencrinitidae Bather, 1899 (for example, in Kesling, 1968) it was resurrected by Broadhead and Strimple (1978, p. 170) as a subfamily, Scoliocystinae, characterized by cystoids with advanced disjunct pectinirhombs with vestibule rims, and transferred to the family Callocystitidae Bernard, 1895. The situation was further complicated when Hecker (1964, pl. 3, figs. 10, 11) illustrated under the name *Scoliocystis* sp. another Ordovician cystoid, which shows strong resemblances to the North American Ordovician genus *Lepadocystis* Carpenter, 1891 and the Lower Silurian genus *Anartiocystis* Ausich et Schumacher, 1984, both of which are callocystitids. *Scoliocystis* sp. differs in so many characters from *S. pumila*, that we do not think it can be included in the same genus. Thus, these taxonomic and nomenclatural problems cannot be settled without a thorough redescription of *Scoliocystis pumila*.

In addition, *Scoliocystis* shows an interesting combination of characters that suggests it is intermediate between the families Cheirocrinidae and Echinoencrinitidae. For example, it has five plates surrounding the periproct (Fig. 1c, 1d), a character that is almost universally present in the Cheirocrinidae (Figs. 1a, 1b, 1g), but otherwise unknown in pectinirhomb-bearing cystoids. However, it has only five radial plates, not the six characteristic of cheirocrinids, but typical of echinoencrinitids and callocystitids (compare Figs. 1a, 1b and 1g with 1c–1f). Furthermore, judging from Jaekel's

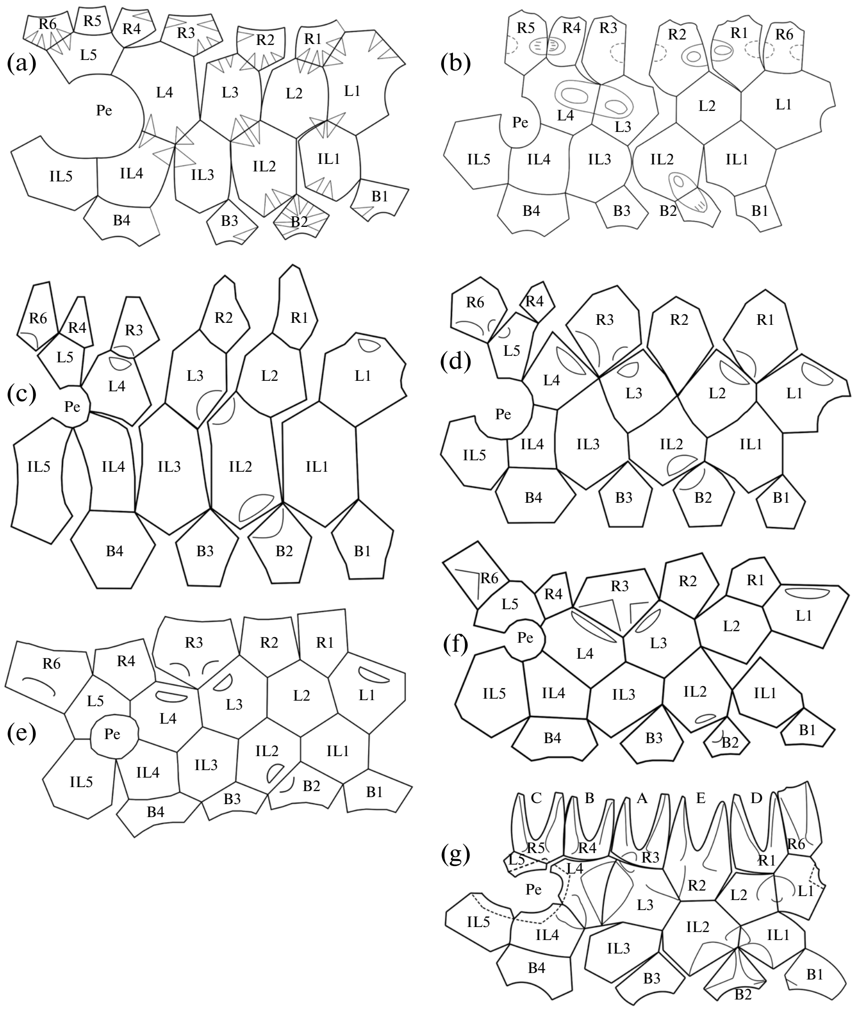


Fig. 1. Plate arrangements in key glyptocystitoid genera. (a) *Cheirocystella* Paul, 1972. (after Paul, 1972, p. 35, text-fig. 9); (b) *Sprinkleocystis* Broadhead and Sumrall, 2003 (after Broadhead and Sumrall, 2003, p. 118, text-fig. 4); (c) *Scoliocystis pumila* (Eichwald, 1859) (after Jaekel, 1899, p. 258, text-fig. 51); (d) *S. thersites* Jaekel, 1899 (after Jaekel, 1899, p. 258, text-fig. 50); (e) *Maennilocystis heckeri* sp. nov.; (f) *Anartiocystis* Ausich et Schumacher, 1984 (after Ausich and Schumacher, 1984, p. 11, text-fig. 2); (g) *Coronocystis angulata* (Wood, 1909) (after Paul, 1972, p. 39, text-fig. 11). Designations: (B1–B4) basal plates, (IL1–IL5) infralateral plates, (L1–L5) lateral plates, (Pe) periproct, (R1–R6) radial plates. Note that *Cheirocystella* and *Sprinkleocystis* have six radial plates and that five plates form the periproct border in both species of *Scoliocystis*.

illustrations, *Scoliocystis* apparently had advanced disjunct pectinirhombs with vestibule rims, otherwise typical of some echinoencrinitids (Broadhead and Strimple's Scoliocystinae) and all callocystitids. Thus, *Scoliocystis* occupies a significant position in the evolution of the glyptocystitoid cystoids, which again cannot be settled without a thorough understanding of its morphology.

Advanced disjunct pectinirhombs with vestibule rims are also found in two other Ordovician genera of glyptocystitoids, *Praepleurocystis* Paul, 1967c, and *Sprinkleocystis* Broadhead and Sumrall, 2003 (Fig. 1b). *Praepleurocystis* shares many characters with other members of the highly specialized family Pleurocystitidae and need not be considered further here. However, *Sprinkleocystis* is possibly much more closely related to *Scoliocystis*. It was originally attributed to the family Cheirocrinidae on the grounds that it had pectinirhombs and six radial plates; both are characters of the Cheirocrinidae. However, it differs from all other known cheirocrinids in having only four plates around the periproct, because plate L5 is apparently missing; only four ambulacra that terminate in a single brachiole and in having advanced pectinirhombs with vestibules. A reduction in the ambulacral system is typical of echinoencrinitids. Furthermore, the theca of *Sprinkleocystis* is a very unusual shape, which resonates with Kesling's (1968, p. S191) comment that Jaekel described *S. pumila* as "stunted." *Sprinkleocystis* also seems to share some characters of the Cheirocrinidae and others that are more typical of the Echinoencrinitidae. Thus we think its evolutionary

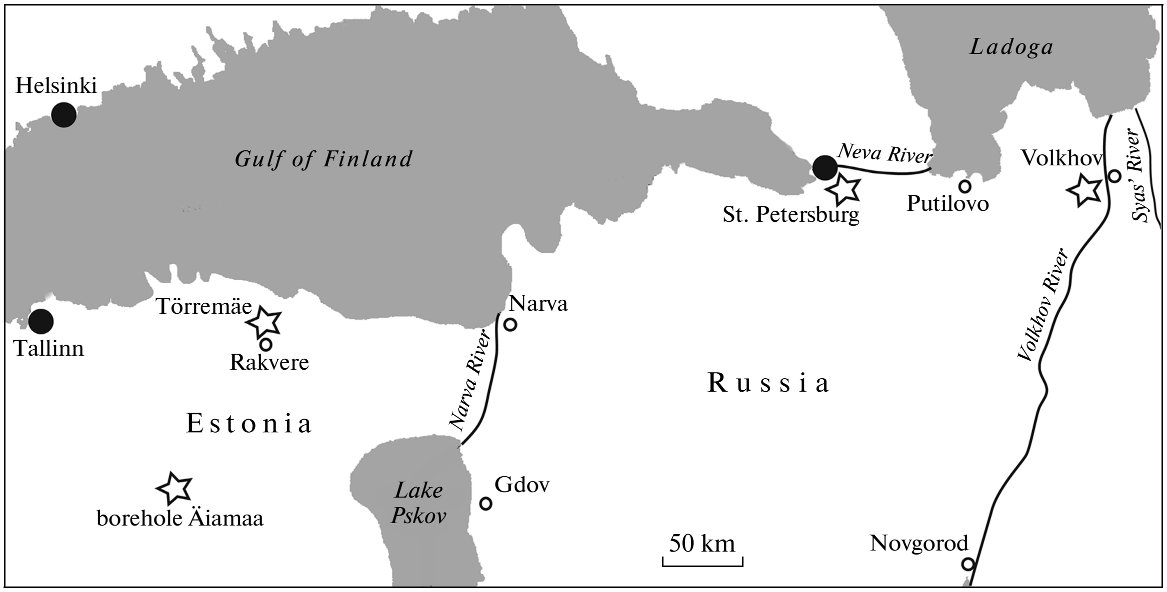


Fig. 2. Map of the localities mentioned in the text (designated by asterisk).

position should be considered at the same time as a reevaluation of *Scoliocystis*.

This paper was initiated when one of us (C. Paul) came across the paper by Rozhnov (2002), in which Jaekel's original specimen of *Scoliocystis thersites* was freshly illustrated (Rozhnov 2002, text-fig. 6). Thus, it was apparent that Jaekel's specimens had not been destroyed during the Second World War, as had previously been believed. In addition, new specimens we attribute to *S. pumila* and "*Scoliocystis* sp." allow a more complete description of these two taxa. The aims of the present paper are to describe the available material of all three species previously attributed to *Scoliocystis* and to discuss the evolution of these and other relevant taxa. The material described in this paper came from the Ordovician of western Russia and adjacent Estonia (Fig. 2). The local stratigraphy is illustrated in Fig. 3, with the key horizons from which cystoids have been recorded indicated on the right hand side.

The specimens examined are housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), and in the Geological Institute of Tallinn Technological University (GIT).

Key Characters

With very few exceptions, all glyptocystitoid cystoids are characterized by a theca composed of up to 27 primary thecal plates arranged in five circlets. They have a fixed plate formula, from the stem attachment upwards, of four basals (B, plural BB), five infralaterals (IL, ILL), five laterals (L, LL), four, five, six, or ten radials (R, RR) and seven orals (O, OO). Variations involve both the number and arrangement of plates. Thus, *Cuniculocystis* Sprinkle and Wahlman, 1994 (family Cuniculocystidae) is unique in having ten radial plates and *Sprinkleocystis* (family Cheirocrinidae) has only four lateral plates (L5 is apparently absent or fused with plate L1; Fig. 1b). However, Paul (1972, p. 41, text-fig. 13, pl. 3, figs. 1–4) illustrated a specimen of *Coronocystis angulata* (Wood, 1909), which also lacked plate L5. In addition, all genera in the families Echinoencrinitidae and Callocystitidae have apparently lost plate R5 (e.g., Figs. 1c–1f) and some echinoencrinitids lack plate R4 as well. In the oldest glyptocystitoid genus, *Macrocystella* Callaway, 1877, and in the oldest cheirocrinid, *Cheirocystella* Paul, 1972 (Fig. 1a), all the plate circlets are closed, which means that, if the plates of a single circlet were isolated, they would form a complete ring. Plate arrangements vary when some plate circlets become open, which occurs when plates from the circlet above and below meet at a common suture (e.g., *Coronocystis* Paul, 1972; Fig. 1g), thus interrupting the intervening plate circlet. In *Coronocystis*, plates IL2 and R2 have a common suture, thus separating plates L2 and L3. An IL2:R2 suture is also universally present in the family Glyptocystitidae. In addition, some taxa have modified plate circlets, in which four plates meet at a point (e.g., *Scoliocystis thersites;* Fig. 1d). This usually arises due to lengthening of rhomb-bearing sutures, as first documented by Sumrall and Carlson (2000), but this is not true of plates IL2, L2, L3, and R2 in *S. thersites*. A few generalizations may be made, for example, that the basal and oral circlets are always closed, but details of which of the other circlets are open and at how many places, form the bases of several generic definitions, especially within the families Cheirocrinidae, Glyptocystitidae, and Callocystitidae.

