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MORPHOLOGIC AND SYSTEMATIC REVISION OF THE SOLUTE *MAENNILIA ESTONICA* (HOMOIOSTELEA, ECHINODERMATA) FROM THE UPPER ORDOVICIAN OF ESTONIA

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ABSTRACT—*Maennilia estonica* Rozhnov and Jefferies was first described as a stem-chordate but restudy shows it is an unusually large homoiostelean echinoderm. Its feeding structure, an erect ambulacrum, extending exothecally from the peristomial frame plates, bears a large internal tunnel that opens directly into the body cavity. This type of feeding appendage is now recognized to be unique to homoiosteles. It bears no evidence for water vascular system impressions adjacent to its food groove. The theca has poorly developed marginal plates and a narrow rim that, in contrast to some other homoiosteles, does not extend over either lower or upper thecal face. *Maennilia* appears to have inhabited the deeper portions of a near-shore environment in limey muds adjacent to a linear zone of bryozoan and microbial bioherms.

INTRODUCTION

THE ECHINODERM class Homoiostelea and its single order Soluta ranges from the lower middle Cambrian to the Lower Devonian. Homoiosteles are essentially flattened, asymmetrical forms that tend towards being bilateral. The feeding structure is always offset laterally from the polar thecal axis and placed marginally or nearly so. Extending from the theca is a two- or three-part stalk that helps define the nearly bilateral symmetry. Thecal plating is mostly tessellate, composed of small, thin, polygonal platelets. The earliest solutes are tessellate plated forms from Laurentia, including three species: *Coleicarpus* and *Castericystis* from the middle Cambrian (Series 3) of Utah (Ubaghs and Robison, 1985, 1988; Daley, 1995, 1996), and a slightly younger Furongian form *Minervacystis*? sp. (Ubaghs, 1963; Sumrall et al., 1997) from Nevada (Zamora et al., in press). The Early Ordovician *Minervacystis* Ubaghs and Caster, 1968 (Montagne Noir, France) is also tesselately plated. Marginal plates in *Maennilia*, Rozhnov and Jefferies, 1996 from the early Late Ordovician of Estonia display the beginning stages of lateral marginal plate evolution. Here, marginals are narrow and do not have extensions over the lateral portions of either the upper or lower face. Other Middle and Late Ordovician Laurentian solutans including: *Syringocrinus*, Billings, 1859, (Middle Ordovician); *Belemnocysties*, Miller and Gurley, 1894, (M. Ord.); I*owacystis*, Thomas and Ladd, 1926, (Middle Ordovician); *Sclaenocystites,* Kolata, 1973, (Middle Ordovician) and *Girvanicystis*, Caster, 1968, (Upper Ordovician) all bear a well-defined set of marginal thecal plates extending over the lateral portions of upper and especially the lower face. The marginals in *Maennilia* appear to represent an independent fusion of thecal plates forming a narrow band of small plated marginals. Coeval (Upper Ordovician) forms in Bohemia; *Dendrocystites* Barrande, 1887, *Dendrocyoides* Jaekel, 1918 and Estonia *Heckericystis* Gill and Caster, 1960 retained the plesiomorphic tesselate plated condition. For unknown reasons Soluta are not represented in Silurian strata but reappear in the Lower Devonian where two thecal patterns are present: the first retaining a polyplated thecae, *Dehmicystis*, Caster, 1968 from Germany and *Rutroclypeus*, Withers, 1933 from Australia, and the second showing fusion of large polyplates into a rigid surface, *Claritacarpus*, Parsley and Sumrall, 2007 from Oklahoma.