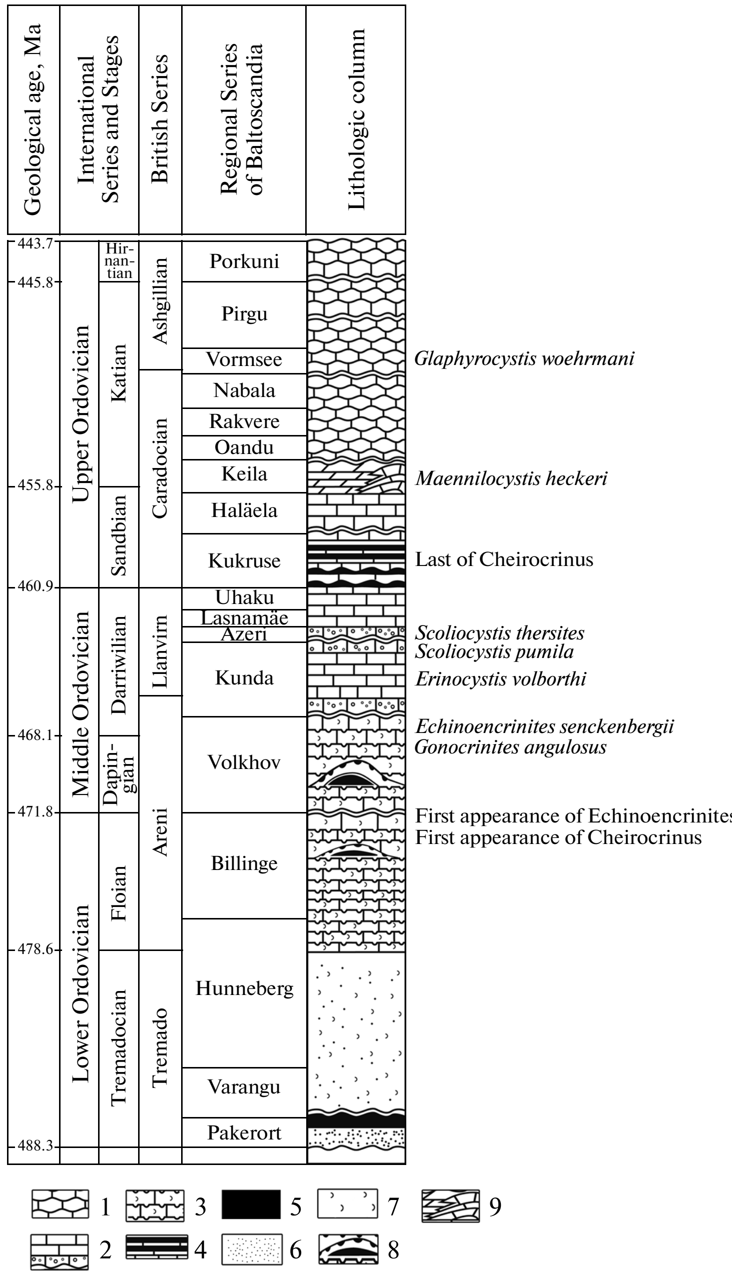


Fig. 3. Regional stratigraphical scheme of the Ordovician of the Baltoscandian Region, correlation with the International Stratigraphic Chart and historical British Chart, and occurrence of cystoids mentioned in the text in this region. Designations: (1) tropical carbonates, (2) warm-water carbonates with ferriferous oolites, (3) cold-water carbonates with glauconite, (4) kukersite shale, (5) schist, (6) quartz sand and sandstone, (7) glauconite, (8) cold-water mud mounds, (9) tropical mud mounds (after Dronov and Rozhnov, 2007, modified).

Finally, the number of plates surrounding the periproct varies widely within the superfamily Glyptocystitoida and may be used to characterize genera and even families, although there are almost always some exceptions to any generalization within families. Even so, in the large family Cheirocrinidae, all but one genus (*Sprinkleocystis*) have five plates surrounding the periproct, which is covered by a flexible, plated periproctal membrane, within which is set a circular anal pyramid at the lower right. This arrangement was inherited from the Macrocystellidae. In most genera of the Pleurocystitidae, the periproctal area increases and the periproct is surrounded by six or even eight thecal plates (see Paul, 1984, p. 81, text-fig. 52). In other families, the tendency is to reduce both the size of the periproct and its cover. Thus, in the family Glyptocystitidae, the periproct is surrounded by four plates (IL4, IL5, L4, and L5) in *Quadrocystis* Sprinkle, 1982 and by IL4, L4, L5, and R4 in *Hesperocystis* Sinclair, 1945, but only three (always IL4, L4, and L5) in

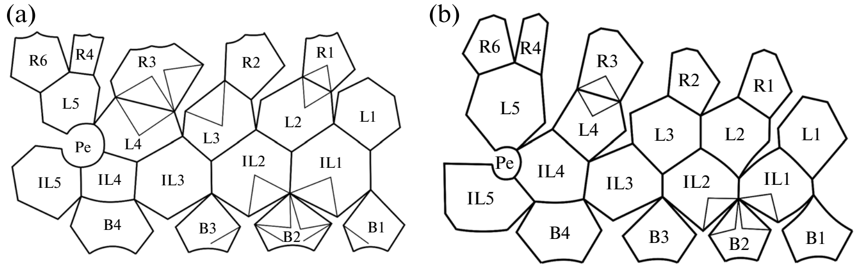


Fig. 4. Plate arrangements in the echinoencrinitid genera: (a) *Gonocrinites* Eichwald, 1840 and (b) *Echinoencrinites* von Meyer, 1826 (after Kesling, 1968, p. S185, fig. 89). Designations: (B1–B4) basal plates, (IL1–IL5) infralateral plates, (L1–L5) lateral plates, (Pe) periproct, (R1–R6) radial plates. Note that *Gonocrinites* has four plates surrounding the periproct.

the other five genera. In addition, as far as is known, in the Glyptocystitidae, the anal pyramid is surrounded by two or three circlets of imbricate auxiliary plates (see Sprinkle 1982, text-figs. 61c, 62f, 64c). In the families Echinoencrinitidae and Callocystitidae, the periproct is typically surrounded by four or three plates (usually, IL4, IL5, and L5 in the latter case, Fig. 4b) and, as far as is known, the anal pyramid is always surrounded by a single circlet of tessellate auxiliary plates. Indeed, apart from *Scoliocystis*, which has five periproct border pates, the monotypic genus *Fusicystis* Terentiev (in Zuykov et al. 2008) and two species currently attributed to *Echinoencrinites* von Meyer, 1826 (*E. angulosus* (Pander, 1830) and *E. lahuseni* Jaekel, 1899), which have four (Fig. 4a), all Ordovician echinoecrinitids have three plates surrounding their periproct. *Echinosphaerites angulosus* Pander, 1830 was made type species of the genus *Gonocrinites* Eichwald, 1840 and we think *Gonocrinites* can usefully be distinguished from *Echinoencrinites* sensu stricto by the number of plates surrounding the periproct. Finally, in the unique genus *Rhombifera* Barrande, 1867 (family Rhombiferidae), the periproct is extremely small and surrounded by just two lateral plates (Kesling, 1962). Its cover is unknown.

A second key character is the presence and nature of the pore structures. *Macrocystella* (family Macrocystellidae) primitively lacks specialized pore structures and merely has thin, tightly folded plates. Three other genera have apparently secondarily lost their pore structures, which are typically pectinirhombs. The only exception is the unique genus *Cuniculocystis*, which has covered epispires. Pectinirhombs show a number of evolutionary changes. They consist of sets of thecal canals called dichopores, which open externally in slits and occur half in one plate and half in an adjacent plate (Paul, 1968b). In conjunct pectinirhombs, the slits run the entire length of the dichopores. In disjunct pectinirhombs, there are two slits one at each end of the dichopores and they function as entrances and exits. All the entrances lie in the same plate and all the exits are in the opposite plate. During growth, the slits start as conjunct dichopores, but when they reach a critical length, a roof of calcite seals the central part of the slit. Thus, in incompletely formed disjunct pectinirhombs, the outermost slits may be conjunct. In addition, the earliest pectinirhombs, whether conjunct or disjunct, are composed of isolated dichopores, called discrete dichopores (Paul, 1968b). The sets of dichopores may also be separated into two demirhombs by a median thicker rib of calcite internally, as in *Cheirocystella* (Fig. 1a). Later, more advanced pectinirhombs are composed of confluent dichopores, in which all the dichopores are connected and, in transverse section, resemble isoclinal folds. The slits of both conjunct and disjunct pectinirhombs with confluent dichopores are surrounded by a strengthening rim of thicker calcite called a vestibule rim. In the disjunct forms, one half rhomb has a vestibule rim that entirely surrounds the slits; the other only has a vestibule rim on the side away from the suture. The half rhombs with closed vestibule rims were the exits for currents that flowed through the dichopores in life. Advanced pectinirhombs occur in all genera of the family Pleurocystitidae, except *Amecystis* Ulrich et Kirk, 1921, *Deltacystis* Sprinkle, 1974, and *Hillocystis* Jell, 1983, which all lack any pectinirhombs. Pleurocystitid pectinirhombs are typically conjunct, but disjunct in the single genus *Praepleurocystis* Paul, 1967c. Advanced, disjunct pectinirhombs with vestibule rims occur in two Ordovician genera of the Echinoencrinitidae, *Scoliocystis* Jaekel, 1899 and *Fusicystis*, and all post-Ordovician genera in the family. They also typify the family Callocystitidae.

A third key character is the nature of the ambulacral system. *Macrocystella* had five short ambulacra confined to the oral surface and the flooring plates of which formed part of the thecal wall. This arrangement was retained in the family Cheirocrinidae, where the flooring plates either lay between the oral plates or, when they extended as in the genus *Coronocystis*, they produced deep sinuses in the radial plates (Fig. 1g). Ambulacra are usually arranged in a 2-1-2 pattern and labeled A-E under the Carpenter system (Carpenter, 1884, 1891) or using Roman numerals I–V under Jaekel's system (Jaekel, 1899). Furthermore, the B and D ambulacra differed from the other three in having the first two brachioles developed on the left of the

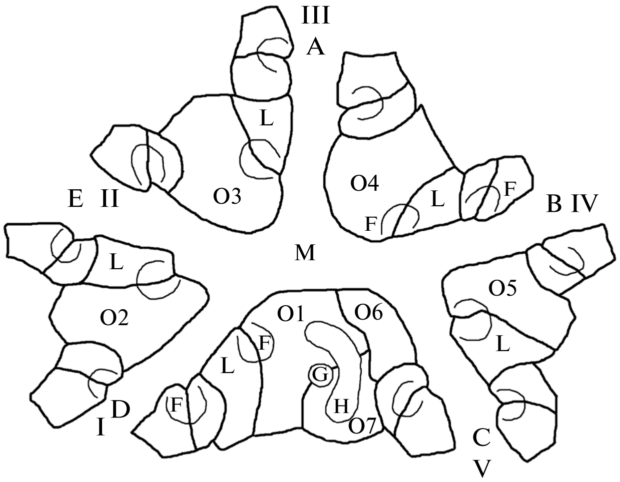


Fig. 5. Oral area of *Lepadocystis moorei* (Meek, 1871), showing the "BD different pattern" of primary brachioles (drawn using camera lucida). Note that looking down the ambulacra from the mouth (M) in the direction of growth, the first two brachiole facets (F) lie to the left in ambulacra B (IV) and D (I). In the other three ambulacra, only the first facet lies to the left. Designations: (A–E, I–V) ambulacra, (G) gonopore, (H) hydropore, (L) "first left ambulacral floor plate" after Sumrall and Waters (2012), (O1–O7) oral plates (after Sumrall and Waters, 2012, text-fig. 1).

ambulacrum, as viewed in the growth direction looking from the mouth towards the tip of the ambulacrum (Fig. 5). In the other three ambulacra, only the first brachiole occurs on the left. Thereafter in all ambulacra, the brachioles alternate regularly. This is called the "BD different pattern" for brevity (Paul, 2014a). As far as is known, all glyptocystitoid genera with five ambulacra (except possibly *Maennilocystis* gen. nov.) have the BD different pattern of primary brachioles. Five ambulacra are typical of the families Glyptocystitidae and Cheirocrinidae, although the unique cheirocrinid genus *Sprinkleocystis* has only four ambulacra with one, rarely two, brachioles each.

Ambulacral systems vary from this ancestral pattern either by reducing the number of ambulacra or, alternatively, by extending them so that they grow epithecally over the other thecal plates. A reduced number of ambulacra is typical of pleurocystitids, most genera of which have two ambulacra composed of a single, large brachiole each, although *Hillocystis* has just one brachiole. All genera of echinoencrinitids have reduced ambulacra. However, the arrangements vary from *Echinoencrinites*, which has five ambulacra, but with no more than three brachioles in each (Bockelie, 1981) to *Glansicystis* Paul, 1967a, with four ambulacra each with one or at most two brachioles or *Tyrrhidiocystis* Broadhead and Strimple, 1978, with three ambulacra each with a single brachiole or *Erinocystis* Jaekel, 1899, with two brachioles or *Osculocystis* Paul, 1967b and *Fusicystis* with just a single brachiole. In addition, the British Silurian genus *Schizocystis* Jaekel, 1895 has two ambulacra with up to five brachioles, all but the terminal one on the left side of the ambulacrum.

Scoliocystis apparently occupies a critical position in the evolution of the glyptocystitoid cystoids in that it has primitive, closed plate circlets and five plates surrounding the periproct, as in the ancestral families Cheirocrinidae and Macrocystellidae, but is the oldest known genus with advanced, disjunct pectinirhombs with vestibule rims. Furthermore, it has a reduced oral area and, even if the details of its ambulacral system remain unknown, this is more characteristic of the family Echinoencrinitidae.

The genus *Sprinkleocystis* also has a puzzling combination of characters. It has only four lateral plates. The plate originally interpreted as L1 is the largest of the laterals and occupies the position of both L5 and L1. If it is the two plates fused together, then *Sprinkleocystis* becomes more typical of the family Cheirocrinidae in that it has six radials, five laterals, and five plates surrounding the periproct (IL4, IL5, L4 plus fused L5 and L1). However, it has advanced disjunct pectinirhombs with vestibule rims and a reduced ambulacral system with four ambulacra with no more than two brachioles each. Both characters are more typical of the family Echinoencrinitidae.

In addition, the new genus *Maennilocystis* (described below) clearly has affinities with the family Callocystitidae in having five recumbent ambulacra and four advanced pectinirhombs in the same positions as the American Lower Silurian callocystitid genus *Anartiocystis*. However, it apparently lacks the BD different pattern of primary brachioles. Even so, with the pattern of brachioles known in only a single ambulacrum (D) in one specimen, it is impossible to judge whether the apparent lack of the BD different pattern is due to a teratological specimen or is a key character of the genus. Thus, it is possible that *Maennilocystis* is the oldest known callocystitid genus. On the other hand, it is also possible that *Maennilocystis* represents a unique echinoencrinitid genus that independently developed relatively long, recumbent ambulacra. The Early Silurian echinoencrinitid genus *Schizocystis* also develops epithecal tips to its ambulacra and has up to the first four brachioles on the left of its two ambulacra. Before discussing these taxa further, it is necessary to describe their detailed morphology as far as it is known.

SYSTEMATIC PALAEONTOLOGY

S u p e r f a m i l y Glyptocystitoida Bather, 1899

D i a g n o s i s (after Paul et al., 2014, emended). Superfamily of dichoporite rhombiferans with well-developed xenomorphic stem consisting of rapidly tapering proximal portion composed of alternating inner and outer annular columnals and distal portion composed of alternating longer and shorter cylindrical columnals; theca composed of four basals, five infralaterals, five laterals, four, five, six, or ten radials, and seven orals.

C o m p o s i t i o n. Families Callocystitidae Bernard, 1895; Cheirocrinidae Jaekel, 1899; Cuniculocystidae Sprinkle et Wahlman, 1994; Cystoblastidae Jaekel, 1899; Echinoencrinitidae Bather, 1899; Glyptocystitidae Bather, 1899; Macrocystellidae Bather, 1899; Pleurocystitidae Neumayr, 1889; and Rhombiferidae Kesling, 1962.

R e m a r k s. The stem is divided into distinct proximal and distal portions. The proximal column tapers rapidly and is composed of annular, inner and outer proximal columnals that articulate across fulcra, the axes of which rotate down the stem. Thus, the proximal stem is highly flexible and could bend in any direction. The distal stem is composed of more cylindrical columnals with a narrow lumen and which often alternate as larger and smaller columnals. When Paul (1968a) redescribed the genus *Macrocystella* and transferred the Macrocystellidae to the glyptocystitoids, it was the structure of the stem and the arrangement of thecal plates that were considered the most significant characters. At that time, only two genera of glyptocystitoids were known to lack pectinirhombs, *Macrocystella* Callaway, 1877 and *Amecystis* Ulrich et Kirk, 1921. Since then, two more genera which lack pore structures have been described, *Deltacystis* Sprinkle, 1974, and *Hillocystis* Jell, 1983. Pectinirhombs are respiratory structures composed of canals called dichopores, which lie within the theca and open to the external environment in slits (Paul, 1968b). They are confined to the superfamily Glyptocystitoida. However, not only are there four known genera of glyptocystitoids that lack pectinirhombs; in addition, Sprinkle and Wahlman (1994) described the unusual glyptocystitoid genus *Cuniculocystis*, which has covered epispires as respiratory structures and apparently ten radial plates. Thus, the presence of pectinirhombs can no longer be considered a diagnostic character of the superfamily.

Family Echinoencrinitidae Bather, 1899
[= Scoliocystidae Jaekel, 1899]

D i a g n o s i s. Glyptocystitoid family with reduced oral area, with theca composed of 26 or 25 plates arranged in five circlets according to the formula: 4 basals (B, plural BB), 5 infralaterals (ILL), 5 laterals (LL), 4 or 5 radials (RR), and 7 orals (OO), with disjunct pectinirhombs.

G e n e r i c c o m p o s i t i o n. *Echinoencrinites* von Meyer, 1826; *Erinocystis* Jaekel, 1899; *Fusicystis* Terentiev in Zuykov et al., 2008; *Glansicystis* Paul, 1967a; *Glaphyrocystis* Jaekel, 1899; *Gonocrinites* Eichwald, 1840; *Osculocystis* Paul, 1967b; *Proctocystis* Regnéll, 1945; *Schizocystis* Jaekel, 1895; *Scoliocystis* Jaekel, 1899; and *Tyrridiocystis* Broadhead et Strimple, 1978.

R e m a r k s. Echinoencrinitids typically have a reduced oral area. In genera with all five ambulacra present, there are rarely if ever more than three brachiole facets per ambulacrum (Jaekel, 1899, Bockelie, 1981). In other genera, the number of ambulacra is reduced and each may contain a single brachiole, so for example, *Erinocystis* Jaekel, 1899 has only two brachioles, whereas *Fusicystis* Terentiev (in Zuykov et al., 2008) and *Osculocystis* Paul, 1967b, have only a single brachiole. Most Ordovician echinoencrinitid genera have disjunct pectinirhombs with discrete dichopores, but *Scoliocystis* and *Fusicystis* have more advanced pectinirhombs with confluent dichopores that open in distinct vestibules (see Paul 1968b, p. 704, text-figs. 16, 18). The echinoencrinitids seem to be a sister group to the family Callocystitidae Bernard (1895). Both families have lost plate R5 in the radial circlet and, as far as is known, they have a periproct that is covered by an anal pyramid and a single circlet of auxillary plates (see discussion in Paul, 2014a). They differ primarily in that the callocystitids have long ambulacra that extend over the other thecal plates, often right down to the stem. Indeed, Paul (2014a) made this the key character separating the two families. Both original species of *Scoliocystis* have reduced oral areas, which suggests they can be included in the Echinoencrinitidae. However, previously it was also possible to group the two families by the possession of a periproct that was never surrounded by more than four thecal plates. Thus, the inclusion of *Scoliocystis*, which has five plates surrounding the periproct, within the family requires some modification of the family characters.

Genus *Scoliocystis* Jaekel, 1899

T y p e s p e c i e s. *Caryocystites pumilus* Eichwald, 1860, by original designation; *Orthoceras* Limestone, vicinity of St. Petersburg (Kunda–Lasnamäe); Darriwilian Stage.

D i a g n o s i s. Echinoencrinitid genus with five plates surrounding periproct, with disjunct pectinirhombs with confluent dichopores and well-developed vestibule rims.

S p e c i e s c o m p o s i t i o n. In addition to the type species, *S. thersites* Jaekel, 1899.

R e m a r k s. The key character that distinguishes *Scoliocystis* from all other genera in the Echinoencrinitidae is the possession of a relatively large, lateral periproct surrounded by five thecal plates, IL4, IL5, L1, L4, and L5 (Figs. 1c, 1d). No other echinoencrinitid has plate L1 contributing to the periproct border. The periproct of *Macrocystella* and all genera of Cheirocrinidae (except *Sprinkleocystis*) is also surrounded by the same five plates and is known to have been covered by an anal pyramid set in an extensive polyplated periproctal membrane. Unfortunately, the cover of the periproct is not preserved in any of the specimens of *Scoliocystis*. Cheirocrinids also differ from echinoencrinitids in having six radial plates and

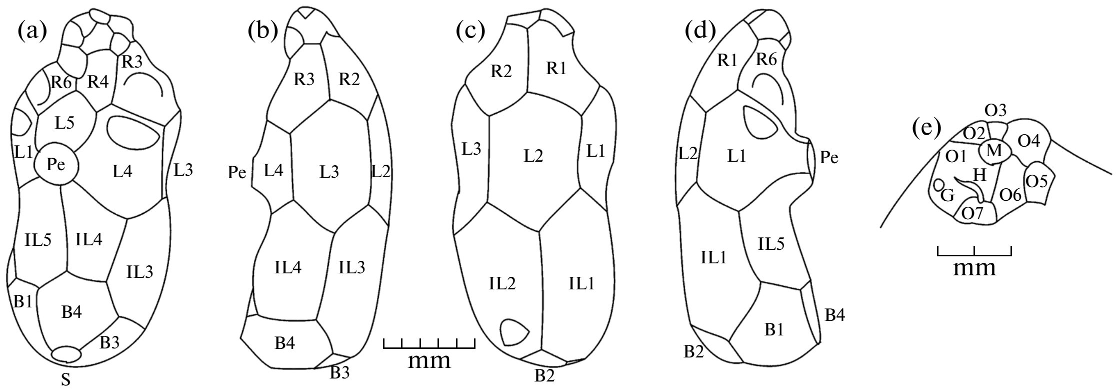


Fig. 6. Theca of *Scoliocystis pumila* (Eichwald, 1859), specimen PIN, no. 4125/910: (a) rear view (slightly displaced); (b) right lateral view; (c) anterior view; (d) left lateral view; (e) enlarged oblique oral view, camera lucida drawing; (S) stem cicatrix; for other designations, see Figs. 1 and 5.

in having their upper pectinirhombs predominantly across radial:radial (R:R) sutures. Both echinoencrinitids and callocystitids lack R:R rhombs, but possess up to five radial:lateral (R:L) rhombs. Furthermore, *Scoliocystis* bears advanced disjunct pectinirhombs with vestibule rims, which are not developed in any known cheirocrinid except *Sprinkleocystis* (discussed below). On balance, we believe *Scoliocystis* has more affinities with the Echinoencrinitidae than with the presumably ancestral Cheirocrinidae.

Scoliocystis pumila (Eichwald, 1860)

Plate 8, figs. 1 and 3

Caryocystites testudinarius (non *Sphaeronites testudinarius* Hisinger, 1828): Eichwald, 1856, p. 68.

Caryocystites pumilus: Eichwald, 1859–1860, p. 629, pl. 32, figs. 19a–19c.

Scoliocystis pumila (Eichwald): Jaekel, 1899, p. 260, text-fig. 36e, p. 196, text-fig. 51, p. 258, text-fig. 52, p. 260, pl. 11, figs. 11, 12; Bassler and Moodey, 1943, p. 39, 188; Kesling, 1968, p. 191; Rozhnov, 2002, p. 533, text-fig. 6.

Scoliocystis pumilus (Eichwald): Paul and Donovan, 2011, p. 438 [non *S. pumila* Jaekel, 1899, pl. 11, fig. 12; see remarks below].

H o l o t y p e. Original figured by Eichwald (1859, pl. 32, figs. 19a–19c). At present, the depository is not known, although Jaekel (1899, p. 260) stated that it was stored in St. Petersburg. Leningrad Region, Pulkovo; Middle Ordovician, Darriwilian Stage, *Orthoceras* Limestone (Kunda–Lasnamäe).

D e s c r i p t i o n (Figs. 1c, 6). The stem is not preserved, but a circular attachment scar visible at the thecal base is about 1.5 mm in diameter (Pl. 8, fig. 1f; S in Fig. 6a).

The theca is elongate, cylindrical, with an oval cross section and bent so that the periproctal side is slightly concave and the side with the basal pectinirhomb weakly convex (Pl. 8, figs. 1b, 1d; Figs. 6b, 6d). The theca is about 20 mm high and 9 mm maximum width with a protrusive periproct (Pl. 8, fig. 1a).

The plates are arranged as shown in Fig. 1c. All circlets are closed and have long IL:IL and L:L sutures. The theca is generally worn, but an isolated plate (probably IL2) shows prominent ridges radiating to the corners and series of finer parallel ridges and grooves set perpendicular to plate edges. In addition, the half rhombs have vestibule rims (Pl. 8, figs. 1a, 1d).

The holotype has four pectinirhombs, B2:IL2, IL2:L3, R3:L4, and R6:L1 (Fig. 1c), but IL2:L3 is not developed on the specimen available to us (Fig. 6c). All rhombs disjunct, although wear may make them appear to be conjunct, with confluent dichopores (Paul, 1968b) and with originally prominent vestibule rims, which are complete on IL2, L1, and L4, marking the exits of the rhombs.

The oral area is present and tapering to a point (Pl. 8, figs. 1a–1f), with seven oral plates, only five of which surround the small mouth (Fig. 6e). The arrangement is unusual in that both O5 and O7 do not form part of the mouth frame.

E x p l a n a t i o n o f P l a t e 8

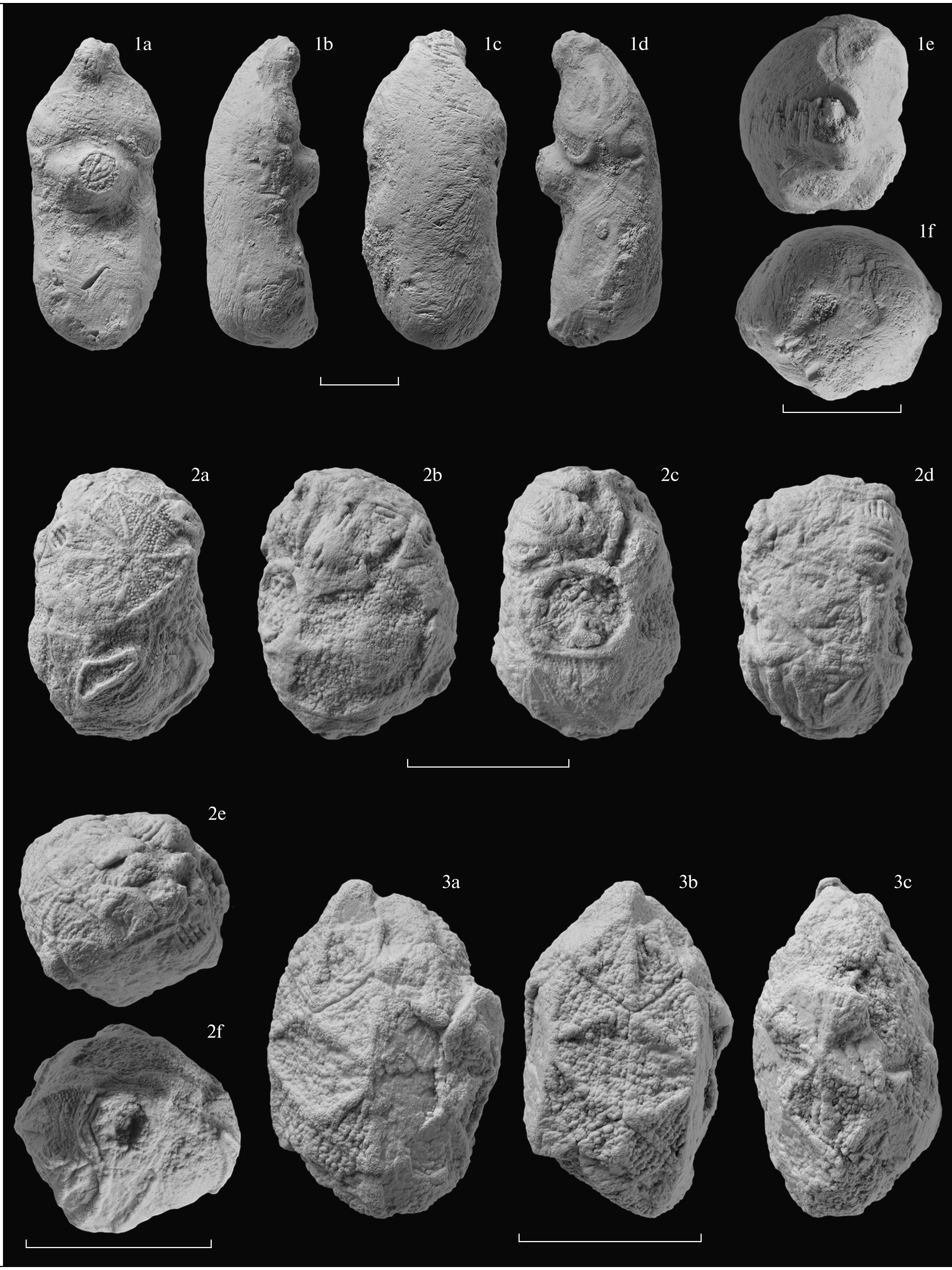
Figs. 1. *Scoliocystis pumila* (Eichwald, 1859): (1) specimen PIN, no. 4125/910, theca: (1a) posterior view (periproct side), (1b) left lateral view, (1c) anterior view, (1d) right lateral view, (1e) oral side (from above), (1f) bottom view (basal); Volkhov, Volkhov River, beach on the left bank, downstream from the dam; Kunda or Azeri, Darriwilian Stage.