Maennilia was originally described as a stem-chordate by Rozhnov and Jefferies, 1996 (also see Daley 1995, 1996) but we hold to the conventional position that it is an echinoderm (e.g., Gill and Caster, 1960; Caster, 1968; Ubaghs, 1968; Parsley and Caster, 1965; Parsley, 1972; Kolata, 1973; Sprinkle, 1976; Kolata, Strimple and Levorson, 1977; Parsley, 1997; Parsley and Sumrall, 2007). Restudy also has shown that some of the thecal morphology as originally documented is inaccurate and in need of revision. Specifically, the theca has a narrow but well developed series of marginal plates. The original illustration showing a pronounced biconvex curvature of upper and lower faces is exaggerated (Rozhnov and Jefferies, 1986, p. 97). Except for the aboral lobe, the general appearance of the theca is more in line with other Ordovician polyplated homoiosteles. The theca and stalk are similar to those of the slightly older Bohemian solute genera, *Dendrocystites* and *Dendrocystoides*. Excellent preservation of the feeding structure clearly demonstrates that this erect ambulacrum is plated differently from other similar structures in other echinoderm classes.

STRATIGRAPHIC SETTING

Specimens of *Maennilia* were collected from an active limestone quarry in the Vazalemma Formation (upper part of the Keila regional stage, Katian, Upper Ordovician) near the village Vazalemma in North Estonia, about 60 km southwest of Tallinn (Fig. 1). This formation consists of medium to thick, coarse-grained, commonly termed ''cystoid limestone'' surrounding both bryozoan and microbial bioherms. Coarse-grained ''cystoid limestones'' are composed mostly of skeletal fragments of the hemicosmitoid rhombiferan echinoderm *Hemicosmites* von Buch, 1840. Insoluble residue found in the cystoid limestone facies averages 1.9 percent and suggests that *Maennilia* collected from this facies, was living in relatively clean, clear water (Põlma, 1982) (Fig. 2).

Bioherms adjacent to *Maennilia* bearing sediments extend about 25 km from east near the village Tuula to west near the village Mããra in an exposure belt 0.5 to 1 km wide. These bioherms are often irregular in plan and size. Their diameter is usually 5 to 50 meters but in rare cases can reach up to 300 m. Their height varies from 1 to 10 m and contacts are sharp with the surrounding sediments. In bioherms dominated

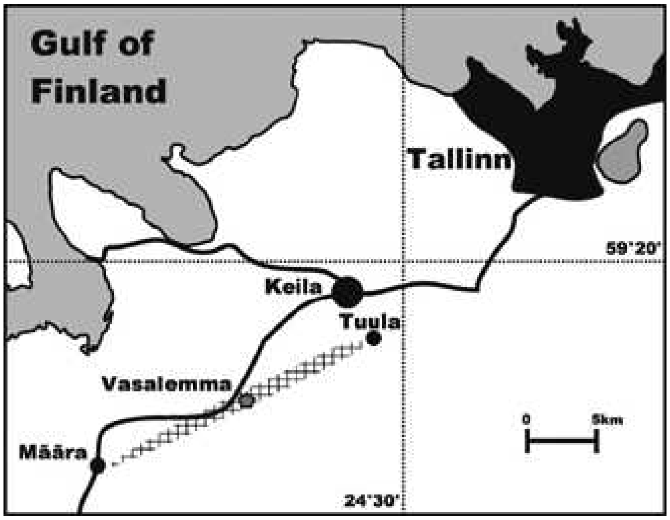

FIGURE *1*—Locality map and outcrop pattern (cross-hatched) of *Maennilia* bearing Vazalemma Formation (Upper Ordovician, northern Estonia).

by bryozoans, the major constituents are large branching trepostomes, (various members of the family Monticuliporidae) and encrusting cyclostomes. In microbial bioherms, sediments are densely cryptocrystalline and yellowish to bluish-gray in color. There are irregular lenticular intercalations of limestone, marl, and clay with conchoidal fracture in both bioherms and surrounding grainstones (Männil 1960, 1966; Rõõmusoks, 1970).

The preservation of *Maennilia* is variable. It is commonly preserved in a thanatocoenosis where many specimens are concentrated most likely resulting from storm transport. Preserved thecae are typically fragmented and partially overlap adjacent specimens on bedding surfaces obscuring the outlines of single individuals. Whitening slabs with numerous individuals with sublimate of NH_4Cl facilitates the discrimination of single individuals. The stele and ambulacral structures in this material are robustly constructed and converse to thecae, are commonly well preserved.