Fig. 2. *Scoliocystis thersites* Jaekel, 1899, holotype PIN, no. 2/1004 (originally figured in Jaekel, 1899, pl. 11, figs. 10, 10a): (2a) anterior view, (2b) left lateral view, (2c) posterior view (periproct side), (2d) right lateral view, (2e) oral side view (from above), (2f) bottom view (basal); vicinity of St. Petersburg; Kunda–Lasnamäe (?), Darriwilian Stage.

Fig. 3. *Echinoencrinites* sp. ?. specimen PN, no. 2/1003, theca, lateral view (originally figured in Jaekel, 1899, pl. 11, fig. 12), vicinity of St. Petersburg, Pulkovo, Kunda-Lasnamae (?); Darriwilian Stage.

All specimens are coated with ammonium chloride. Scale bars, 5 mm.

Plate 8



The oral area is worn in the available theca, so no details of brachiole facets can be made out (Pl. 8, fig. 1e). Hence, the number of ambulacra and of brachioles is unknown, but must have been small.

The periproct is strongly protrusive (Pl. 8, figs. 1a, 1b, 1d; Pe in Figs. 6a, 6b, 6d), circular, with a prominent rim (Pl. 8, figs. 1a, 1b, 1d). The anal opening is 2.5 mm in diameter and surrounded by five thecal plates, IL4, IL5, L1, L4, and L5 (Figs. 1c, 6a).

The hydropore is a narrow, curved slit across the O1:O7 suture, but developed to a much greater extent in O1 (H in Fig. 6e).

The gonopore is very small, in the shape of a circular opening below and to the left of the hydropore and apparently entirely within plate O1 (G in Fig. 6e).

Remarks. An unusual feature of Eichwald's original enlarged figure of the holotype (Eichwald, 1859, pl. 32, fig. 19c) is that it shows the stem facet, periproct, and oral opening in a single lateral view. Nevertheless, this is an accurate depiction of the periproctal view due to the slight curvature of the theca (Pl. 8, figs. 1b, 1d). Eichwald's figures (Eichwald, 1859–1860, pl. 32, fig. 19a) are all upside down compared with the modern conventional orientation, but depict a lateral view showing the protrusive periproct and swollen area, where the basal pectinirhomb is (Eichwald's fig. 19a), the relatively featureless anterior view (fig. 19b) and an enlarged periproctal (posterior) view (fig. 19c). The plate outlines are shown, but Eichwald did not depict the oral circlet. In addition, he did not show, or mention in the original description, any of the rhombs. Jaekel (1899, pl. 11, figs. 11, 12) illustrated a conical oral area of a damaged theca and two isolated thecal plates showing one of the pectinirhombs with strongly raised vestibule rims. The former specimen is now so badly preserved that we cannot identify it with certainty, but think it may have been a specimen of *Echinoencrinites* originally (Pl. 8, figs. 3a–3c). It has a much stronger ornament and lacks any sign of a large, lateral periproct. Whatever its true systematic affinities, we are sure it is not a specimen of *Scoliocystis pumila*. The isolated plate agrees well with Jaekel's fig. 11 and we suspect that the part of the other plate shown was probably restored. Neither specimen shows enough information to justify Jaekel's plate diagram (Jaekel, 1899, p. 258, text-fig. 51) or the lateral view of the theca (p. 260, text-fig. 52) and we believe these were based on Eichwald's original type specimen. The newly discovered complete theca shows all the features of Eichwald's type, except the rhomb across the IL2:L3 suture. This is an unusual position for a pectinirhomb and has not been reported in any other echinoencrinitid as far as we are aware. The precise number of pectinirhombs often varies in other species of echinoencrinitids, so we believe that this difference is insignificant compared with the unusual thecal shape and plate arrangement. Both Eichwald's original figures (at natural size) and Jaekel's explicit statement that the theca was 17 mm high indicate that our specimen is different (20 mm high). However, with only two specimens showing most details, it is impossible to tell whether any differences are merely individual variation or are taxonomically significant.

An unusual feature of our complete specimen is that five plates (O1, O2, O3, O4, and O6) surround the mouth (Fig. 6e). It is more common to find either four or six orals forming the mouth frame. *Echinoencrinites* typically has six (all but O7; Bockelie, 1981, text-figs. 2, 4). Paul (1967a, p. 347, text-fig. 39) figured a specimen of the Silurian echinoencrinitid *Glansicystis* Paul, 1967a with six plates (all but O7) forming the mouth frame and another example of the same species (Paul, 1968c, p. 417, text-fig. 4) with only four mouth frame plates (O1, O3, O4, and O6).

Material. In addition to the holotype, one more complete theca, specimen PIN, no. 4125/910, and a single isolated plate, probably IL2 (specimen PIN, no. 2/1002).

Scoliocystis thersites (Jaekel, 1899)

Plate 8, fig. 2

Scoliocystis thersites: Jaekel, 1899, p. 260, text-fig. 36a, p. 196, text-fig. 50, p. 258, pl. 11, fig. 10; Bassler and Moodey, 1943, pp. 39, 188; Hecker, 1964, p. 39, text-figs. 24, 25a, 25b; Kesling, 1968, p. S191, text-fig. 92, 93, p. 188, p. 190, text-figs. 94, 2a, 2b; Paul and Donovan, 2011, p. 438.

Holotype. PIN, no. 2/1004 (originally figured by Jaekel, 1899, pl. 11, fig. 10); Leningrad Region, Pulkovo (?); Middle Ordovician, Darriwilian Stage (?Kunda–Lasnamäe).

Description (Figs. 1d, 7). The stem is not preserved, but a circular attachment scar visible at the base of the theca is about 1.0 mm in diameter (Pl. 8, fig. 2f).

The theca is oval, about 8 mm high and 5.4 mm maximum width, rather worn, without a protrusive periproct (Pl. 8, figs. 2a–2d; Fig. 7).

The plates are arranged as shown in Fig. 1d. All circlets are closed and plates are more or less equidimensional. Some laterals only just meet at a point, but the lateral circlet is modified rather than truly open (Fig. 7). The plates bear an ornament of radiating ridges and granules (e.g., Pl. 8, figs. 2a, 2d).

Pectinirhombs are only six in all, B2:IL2, R1:L2, R3:L3, R3:L4, R6:L5, and R6:L1. Pectinirhomb R6:L5 is very small, with no more than five dichopores. Pectinirhombs have prominent vestibule rims, when not damaged (Pl. 8, fig. 2a).

The oral area is flattened and worn, with details of plate arrangement obscured (Pl. 8, fig. 2e; Fig. 7a).

The periproct is relatively large, rounded angular, with a prominent marginal rim (Pl. 8, fig. 2c). The anal opening is 2.2 mm in diameter and surrounded by five thecal plates IL4, IL5, L1, L4, and L5 (Figs. 1d, Pe in 7d).

The hydropore and gonopore are not certainly detected in the worn oral area (Pl. 8, fig. 2e).

R e m a r k s. Jaekel (1899, p. 260) mentioned two specimens and said the species was 7–10 mm high. His plate diagram (Jaekel, 1899, p. 258, text-fig. 50) shows only five pectinirhombs, but the illustrated example (pl. 11, fig. 10a) shows the additional small R6:L5 pectinirhomb. The only specimen available to us is now rather worn and the details of the oral area in particular are not clear. Jaekel (1899, p. 260) stated explicitly that there were five ambulacra. We cannot confirm this, although at least five (and probably seven) oral plates are present.

The two species of *Scoliocystis* seem to be distinct. Both share the plesiomorphic character of having five plates forming the periproct border, although the nature of the cover remains unknown. Equally, they both share the advanced character of disjunct pectinirhombs, with confluent dichopores and well-developed vestibule rims. This combination of characters is sufficient to define a distinct genus, which we would include in the family Echinoencrinitidae. This requires a slightly modified diagnosis of the family. Although available material of neither species preserves the oral area in sufficient detail to describe the ambulacral system adequately, it must have been restricted. Jaekel (1899, p. 260, text-fig. 52) tentatively restored two brachioles in *S. pumila* and stated that five ambulacra occurred in *S. thersites*. If these two interpretations are true, we do not think that the two species can be accommodated in the same genus. However, we tentatively retain them together in *Scoliocystis* until such time as positive evidence of different ambulacral systems is discovered. The material available to us suggests that the ambulacral systems of both species were restricted to the oral area and, if five ambulacra were present, they probably had only a single brachiole each. Thus, we think the third species that has been attributed to *Scoliocystis* (*S.* sp. of Hecker, 1964, pl. 3, figs. 10, 11a, 11b, described below) cannot be included in the genus *Scoliocystis*. It has five ambulacra that extend onto the lateral plate circlet and a periproct surrounded by only four plates (IL4, IL5, L4, L5). The extensive recumbent ambulacra exclude it from the family Echinencrinitidae as we understand it.

M a t e r i a l. Jaekel (1899, p. 260) mentioned that two examples existed in St. Petersburg, but we have only seen the illustrated type specimen. Furthermore, all illustrations subsequent to Jaekel (1899) depict the same specimen.

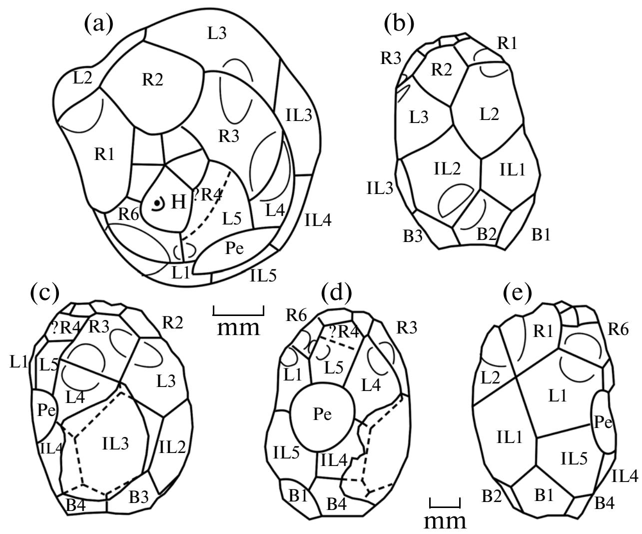


Fig. 7. Theca of the holotype (?lectotype) of *Scoliocystis thersites* Jaekel, 1899, PIN, no. 2/1004: (a) enlarged oblique oral view; (b) anterior view; (c) right lateral view; (d) slightly displaced posterior view; (e) left lateral view (after Rozhnov, 2002, text-fig. 6). Note the small rhomb L5:R6. For designations, see Figs. 1 and 5. Drawn using camera lucida.

Genus *Echinoencrinites* von Meyer, 1826

T y p e s p e c i e s. *Echinoencrinites senckenbergii* von Meyer, 1826; by monotypy, from the "Vaginatenkalk or glauconitkalk" (basal Darriwilian) near St. Petersburg, Russia (von Meyer, 1826) (Fig. 2).

D i a g n o s i s. Echinoencrinitid genus with all plate circlets closed, three plates surrounding periproct, disjunct pectinirhombs with discrete dichopores and five ambulacra with up to three brachioles each (Fig. 4b).

S p e c i e s c o m p o s i t i o n. In addition to the type species, *E. laevigatus, E. reticulatus, E. striatus* (see Jaekel, 1899). Phleger (1935) elevated some of Jaekel's (1899) varieties to specific level.

C o m p a r i s o n. *Echinoencrinites* is readily distinguished from *Erinocystis* Jaekel, 1899 and *Proctocystis* Regnéll, 1945, because both the latter genera have an open IL circlet with a B3:L3 suture, a markedly produced periproct and just two brachioles. In addition, *Proctocystis* has only four radial plates. *Echinoencrinites* differs from *Glaphyrocystis* Jaekel, 1899, which also has only four radial plates and an open radial circlet; plate L5 separates R3 from R6. Finally, *Echinoencrinites* can be distinguished from the closely similar genus *Gonocrinites* Eichwald, 1840, because it has three not four plates surrounding the periproct.

Genus *Gonocrinites* Eichwald, 1840

T y p e s p e c i e s. *Echinosphaerites angulosus* Pander, 1830, by original designation, from the "Vaginatenkalk" (basal Darriwilian) near St. Petersburg, Russia (Fig. 2).

D i a g n o s i s. Echinoencrinitid genus with all plate circlets closed, four plates surrounding periproct, disjunct pectinirhombs with discrete dichopores and five ambulacra with up to three brachioles each (Fig. 4a).

S p e c i e s   c o m p o s i t i o n. In addition to the type species, *G. lahuseni* (Jaekel, 1899).

C o m p a r i s o n. *Gonocrinites* has previously been considered a junior synonym of *Echinoencrinites* von Meyer, 1826 (see Jaekel, 1899; Kesling, 1968), but we believe the presence of four plates surrounding the periproct is generically significant, providing a link between *Scoliocystis* with five periproct border plates and other Ordovician echinoencrinitid genera with three. Jaekel (1899, p. 247, unnumbered diagram) thought that "*E.*" *lahuseni* was the most primitive species of *Echinoencrinites* and gave rise to a phylogenetic side branch that included *E. angulosus* and its varieties. Jaekel's ideas are consistent with our interpretation that *Gonocrinites* occupies a phylogenetic position between *Scoliocystis* and *Echinoencrinites* sensu stricto.

Although the number of pectinirhombs does not seem to be fixed in several species of echinoencrinitids, there does seem to have been an overall reduction in number. Again, Jaekel (1899, p. 243, fig. 47) produced a plate diagram of *"E." lahuseni* with seven pectinirhombs, four basal and three upper, whereas the type species of *Echinoencrinites*, *E. Senckenbergii,* often has only three, but sometimes five. Phleger (1935, p. 200) introduced the new genus *Eutretocystis* for forms of *Echinoencrinites* with two pectinirhombs on plate R3. However, most subsequent authors have regarded this as merely variation in pectinirhomb number and treated *Eutretocystis* as a junior synonym of *Echinoencrinites*. We are inclined to agree.

Family Callocystitidae Bernard, 1895 emend. Paul, 2014b

D i a g n o s i s. Glyptocystitoid family with recumbent ambulacra extending over thecal plates, often reaching stem; with theca composed of 26 plates arranged in five circlets according to formula: 4 basals, 5 infralaterals, 5 laterals, 5 radials, and 7 orals; with five or fewer pectinirhombs always in positions B2:IL2, R1:L2, R3:L3, R3:L4, and R6:L1.

G e n e r i c   c o m p o s i t i o n. Genera *Adocetocystis* Koch et Strimple, 1968; *Anartiocystis* Ausich et Schumacher, 1984; *Apiocystites* Forbes, 1848; *Brockocystis* Foerste, 1914; *Callocystites* Hall, 1852; *Coelocystis* Schuchert, 1903; *Hallicystis* Jaekel, 1899; *Jaekelocystis* Schuchert, 1903; *Lepadocystis* Carpenter, 1891; *Lepocrinites* Conrad, 1840; *Lipsanocystis* Ehlers et Leighley, 1922; *Lovenicystis* Regnéll, 1945; *Maennilocystis* gen. nov.; *Novacystis* Paul et Bolton, 1991; *?Prunocystites* Forbes, 1848; *Pseudocrinites* Pearce, 1843; *Salirocystis* Paul, 2014b; *Sphaerocystites* Hall, 1859; *Staurocystis* Haeckel, 1896; *Strobilocystites* White, 1876; *Tetracystis* Schuchert, 1904; and *Troosticystis* Paul et Donovan, 2011.

R e m a r k s. As mentioned above, we think the key character separating the two families Callocystitidae and Echinoencrinitidae is the nature of the ambulacral system. In echinoencrinitids, it is reduced, with all brachioles close to the mouth and commonly fewer than five ambulacra or brachioles. In callocystitids, the ambulacral system is more extensive, with ambulacra developed on the other thecal plates and frequently reaching the stem. The number of ambulacra may be reduced, from five to four or two, but the structure of having ambulacral flooring plates developed on top of thecal plates is retained. *Schizocystis* Jaekel, 1895 is the only genus attributed to the Echinoencrinitidae in which the two ambulacra extend onto radial and lateral plates.

In addition, callocystitids always have advanced disjunct pectinirhombs with confluent dichopores and well-developed vestibule rims. Broadhead and Strimple (1978) suggested transferring the Silurian genera *Schizocystis* Jaekel, 1895, *Glansicystis* Paul, 1967a, and *Osculocystis* Paul, 1967b from the Echinoencrinitidae to Callocystitidae largely on the character of their pectinirhombs, and they also added the new Devonian genus *Tyrridiocystis* Broadhead and Strimple, 1978. This group of genera constituted the subfamily Scoliocystinae, as defined by Broadhead and Strimple (1978). However, it is now known that Ordovician echinoencrinitids, including *Fusicystis* and *Scoliocystis*, also had the same advanced disjunct pectinirhombs, so Paul (2014a) suggested transferring these genera back to the Echinoencrinitidae on the grounds that advanced pectinirhombs with vestibules were present in undoubted echinoencrinitids as well as all callocystitids.

Genus *Maennilocystis* Paul et Rozhnov, gen. nov.

E t y m o l o g y. In honor of the Estonian paleontologist R. Männil.

T y p e   s p e c i e s. *Maennilocystis heckeri* sp. nov.

D i a g n o s i s. Callocystitid genus with five ambulacra apparently without BD different pattern of primary brachioles, with four pectinirhombs (B2:IL2, R3:L3, R3:L4, and R6:L1) and closed radial circlet.

S p e c i e s   c o m p o s i t i o n. Perhaps, in addition to the type species, the genus *Maennilocystis* includes *Lepadocystis clintonensis* Parks, 1910, but to confirm this statement requires reexamination of Parks' species.

R e m a r k s. Four other callocystitid genera, *Lepadocystis* Carpenter, 1891, *Brockocystis* Foerste, 1914, *Anartiocystis* Ausich et Schumacher, 1984, and *Novacystis* Paul et Bolton, 1991, have five ambulacra and four or more pectinirhombs. Of these, *Lepadocystis* differs in having five pectinirhombs (R1:L2 as well as the four found in *Maennilocystis*) and an open radial circlet, in which L5 is inserted between R4 and R6. The other three genera have the same four pectinirhombs as in *Maennilocystis*, but *Anartiocystis* also has an open radial circlet, in which L5 lies between R4 and R6 (Fig. 1f). *Novacystis* has open lateral and radial circlets, because R4 forms part of the periproct border and separates L4 and L5, as well as L5 interrupting the radial circlet (see Sumrall and Brett, 2002, p. 737, text-fig. 4). *Brockocystis* comes closest to *Maennilocystis* in that it also has a closed radial circlet, but it has inflated hollow thecal plates and a modified proximal stem that forms a hollow bead-like structure. Both the latter two characters are thought sufficient to characterize a genus, so we feel it would require too much modification of the generic diagnosis to include *Maennilocystis heckeri* in *Brockocystis*.

Furthermore, as far as is known, all other callocystitid genera with five ambulacra have the "BD different pattern" of primary brachioles, in which ambulacra B and D have the first two brachioles developed on the left, as viewed looking in the direction of ambulacral growth, whereas the other three ambulacra have only the first brachiole developed on the left (see Paul, 2014b). Thereafter, all five ambulacra have brachioles alternating regularly on opposite sides of the ambulacral axis. One of the specimens of *M. heckeri* has ambulacrum D well preserved (Pl. 9, figs. 2d, 2e; Fig. 8). It shows five brachiole facets with only the first on the left. In all callocystitids, only three patterns of primary brachioles occur, the BD different pattern, the "B-E the same pattern," which only occurs in genera with four ambulacra in all four of which only the first brachiole branches off to the left and brachioles alternate regularly throughout. In *Pseudocrinites* Pearce, 1843, there are only two ambulacra, both of which have the first two brachioles branched off to the left and, thereafter, brachioles alternate regularly. Thus, *Maennilocystis* differs from all other callocystitid genera with five ambulacra in having a single brachiole on the left in ambulacrum D. Available specimens are not sufficiently well preserved to see if this is also true of other ambulacra, especially ambulacrum B.

Parks (1910) described a new species as *Lepadocystis clintonensis,* which has not been redescribed adequately since. *L. clintonensis* has five ambulacra, four pectinirhombs, and apparently a closed radial circlet (see Parks, 1910, p. 405, text-fig. 2), but it lacks the inflated plates of *Brockocystis*. The arrangement of primary brachioles remains unknown. At present, it shares with *Maennilocystis* five ambulacra, four pectinirhombs, and a closed radial circlet, which is sufficient to suggest it may also be a species of *Maennilocystis.* If this is the case, the genus ranges from the Ordovician (Lower Katian) to Lower Silurian (Llandovery).

Maennilocystis heckeri Paul et Rozhnov, gen. et sp. nov.

Plate 9, figs. 1–3

Scoliocystis sp.: Hecker, 1964, pl. 3, figs. 10, 11a, 11b; Paul and Donovan, 2011, p. 438, text-figs. 7a–7d; Paul, 2014a, p. 202.

E t y m o l o g y. In memory of R.F. Hecker.

H o l o t y p e. GIT, no. 640-110 (originally figured by Hecker, 1964, pl. 3, figs. 11a, 11b); Estonia, village of Törremäe near Rakvere; Upper Ordovician, lower part of the Katian Stage, Oandu Regional Stage.

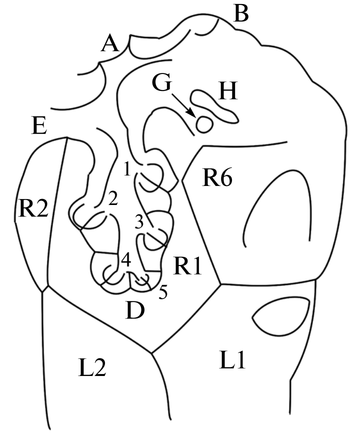


Fig. 8. *Maennilocystis heckeri* gen. et sp. nov., ambulacrum D in paratype GIT 640-58-1: (1–5) brachioles from D^1 to D^5. For other designations, see Figs. 1 and 5. Brachioles alternate regularly on either side of ambulacrum D. Drawn using camera lucida.

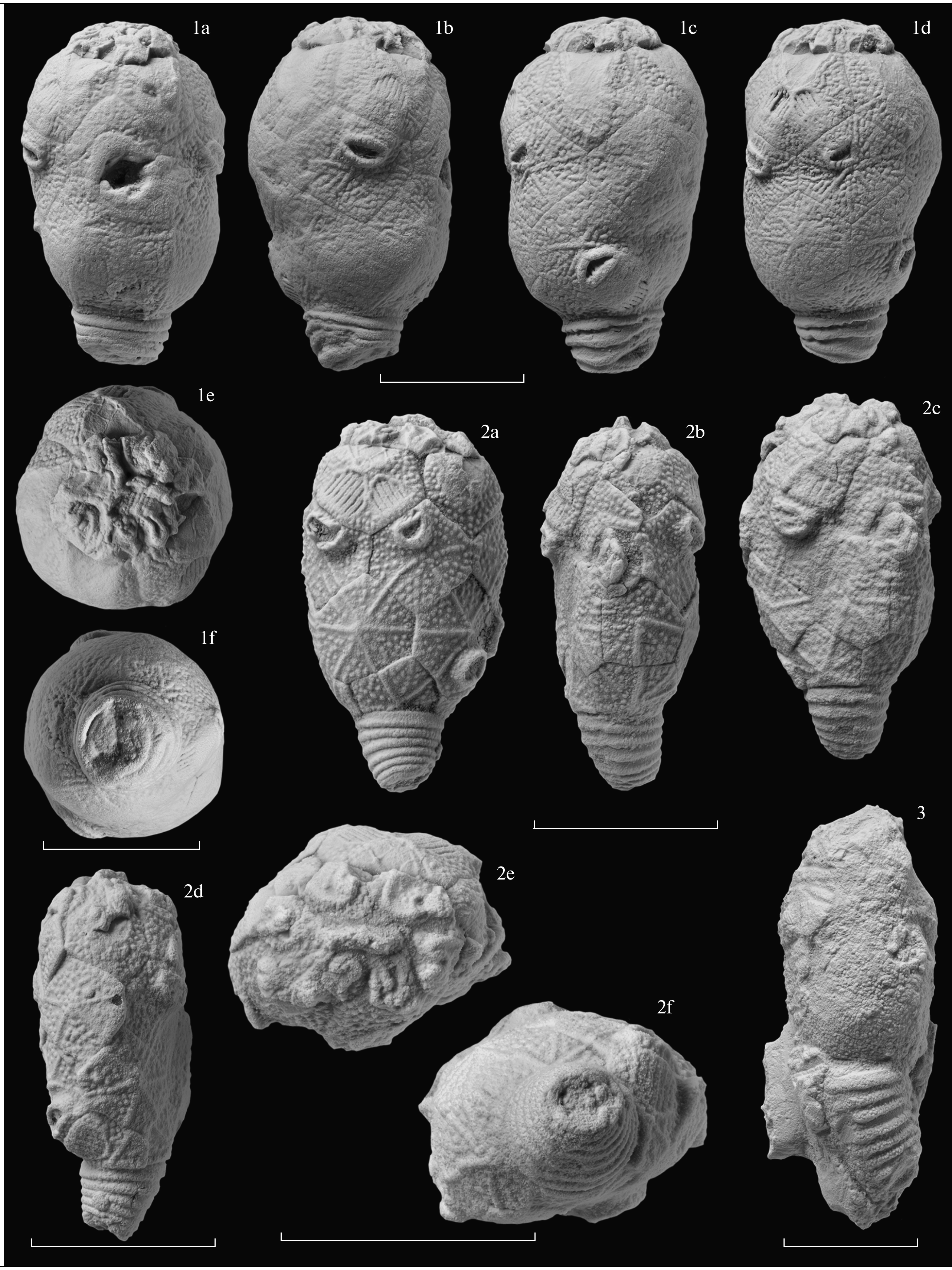
D e s c r i p t i o n (Figs. 1f, 8, 9). In the holotype and both paratypes, the topmost few columnals of the proximal stem remain attached (Pl. 9, figs. 1a–1d, 2a–2d, 3). The proximal stem reaches 3.5 mm in diameter in the holotype and 2.3 mm in diameter in paratype GIT, no. 640-58-1, where it tapers to 1.2 mm in 2.2 mm of length. The proximal stem has outer proximals ornamented with a simple keel with fine granular ornament in paratype GIT, no. 640-111, which preserves six pairs of proximals (Pl. 9, figs. 2a–2d). The distal part of the stem is unknown.