Remains of *Maennilia* are more common on bedding planes near bryozoan bioherms and are less so near microbial bioherms. Rarely, individuals are preserved on the slopes of bioherms with the anterior end of the theca facing into the inferred paleo-current. Most commonly, remains of *Maennilia* are clustered and covered with marl or calcareous clay on a bedding surface of the coarse-grained limestone. This indicates that animals' deaths and accumulation were the probable result of severe storms that lead to the significant disruption of many thecae and their displacement from deeper offshore habitats. There is almost no evidence for bioturbation in these muds and portions of the skeleton and even nearly complete skeletons are preserved undisturbed by infauna. Where specimens are deposited in clusters, dorsal and ventral surfaces are about equal in number facing upwards. Those surviving transport were probably killed because of a lack of oxygen in the smothering mud.

MORPHOLOGY AND EVOLUTION OF THE HOMOIOSTELEAN FEEDING STRUCTURE

In *Maennilia* the feeding structure is commonly well preserved, essentially complete and little distorted. Fortuitous breakage of some specimens gives a nearly complete picture of its internal structure. Although externally it looks like an enlarged brachiole, internally the morphology of these two structures is significantly different in detail. Structural details discussed herein for *Maennilia* hold, with minor modifications, for all homoiostelians.

The solutan erect ambulacrum has a biserially arranged set of ambulacral plates emerging exothecally from the circumoral frame of unknown construction. Possibly unique to *Maennilia* is a proximal series of three or four platelet circlets (sleeve plates of Rozhnov and Jefferies, 1996) that encircle the proximal perimeter of the exothecal ambulacrum. These platelets span about a two-ambulacral plate thick gap between the theca and the proximal-most pair of ambulacral floor and cover plates. The sleeve plates are interpreted as ambulacral floor plates that have fragmented and give the basal part of the exothecal ambulacrum greater flexibility. This interesting feature does not inform either the general morphology of the appendage or the phylogenetic position of this taxon.

Although the peristome is homologous among echinoderms, the frame plating that borders the peristome may or may not be homologous with oral frame borders of other coeval echinoderms. The problem cannot be reconciled largely because of lack of understanding of the internal details of the solute peristome.

The erect ambulacrum of *Maennila* differs from erect ambulacra in blastozoans (e.g., Sprinkle, 1975; Parsley, 1982; Sumrall, 1997; Dean and Smith, 1998; Parsley and Zhao 2006; Sprinkle and Collins, 2006; Sprinkle et al., 2011). In *Maennilia* the erect paired plates radiating out from the sleeve platelets have no sutural contact with thecal plates. This is an apomorphic condition for *Maennilia* and is not representative of solutes as a whole where ambulacral plates extend outwards directly from the oral frame and do not contact thecal plates.

In blastozoans bearing erect ambulacra, there is typically a series of recumbent ambulacral floor plates, commonly without a tunnel extending from the body cavity, radiating from the centrally positioned peristomial area that distally becomes elevated above the theca to form an erect appendage. In such blastozoans, secondary appendages (brachioles) arise from these floor plates as gracile feeding appendages that typically are plated biserially (Sprinkle, 1973). The solute ambulacrum was interpreted as ambulacrum A by Sumrall and Wray (2007) based on symmetry arguments but it clearly has a different evolutionary history and is not directly comparable. The evidence is clear that brachioles (sensu Sprinkle, 1973) are not homologous with erect ambulacra in solutes.

Brachioles are small thin feeding appendages that arise from ambulacral floor plates in various arrangements with respect to the underlying floor plates (Sprinkle, 1973; Sumrall, 1997).

A significant variable in blastozoans is in the family Dibrachicystidae Zamora and Smith, 2012, where two middle Cambrian genera, *Dibrachiacystis* Zamora and Smith, 2012 (Murero Formation, northern Spain) and *Vizcainoia* Zamora and Smith, 2012 (Montagne Noir, southern France) have paired, variably organized, arm-like feeding structures that arise seamlessly, antero-laterally, near the anterior end of the theca. These feeding structures have a tunnel or lumen that opens directly into the theca. Tall pointed cover plates arch over the food collecting surface. These structures help argue for the plasticity of feeding structures in the blastozoans (Zamora and Smith, 2012).