The theca is oval (Pl. 9, figs. 1a–1d), about 10.4 mm high and 6.5 mm maximum diameter in the holotype, with five ambulacra, which spread onto the radial plates (Pl. 9, figs. 1a, 1c–1e, 2e). Paratype GIT, no. 640-58-1 is only 8 mm high (Pl. 9, fig. 3).

The plates are arranged as in Fig. 1f. All circlets are closed and the plates are more or less equidimensional, with a clear suture between plates R4 and R6 above L5 (Pl. 9, fig. 1a, above). Plates are ornamented, with fine radiating ridges passing to the middle of plate sutures and with fine tubercles between in paratype GIT, no. 640-111 (Pl. 9, figs. 2a–2d), but weaker ridges and a more irregular, malleated ornament in the holotype (Pl. 9, figs. 1a–1d). Paratype GIT, no. 640-58-1 apparently lacks radiating ridges and has just fine, granular ornament, but is poorly preserved (Pl. 9, fig. 3).

Pectinirhombs are four in number, B2:IL2, R3:L3, R3:L4, and R6:L1, with obvious vestibule rims, those in half-rhombs IL2, L1, L3, and L4 are closed (Pl. 9, figs. 1b–1d, 2a, 2c, 2d; Figs. 1f, 9). In the holotype and both paratypes, rhomb R3:L3 has five dichopores; the other three rhombs have seven each as far as is known (Pl. 9, fig. 2a).

Plate 9



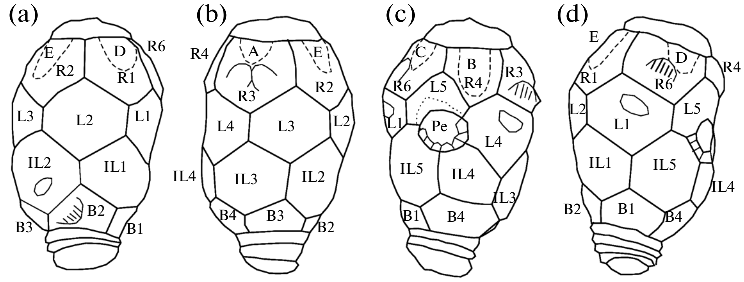


Fig. 9. Theca of the holotype of *Maennilocystis heckeri* gen. et sp. nov., GIT 640-110: (a) anterior lateral view; (b) right lateral view; (c) posterior view; (d) left lateral view. For designations, see Figs. 1 and 5. Drawn using camera lucida. Note that the ambulacra extend onto the radial plates, plates R4 and R6 have a common suture and seven auxiliary plates are preserved in the periproct.

The oral area is flat, with the usual seven orals and five ambulacra (Pl. 9, fig. 2e) that extend down nearly to the lower margins of the radial plates (Pl. 9, figs. 1a–1d; Fig. 9). In paratype GIT, no. 640-58-1, ambulacrum C appears to have four and ambulacrum D five brachiole facets. In ambulacrum D, only the first facet branches to the left (Fig. 8). Ambulacra have broad main food grooves that give rise to oblique lateral food grooves. Some ambulacral cover plates are preserved in the holotype and paratype GIT, no. 640-58-1, but the details cannot be made out.

The periproct is small, rounded angular orifice, 2.2 mm across, with suggestions of a marginal rim (Pl. 9, fig. 1a; *Pe* in Figs. 1f, 9c). The anal opening is surrounded by four thecal plates IL4, IL5, L4, and L5 (Figs. 1f, 9c). Seven or eight plates of the auxiliary ring are preserved in the holotype (Pl. 9, figs. 1a, 2b; Fig. 9C). Paratype GIT, no. 640-58-1 preserves the anal pyramid of five anal pates as well as an almost complete auxiliary circlet of an estimated nine or ten plates (Pl. 9, fig. 2b).

The hydropore is in the shape of a slightly curved, oval area surrounded by a distinct rim and set almost along the oral-aboral direction in paratype GIT, no. 640-58-1 (Pl. 9, figs. 1e, 2e; *H* in Figs. 1f, 8).

The gonopore is preserved in the holotype and paratype GIT, no. 640-58-1 as a small pit to the left of the hydropore (Pl. 9, figs. 1e, 2e; *G* in Figs. 1f, 8).

R e m a r k s. Hecker (1964, pl. 3, figs. 10, 11a, 11b) first illustrated this species under the name *Scoliocystis* sp. The original specimens were collected by Dr. R. Männil. Thus, we are acknowledging the scientific contributions of both scientists in our new specific name. *Maenillocystis heckeri* has strong affinities with the family Callocystitidae. Indeed, apart from the closed radial circlet and apparent lack of the BD different pattern of primary brachioles, it is identical to the North American Lower Silurian genus *Anartiocystis*. We are unable to determine whether or not the apparent lack of the BD different pattern of primary brachioles is a generic character or merely an anomaly of a single individual. Currently, the possession of recumbent ambulacra which spread down the theca over the radial and other thecal plates is the key character of the family Callocystitidae. So, for the present we are assigning *Maennilocystis* to that family. In doing so, *Maennilocystis* becomes the oldest known callocystitid genus as it comes from the basal Katian of Estonia (Fig. 2). The previously oldest known species of callocystitids were *Lepadocystis moorei* and *L. decorus* Sumrall and Carlson, 2000, both of which come from the Upper Katian of the United States. Finally, the Canadian Lower Silurian species "*Lepadocystis clintonensis* Parks, 1910" may be another species of *Maennilocystis*, but it needs redescription to be sure of its affinities.

M a t e r i a l. In addition to the holotype, two paratypes, more or less complete thecae. One comes from the Oandu Regional Stage, Törremäe near Rakvere, the other is from the Keila Regional Stage, borehole Äiamaa (depth of 183.93 m). Both localities are correlated with the lower part of the Katian Stage (Fig. 2).

E x p l a n a t i o n o f P l a t e 9

Figs. 1–3. *Maennilocystis heckeri* gen et sp. nov.: (1) holotype GIT, no. 640-110 (originally figured in Hecker, 1964, pl. 3, fig. 11a): (1a) posterior view (periproct side), (1b) left lateral view, (1c) anterior view, (1d) right lateral view, (1e) oral side view (from above), (1f) bottom view (basal); (2) paratype GIT, no. 640-112 (originally figured in Hecker, 1964, pl. 3, fig. 10): (2a) right lateral view, (2b) posterior view (periproct side), (2c) left lateral view, (2d) anterior view, (2e) oral side view (from above), (2f) bottom view (basal); Estonia, village of Törremäe near Rakvere; Oandu, Katian Stage; (3) paratype GIT, no. 640-58-1, lateral view; Estonia. borehole Äiamaa, 183.93 m of depth; Keila Regional Stage, basal Katian Stage.

All specimens are coated with ammonium chloride. Scale bars, 5 mm.

Family Cheirocrinidae Jaekel, 1899

D i a g n o s i s. Glyptocystitoid family with six radial plates; large periproct usually surrounded by five thecal plates, but always with plate L1 contributing to border and covered with flexible, plated integument within which simple anal pyramid located at lower right.

C o m p o s i t i o n. Genera *Acanthalepis* McCoy, 1846; *Cheirocrinus* Eichwald, 1856; *Cheirocystella* Paul, 1972; *Cheirocystis* Paul, 1972; *Coronocystis* Paul, 1972; *Hadrocystis* Sprinkle, 1974; *Homocystites* Barrande, 1887; and *Sprinkleocystis* Broadhead et Sumrall, 2003.

R e m a r k s. The diagnosis is simplified from Paul (1984, p. 97) due to the description of *Sprinkleocystis ektopios*. This unusual genus has only four ambulacra and also only four plates surrounding the periproct. Prior to its description, all known cheirocrinids had five ambulacra and five periproct border plates, including a single specimen of *Coronocystis angulata*, which also lacks plate L5, but has plate R5 forming that part of the periproct border (see Paul, 1972, p. 41, fig. 13). Broadhead and Sumrall (2003) did not provide a diagnosis of the family Cheirocrinidae largely because of the difficulty of adequately distinguishing the families Cheirocrinidae and Glyptocystitidae. However, no glyptocystitid has more than four plates surrounding the periproct and all but *Quadrocystis* and *Hesperocystis* have only three (always IL4, L4, and L5). *Hesperocystis* has plates IL4, L4, L5, and R4 forming the periproct border (Sprinkle, 1982, fig. 63b, p. 257), whereas *Quadrocystis* has plates IL4, IL5, L4, and L5 (Sprinkle, 1982, p. 271, fig. 66b). Thus, in no glyptocystitid genus does plate L1 contribute to the periproct border. In addition, as far as is known, in the Glyptocystitidae, the cover of the periproct consists of an anal pyramid surrounded by two or three circlets of imbricate auxiliary plates (see Sprinkle, 1982, text-figs. 61c, 62f, 64c). Glyptocystitids also have a distinctive type of pectinirhomb, which Sinclair (1948, p. 306) called "montidisjunct," but which are just large, angular, disjunct pectinirhombs with many dichopores and with incomplete vestibule rims. No cheirocrinid has this type of pectinirhomb, not even *Sprinkleocystis*, which has pectinirhombs with small rounded vestibule rims and never more than seven dichopores (Broadhead and Sumrall, 2003, p. 117, table 2). Thus, it is not difficult to distinguish the two families. However, almost certainly the family Cheirocrinidae, as currently defined, includes evolutionary lineages that lead to other glyptocystitoid families. It is the stem group of pectinirhomb-bearing glyptocystitoids. Thus, it is a paraphyletic group and includes a wide range of character states. For example, all types of pectinirhomb, including the rare and specialized multidisjunct form, occur in genera of the family Cheirocrinidae as currently understood. Plate arrangements with all plate circlets closed occur in the genera *Cheirocystella*, *Cheirocystis* Paul, 1972, and *Homocystites* Barrande, 1887, whereas the lateral plate circlet is open in the genera *Cheirocrinus* Eichwald, 1856 and *Coronocystis* Paul, 1972, where there is always a suture between plates IL2 and R2, which separate L2 from L3 (Paul, 1972). This character also occurs in all glyptocystitid genera. Thus, it seems likely that the entire family Glyptocystitidae evolved from cheirocrinids with open lateral circlets. On the other hand, the families Echinoencrinitidae and Callocystitidae appear to have arisen from cheirocrinids with closed circlets and reduced oral areas.

Genus *Sprinkleocystis* Broadhead et Sumrall, 2003

T y p e s p e c i e s. *Sprinkleocystis ektopios* Broadhead et Sumrall, 2003, by original designation, from the lower part of the Benbolt Formation (Upper Sandbian) of eastern Tennessee, United States.

D i a g n o s i s (after Broadhead and Sumrall, 2003, modified). Cheirocrinid genus with four reduced ambulacra, only four lateral plates, and only four plates (IL4, IL5, L4, and L1) forming the periproct surround, with small protuberant pectinirhombs with confluent dichopores.

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

R e m a r k s. *Sprinkleocystis* differs from all other cheirocrinid genera in having only four ambulacra with one or two brachioles each. Ambulacrum A is not developed. It also differs in lacking plate L5, thus having only four lateral plates and, hence, having only four plates forming the periproct border. In addition, no other cheirocrinid genus has disjunct pectinirhombs with confluent dichopores. *Homocystites* has conjunct pectinirhombs with confluent dichopores, but all other genera have discrete dichopores. Broadhead and Sumrall (2003, p. 119) stated that the pectinirhombs were only disjunct when mature, but this is true of all disjunct pectinirhombs, which start with conjunct dichopores and become disjunct as they grow larger.

Sprinkleocystis ektopios Broadhead et Sumrall, 2003

Sprinkleocystis ektopios: Broadhead and Sumrall, 2003, p. 119, text-figs. 2.1, 3, 4, 5.1, 6.

H o l o t y p e. University of Iowa, SUI 95248; United States, East Tennessee; upper part of the Sandbian, Benbolt Formation.

D e s c r i p t i o n (Figs. 1b, 10). The stem is unknown, except that the topmost outer columnal remains attached in a recess to the base of the theca in the holotype, SUI 95248 and paratype SUI 95255 (see Broadhead and Sumrall, 2003, text-figs. 3.15-16). They are typical annular glyptocystitoid outer proximals, with a large lumen and two fulcra for articulation with the next lower inner columnal. The positions of the fulcra with respect to thecal landmarks vary in the two specimens, suggesting that the orientation of the fulcral axes varied down the stem as first reported by Paul (1968a, p. 585, text-figs. 1, 2) in *Macrocystella*.

Ornament of the outer proximal columnals is unknown.

The theca is small, reaching a maximum of 13 mm high by 7 mm wide; very irregular in shape, with protruding pectinirhombs and periproct, above which is a distinct concave groove; with a flat oral surface, on which four short ambulacra are developed and a distinct quadrate basal concavity. Strong ridges connect plates B4-IL4, B1-IL5, and IL2-IL3.

The plates are arranged as in Fig. 1b, with all plate circlets closed. Plate L1 is unusually large, possibly the result of fusion of plates L5 and L1; as a result, only four lateral plates are present and only four plates (IL4, IL5, L4, and L1) surround the periproct. Plates are generally weakly ornamented, although several specimens show more or less strong fine growth lines. Almost certainly these are the result of weathering.

Pectinirhombs are disjunct, with confluent dichopores developed on raised oval areas of the theca. Usually four, B2:IL2, L4:L3, R1:R2, and R4:R5, but developed on seven locations in all, the additional positions being R3:R2, R5:R6, and R6:R1. Six, possibly all seven, are developed on paratype SUI 95249. Otherwise, not more than four are known on any other specimen (Broadhead and Sumrall, 2003, pl. 2, p. 117). All are very small with no more than seven, usually only 3–5, dichopores.

The oral area is generally flat, with two wide ambulacral grooves that divide near their tips to give the four ambulacra B-E (Fig. 10). Ambulacrum A is absent. Grooves are covered with a biseries of cover plates in paratype SUI 95249. One or rarely two pairs of ambulacral flooring plates occur at the distal ends of the ambulacra, indicating that not more than two brachioles occurred in each ambulacrum, but the brachioles themselves are unknown. The mouth is oval, about 1 mm across, by 0.5 mm and lies entirely within the broad primary food grooves. It is surrounded by plates O1, O3, O4, and O6. The ambulacral grooves have strongly raised rims.

The periproct is rounded, about 1.5–2.0 mm across, with a prominent raised rim and a deep groove in the surface of the theca immediately above it. It is surrounded by only four thecal plates and covered by a plated periproctal membrane, a few plates of which remain attached in the holotype. The anal pyramid is unknown.

The hydropore is relatively large, boomerang-shaped, about 1 mm long in a prominence on the oral surface in the CD interambulacrum; developed across the O1:O7 suture.

The gonopore is a smaller circular pore below (aboral to) the hydropore, which curves around it slightly and is covered by a small gonal pyramid of three or four plates. It is also developed across the O1:O7 suture.

R e m a r k s. In pectinirhombs, the direction of current flow can be determined from the relative length of the slits in each plate. Longer slits indicate entrances (see Paul, 1968b, p. 720, text-fig. 30). Thus, currents flowed from B2 to IL2, from L4 to L3, from R1 to R2, from R3 to R2, from R4 to R5, from R6 to R5, and from R1 to R6. This pattern is consistent with patterns seen in *Cheirocrinus* and *Glyptocystites* (see Paul, 1968b, p. 720, fig. 30). Generally, where more than one half rhomb occurs in a single plate all are either exits or entrances, although the odd exception does occur. For example, three half rhombs occur on plate L3 in *Glyptocystites* and all are exits. Furthermore, in both the Echinoencrinitidae and Callocystitidae there are commonly R3:L3 and R3:L4 rhombs and again R3 contains the entrances to both rhombs. Similarly, B2 has up to four half rhombs in it and they are always entrances. This common pattern of occurrence suggests that various internal coelomic cavities were oxygenated by specific rhombs or sets of rhombs. Cheirocrinids and glyptocystitids commonly have R:R rhombs, whereas these are unknown in the families Echinoencrinitidae and Callocystitidae, where the upper rhombs are usually R:L rhombs.

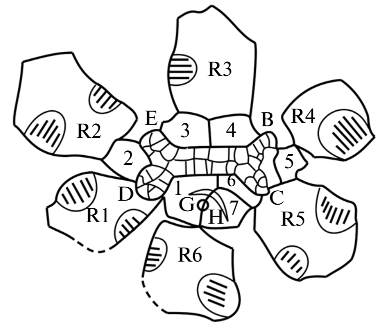


Fig. 10. *Sprinkleocystis ektopios* Broadhead et Sumrall, 2003, diagram of the oral plating and ambulacra in paratype SUI 95249 (after Broadhead and Sumrall, 2003, text-fig. 2.1). For designations, see Figs. 1 and 5. Note that ambulacrum A is not developed.

Sprinkleocystis is a relatively small cystoid, but even so has a small number of rhombs with very few dichopores. One can only surmise that its total respiratory capacity via the rhombs was small. Interestingly, it also has a reduced ambulacral system with less than eight, probably only five or six, brachioles. Although the length of the brachioles is unknown, one can again surmise that its feeding capacity was also reduced. The small, specialized pectinirhombs may well have provided enough oxygen to metabolize all the food it could gather.

There is no obvious reason why the A ambulacrum should have failed to develop in *Sprinkleocystis*. The ambulacral grooves are confined to the oral surface, so it is not possible to argue that the position of the pectinirhombs could have interfered with its development, as appears to have been the case in the Callocystitidae (Paul, 2014b).

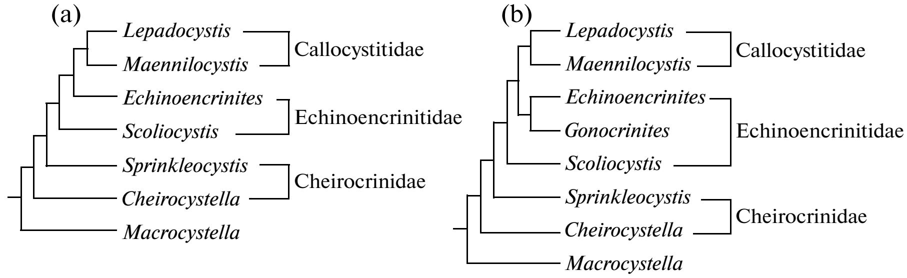


Fig. 11. Two cladograms for the genera discussed in the text: (a) without distinguishing *Gonocrinites* from *Echinoencrinites* (consistency index is 0.86, retention index is 0.86); (b) distinguishing *Gonocrinites* from *Echinoencrinites* (consistency index is 0.88, retention index is 0.89).

Rather like *Scoliocystis*, *Sprinkleocystis* has a combination of primitive and advanced characters. It has six radial plates, with some R:R rhombs, which is typical of other members of the family Cheirocrinidae. However, it has advanced pectinirhombs with confluent dichopores and vestibule rims, plus it is unique in having only four ambulacra with very few brachioles, characters otherwise unknown in the Cheirocrinidae, but more typical of the Echinoencrinitidae and Callocystitidae.

M a t e r i a l. Holotype and 11 paratypes, SUI 95249–95259, of which at least nine are more or less complete thecae.

PHYLOGENETIC RELATIONSHIPS

A simple cladogram, including seven genera, *Macrocystella, Cheirocystella, Sprinkleocystis, Scoliocystis, Echinoencrinites, Maennilocystis,* and *Lepadocystis,* produced a single most parsimonious tree as a simple ladder with the genera in that order (Fig. 11a). It was rooted on *Macrocystella,* because we think the possession of dichopores is an advanced character within the superfamily, primitively absent from *Macrocystella* (Paul, 1968a). Except for the last two, attempting to group the genera into the currently accepted families increases the tree length. Thus, this makes a good starting point for a discussion of the evolutionary position of *Scoliocystis*. *Cheirocystella* (family Cheirocrinidae) can be derived from *Macrocystella* (family Macrocystellidae) by the acquisition of dichopores, which form primitive conjunct pectinirhombs that are always composed of pairs of demirhombs, as far as is known (Paul, 1972). *Cheirocystella* has many pectinirhombs, the number and positions of which were not fixed (Paul, 1972). *Sprinkleocystis* (family Cheirocrinidae) has fewer advanced disjunct pectinirhombs with vestibules, only four lateral plates and, as a result, only four plates surround the periproct. It is also unique among currently accepted cheirocrinid genera in having only four ambulacra with at most two brachioles each. However, it retains many of the features of both *Cheirocystella* and *Macrocystella*, such as closed plate circlets, six radial plates with radial : radial pectinirhombs and a large periproct covered by a flexible plated periproctal membrane. The number and position of the pectinirhombs also vary, as in many cheirocrinids (see, for example, Sprinkle, 1974, table 1, p. 1185).

Scoliocystis (family Echinoencrinitidae) differs from all three preceding genera in having only five radial plates; R5 fails to develop. In addition, it has a variable number of radial:lateral pectinirhombs, but no radial:radial rhombs. However, it retains the primitive plate arrangement around the periproct with five plates (IL4, IL5, L1, L4, and L5) surrounding a relatively large opening. It also has a reduced oral area, the precise details of which remain unknown, but it can-

Table 1. Character states in *Scoliocystis* cladograms

Character	Plesiomorphic	Apomorphic
Dichopores	Absent	Present
Vestibules	Absent	Present
No of radials	Six	Five
L1 in periproct border	Present	Absent
L4 in periproct border	Present	Absent
Epithecal ambulacra	Absent	Present
Radial circlet	Closed	Open at L5

Plesiomorphic character state coded as 0, apomorphic as 1.

Table 2. Character matrix for *Scoliocystis* cladograms

Taxon	1	2	3	4	5	6	7
Macrocystella	0	0	0	0	0	0	0
Cheirocystella	1	0	0	0	0	0	0
Sprinkleocystis	1	1	0	0	0	0	0
Scoliocystis	1	1	1	0	0	0	0
Echinoencrinites	1	0	1	1	1	0	0
Maenillocystis	1	0	1	1	0	1	0
Lepadocystis	1	1	1	1	0	1	1
Gonocrinites	1	1	1	1	0	0	0

not have had more than one brachiole per ambulacrum. Indeed, Jaekel (1899, p. 260, text-fig. 52) reconstructed the type species *S. pumila* with just two brachioles. *Echinoencrinites* (family Echinoencrinitidae) has five ambulacra with at most three brachioles each, in a reduced oral area. It also has only three plates surrounding the periproct (IL4, IL5, and L5) and again a variable number of R:L, but no R:R rhombs. The disjunct pectinirhombs retain the more primitive discrete dichopores and entirely lack vestibules. *Maennilocystis* (family Callocystitidae) has four plates surrounding the periproct (IL4, IL5, L4, L5), only five radial plates, and three disjunct R:L rhombs (R3:L3, R3:L4, R6:L1) with vestibules. It also has the evolutionary novelty of five epithecal ambulacra developed on the radial plates. Finally, *Lepadocystis* Carpenter, 1891 (family Callocystitidae) has the same four periproct border plates, five recumbent ambulacra that reach the infralateral plates and five advanced disjunct pectinirhombs with vestibules.

Thus, the key evolutionary innovations are as follows:

(1) The appearance of dichopores in the change from *Macrocystella* to *Cheirocystella*.

(2) The appearance of disjunct pectinirhombs with vestibules in *Sprinkleocystis* (plus the reduction of the number of rhombs and loss of ambulacrum A).

(3) The loss of plate R5 in *Scoliocystis,* which unites the families Echinoencrinitidae and Callocystitidae.

(4) The loss of plate L1 from the periproct border, first seen in *Gonocrinites* and followed by the loss of plate L4 in all other Ordovician echinoencrinitid genera, except *Fusicystis* Terentiev (Zuykov et al., 2008).

(5) The development of recumbent ambulacra in *Maenillocystis* and *Lepadocystis* and all other genera of Callocystitidae as currently understood (Paul, 2014a, 2014b).

In particular, there seems to be an important trend in the number of plates surrounding the periproct. This makes us consider it desirable to distinguish those species of *Echinoencrinites* sensu lato*,* which have four plates surrounding the periproct (and usually a larger number of pectinirhombs) from those with only three periproct border plates. Fortunately, the name *Gonocrinites* Eichwald, 1840 is available for species with four periproct border plates. Furthermore, making this distinction and including the genus *Gonocrinites* in the cladogram, produces the interesting feature of grouping *Echinoencrinites* and *Gonocrinites* (but not *Scoliocystis*) in a separate branch of the phylogenetic tree (Fig. 11b). Thus, it seems that *Scoliocystis* might best be regarded as a stem group for the Echinoencrinitidae + Callocystitidae.

CONCLUSIONS

We have systematically revised a few key genera in the superfamily Glyptocystitoida on the basis of some original specimens plus new material.

Scoliocystis pumila (Eichwald, 1860), type species of *Scoliocystis* Jaekel, 1899, is characterized by a curved, elongate theca with an oval cross section, five plates surrounding the periproct (IL4, IL5, L1, L4, and L5), plus advanced disjunct pectinirhombs with confluent dichopores and well-developed vestibule rims. It shares more characters with members of the family Echinoencrinitidae than with those of the Cheirocrinidae and was probably a stem-group genus of the clade Echinoencrinitidae + Callocystitidae.

The genus *Gonocrinites* Eichwald, 1840, type species *Echinosphaerites angulosus* Pander, 1830, is resurrected for two species of *Echinoencrinites* sensu lato with four plates surrounding the periproct (IL4, IL5, L4, and L5).

Echinoencrinites sensu stricto, type species *E. senckenbergii* von Meyer, 1826, is characterized by three plates surrounding the periproct (IL4, L4, and L5).

Scoliocystis sp. (Hecker, 1964) is redescribed as *Maennilocystis heckeri* gen. et sp. nov. and referred to the family Callocystitidae based on its five recumbent ambulacra. It becomes stratigraphically the oldest member of the Callocystitidae.

The genus *Sprinkleocystis,* type species *S. ektopios* Broadhead et Sumrall, 2003, is accepted as an unusual cheirocrinid cystoid with only four lateral plates (L1–L4), four periproct border plates (IL4, IL5, L1 and L4), four ambulacra (ambulacrum A is missing) plus advanced disjunct pectinirhombs with confluent dichopores and well-developed vestibule rims. The last character arose independently in *Scoliocystis* and *Sprinkleocystis*.

A provisional cladogram for key genera suggests that the families Echinoencrinitidae and Callocystitidae arose from cheirocrinids with closed plate circlets by the loss of plate R5 and the substitution of radial:lateral pectinirhombs for radial:radial pectinirhombs. Echinoencrinitids are characterized by reduced ambulacra and oral areas; callocystitids display extensive ambulacra recumbent on primary thecal plates. Some Ordovician genera in both families independently developed advanced disjunct pectinirhombs with confluent dichopores and well-developed vestibule rims.

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REFERENCES

Ausich, W.I. and Schumacher, G.A., New Lower Silurian rhombiferan cystoid (Echinodermata, Callocystitidae) from southwestern Ohio, *J. Paleontol.,* 1984, vol. 58, pp. 9–15.

Barrande, J., *Système Silurien du Centre de la Bohème. Première Partie: Recherches Paléontologiques,* vol. 3: *Classe des Mollusques. Ordre des Ptéropodes,* Prague: W. Waagen, 1867.

Barrande, J., *Système Silurien du Centre de la Bohème. Première Partie: Recherches Paléontologiques,* vol. 7: *Classe des Echinodermes. Ordre des Cystidées,* Prague: W Waagen, 1887.

Bassler, R.S. and Moodey, M.W., Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms, *Geol. Soc. Am. Spec. Pap.,* 1943, no. 45, pp. 1–733.

Bather, F.A., A phylogenetic classification of the Pelmatozoa, *Rep. Brit. Ass. Advance. Sci.*, 1899, vol. 68, pp. 916–923.

Bernard, F., *Eléments de Paléontologie,* Paris: J.-B. Ballière et Fils, 1893–1895.

Bockelie, J.F., The oral area of *Echinoencrinites* von Meyer. 1826, *Norsk Geol. Tidsskr.,* 1981, vol. 61, pp. 79–82.

Broadhead, T.W. and Strimple, H.L., Systematics and distribution of the Callocystitidae (Echinodermata, Rhombifera), *J. Paleontol.,* 1978, vol. 52, pp. 164–177.

Broadhead, T.W. and Sumrall, C.D., Heterochrony and paedomorphic morphology of *Sprinkleocystis ektopios,* new genus and species (Rhombifera, Glyptocystida[sic]) from the Middle Ordovician (Caradoc) of Tennessee, *J. Paleontol.,* 2003, vol. 77, pp. 113–120.

Callaway, C., On a new area of Upper Cambrian rocks in south Shropshire, with a description of a new fauna, *Quart. J. Geol. Soc., Lond.*, 1877, vol. 33, pp. 652–672.

Carpenter, P.H., Report upon the Crinoidea collected during the voyage of HMS Challenger during the years 1873–76: Part 1. General morphology with descriptions of the stalked crinoids, *Rep. Sci. Res. Voy. HMS Challeng., Zool.,* 1884, vol. 11, pp. 1–442.

Carpenter, P.H., On certain points of the morphology of the Cystidea, *J. Linn. Soc. (Zool.),* 1891, vol. 34, pp. 1–52.

Dronov, A. and Rozhnov, S., Climatic changes in the Baltoscandian Basin during the Ordovician: Sedimentological and palaeontological aspects, *Acta Palaeontol. Sin.,* 2007, vol. 46, suppl. no., pp. 108–113.

Ehlers, G.M. and Leighley, J.B., *Lipsanocystis traversensis*, a new cystid from the Devonian of Michigan, *Pap. Michigan Acad. Sci. Arts Lett.,* 1922, vol. 2, pp. 155–160.

Eichwald, E., Sur la système Silurien d l'Esthonie, *J. Méd. Hist. Nat. Acad. Méd. St Petersburg*, 1840, vol. 1, pp. 1–222.

Eichwald, E., Beitrag zur geographischen Verbreitung der fossilien Thiere Russlands: Alte Periode, *Bull. Soc. Imp. Natur. Moscou,* 1856, vol. 29, pp. 88–127.

Eichwald, E., *Lethaea Rossica ou Paléontologie de la Russie: Ancienne Période: Atlas, Text,* Stuttgart: Schweizerbart, 1859–1860.

Foerste, A.F., Notes on Agelacrinidae and Lepadocystinae with descriptions of *Thresherodiscus* and *Brockocystis*, *Bull. Sci. Labs. Denison Univ.*, 1914, vol. 17, pp. 399–487.

Forbes, E., On the Cystideae of the Silurian rocks of the British Isles, *Mem. Geol. Sur. UK,* 1848, vol. 2, part 2, pp. 483–538.

Haeckel, E.H.P.A., Amphorideen und Cystoideen. Beiträge zur Morphologie und Phylogenie der Echinodermen In: Festschrift zum Siebenzigsten Geburtstage von Carl Gegenbauer am 21 August 1896. 1896, Erster Band, W. Engelmann, Leipzig, pp. 1–180.

Hall, J., *The Natural History of New York: Part 6. Palaeontology of New York,* 1852, vol. 2 (containing descriptions of the organic remains of the Lower Middle Division of the New-York System), Albany, New York: D. Appleton, and Wiley and Putnam.

Hall, J., *The Natural History of New York: Part 6. Palaeontology of New York,* 1859, vol. 3 (Descriptions of the organic remains of the lower Helderberg group and the Oriskany sandstone), Albany, New York: D. Appleton, and Wiley and Putnam.

Hecker, R.F., Class Cystoidea, *Osnovy paleontologii. Iglokozhie, gemikhordovye, pogonofory i shchetinkochelyustnye,* Hecker, R.F., Ed., Moscow: Nedra, 1964, pp. 30–45.

Hisinger, W., *Anteckningar I Physik och Geognosi under resor uti Sverige och Norrige,* Stockholm, 1828, vol. 4.

Jaekel, O., Über die Organization der Cystoideen, *Deutsche Zoologische Geselschaft Verhandlungen auf der fünften jahresversammlung zu Strassburg,* 1895, vol. 5, pp. 109–121.

Jaekel, O., *Stammesgeschichte der Pelmatozoen: 1. Thecoidea und Cystoidea,* Berlin: Julius Springer, 1899.

Jell, P., Early Devonian echinoderms from Victoria (Rhombifera, Blastoidea and Ophiocistioidea), *Mem. Assoc. Austral. Palaeontol.,* 1983, vol. 1, pp. 209–235.

Kesling, R.V., An interpretation of *Rhombifera bohemica* Barrande, 1867, an unusual hydrophoridean cystoid, *Contrib. Mus. Paleontol. Univ. Michigan,* 1962, vol. 17, pp. 277–289.

Kesling, R.V., Cystoids, in *Treatise on Invertebrate Paleontology: Part S. Echinodermata 1 (1),* Boulder, Lawrence: Geol. Soc. Amer.; Univ. Kansas Press, 1968. P. 85–267.

Koch, D.L. and Strimple, H.L., A new Upper Devonian cystoid attached to a discontinuity surface, *Iowa Geol. Surv., Rep. Invest.,* 1968, no. 5, pp. 1–49.

McCoy, F., A synopsis of the Silurian fossils of Ireland, Dublin, 1846.

Meyer, H., von, Beschreibung des Echino-Encrinites Senckenbergii, einer neu entdeckten Versteinerung, *Archiv Ges. Natur. Herausgegeben K.W.G. Kastner,* 1826, vol. 7, pp. 185–192.

Neumayr, M., *Die Stämme des Thierreiches: Wirbellose Thiere,* Wien and Prag: Tempsky, 1889, vol. 1.

Pander, C.H., *Beiträge zur Geognosie des Russischen Reiches,* St. Petersburg: Karl Kray, 1830.

Parks, W.A., A new cystid from the Clinton Formation of Ontario—*Lepadocystis clintonensis, Am. J. Sci.,* 1910, vol. 29, pp. 404–406.

Paul, C.R.C., The British Silurian cystoids, *Bull. Brit. Mus. (Natur. Hist.) Geol.,* 1967a, vol. 13, pp. 299–355.

Paul, C.R.C., *Osculocystis,* a new British Silurian cystoid, *Geol. Mag.,* 1967b, vol. 104, pp. 449–454.

Paul, C.R.C., The functional morphology and mode of life of the cystoid *Pleurocystites*, E. Billings, 1854, *Echinoderm Biol. Symp. Zool. Soc. London,* 1967c, vol. 20, pp. 105–123.

Paul, C.R.C., *Macrocystella* Callaway, the earliest glyptocystitid cystoid, *Palaeontology* 1968a, vol. 11, pp. 580–600.

Paul, C.R.C., Morphology and function of dichoporite pore structures in cystoids, *Palaeontology,* 1968b, vol. 11, pp. 697–730.

Paul, C.R.C., Notes on cystoids, *Geol. Mag.*, 1968c, vol. 105, pp. 413–420.

Paul, C.R.C., *Cheirocystella antiqua* gen. et sp. nov. from the Lower Ordovician of Western Utah, and its bearing on the evolution of the Cheirocrinidae (Rhombifera: Glyptocystitida), *Brigham Young Univ. Geol. Stud.,* 1972, vol. 19, pp. 15–63.

Paul, C.R.C., British Ordovician cystoids: Part 2, *Monogr. Palaeontogr. Soc. London,* 1984, vol. 136, pp. 65–152.

Paul, C.R.C., *Callocystites fresti* sp. nov., and the significance of ambulacral branching in the Callocystitidae (Echinodermata, Glyptocystitoida), *Geol. J.,* 2014a, vol. 50, pp. 189–209.

Paul, C.R.C., A cystoid with two left facets: The significance of *Tetracystis* in the evolution and classification of the Callocystitidae (Echinodermata, Glyptocystitoida), *Geol. J.,* 2014b. DOI: 10:1002/gj.2578

Paul, C.R.C. and Bolton, T.E., A new Middle Silurian callocystitid cystoid from the Lake Timiskaming Region, Northern Ontario, *Bull. Geol. Surv. Can.,* 1991, vol. 412, pp. 35–42.

Paul, C.R.C. and Donovan, S.K., A review of the British Silurian cystoids, *Geol. J.,* 2011, vol. 46, pp. 434–450.

Paul, C.R.C., Donovan, S.K., Muir, L.A., et al., Primitive Ordovician (Floian) echinoderms from Sandu, Guizhou Province, South China, and their significance, *Geol. J.,* 2014, vol. 51, pp. 143–156.

Pearce, J.C., On an entirely new form of encrinite from the Dudley Limestone, *Proc. Geol. Soc., Lond.*, 1843, vol. 4, pp. 1–160.

Phleger, F.B., Some Ordovician cystids from Russia, *Bull. Mus. Compar. Zool., Harvard Coll.,* 1935, vol. 76, pp. 191–201.

Regnéll, G., Non-crinoid Pelmatozoa from the Paleozoic of Sweden, *Meddel. Lunds Geol.–Min. Inst.*, 1945, no. 108, pp. 1–255.

Rozhnov, S.V., Morphogenesis and evolution of crinoids and other pelmatozoan echinoderms in the Early Paleozoic, *Paleontol. J.,* 2002, vol. 36, suppl. no. 6, pp. 525–674.

Rozhnov, S.V., Sibling echinoderm taxa on isolated Ordovician continents: Problem of center of origin, *Bull. Geosci.,* 2010, vol. 85, no. 4, pp. 671–678.

Schuchert, C., On new Siluric Cystidea, and a new *Camarocrinus*, *Am. Geol.,* 1903, vol. 32, pp. 230–240.

Schuchert, C., On Siluric and Devonic Cystidea and *Camarocrinus*, *Smithson. Misc. Coll.,* 1904, vol. 2, pp. 201–272.

Sinclair, G.W., An Ordovician faunule from Quebec, *Can. Field Nat.*, 1945, vol. 59, pp. 71–74.

Sinclair, G.W., Some Ordovician echinoderms from Oklahoma, *Am. Mid. Nat.,* 1845, vol. 34, pp. 707–716.

Sinclair, G.W., Three notes on Ordovician cystids, *J. Paleontol.,* 1948, vol. 22, pp. 301–314.

Sprinkle, J., New rhombiferan cystoids from the Middle Ordovician of Nevada, *J. Paleontol.,* 1974, vol. 48, pp. 1174–1201.

Sprinkle, J., Cylindrical and globular rhombiferans, in *Echinoderm faunas from the Bromide Formation (Middle Ordovician) of Oklahoma,* Univ. Kansas Paleontol. Contrib., 1982, Monogr. 1. pp. 231–273.

Sprinkle, J. and Wahlman, G.P., New echinoderms from the Early Ordovician of West Texas, *J. Paleontol.,* 1994, vol. 68, pp. 324–338.

Sumrall, C.D. and Brett, C.E., A revision of *Novacystis hawkesi* Paul and Bolton 1991 (Middle Silurian: Glyptocystitida, Echinodermata) and the phylogeny of early callocystitids, *J. Paleontol.,* 2002, vol. 76, pp. 733–740.

Sumrall, C.D. and Carlson, D.T., Suture modification and pectinirhomb growth in *Lepadocystis decorus,* a new species of callocystitid glyptocystitid rhombiferan (Echinodermata) from Illinois, *J. Paleontol.,* 2000, vol. 74, pp. 487–491.

Sumrall, C.D. and Waters, J.A., Universal element homology in glyptocystitoids, hemicosmitoids, coronoids and blastoids: Steps towards echinoderm phylogenetic reconstruction in derived Blastozoa, *J. Paleontol.,* 2012, vol. 86, pp. 956–972.

Ulrich, E.O. and Kirk, E., *Amecystis*, a new genus of Ordovician Cystidea, *Proc. Biol. Soc. Wash.*, 1921, vol. 34, pp. 147–148.

White, C.A., Description of new species of fossils from the Palaeozoic rocks of Iowa, *Proc. Acad. Nat. Sci. Philad.,* 1876, vol. 28, pp. 27–34.

Wood, E., A critical summary of Troost's unpublished manuscript on the crinoids of Tennessee, *Bull. US Nat. Mus.*, 1909, vol. 64, pp. 1–150.

Zuykov, M.A., Terentiev, S.S., and Harper, D.A.T., New endemic brachiopod and echinoderm genera from the Upper Ordovician of the St Petersburg region, northwestern Russia, *Geol. Fören. Stockholm Förhandl.,* 2008, vol. 130, pp. 87–93.

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