Because the feeding appendage of solutes arises directly from the peristomial border it is, therefore, interpretable as an erect ambulacrum as is evidenced by the biserial plating of the floor plates and overlying cover plates. Because it extends

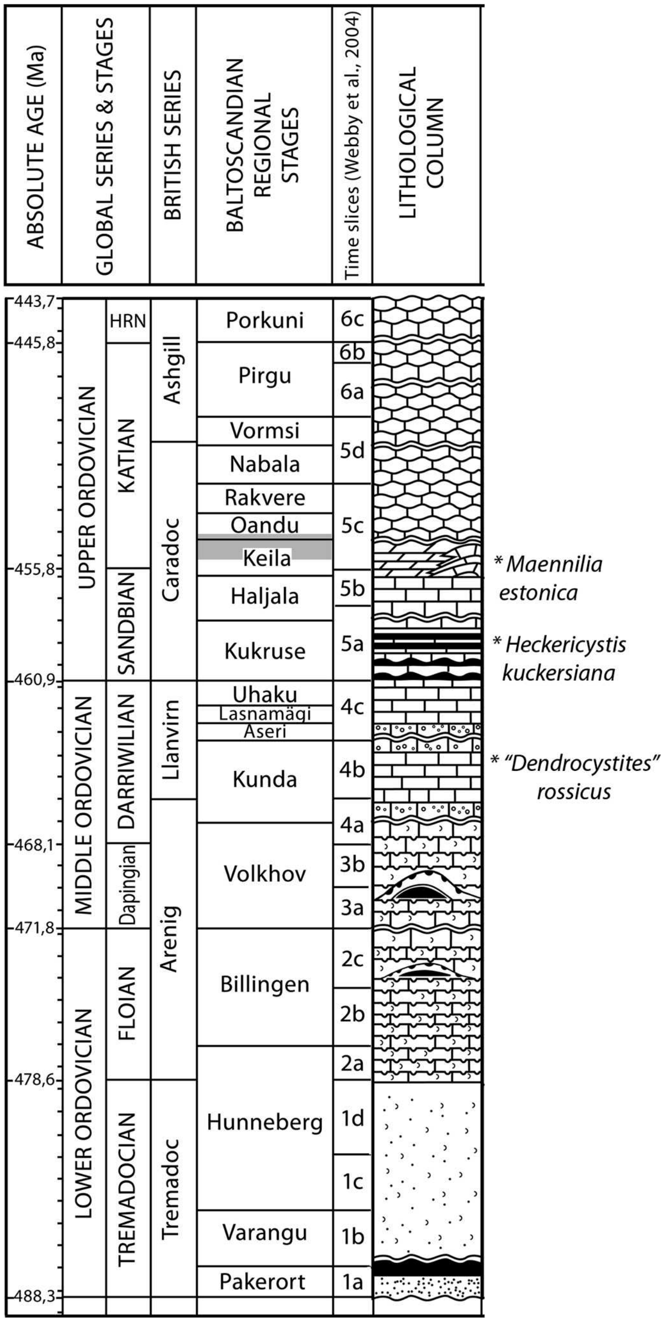

FIGURE 2—Lithologic column of the Estonian Ordovician. Shaded area is position of the Vazalemma Formation which contains *Maennilia.*

directly from the oral frame and has no thecal involvement it is interpreted as an independent evolutionary novelty. Calling this structure a brachiole (sensu Sprinkle, 1973) confuses the meaning of terminology and confounds phylogenetic reconstruction (Sumrall, 2010).

There is a large tunnel (not homologous with the lumen in crinoids and in some blastozoans) within the floor and sleeve plates that opens directly into the theca. Why early solutes have such large ambulacral tunnels is unknown. Younger genera, especially Laurentian forms, seem to have somewhat reduced the diameter of their ambulacral tunnels. The tunnel opens directly (through the sleeve plates) into the thecal cavity. This arrangement is unknown in erect ambulacra of other stemmed echinoderms but has analogy in the erect ambulacra of plesiomorphic crinoids. In crinoids, erect ambulacra are composite structures that bear biserial ambulacral floor plates overlaying uniserial plates derived from an extension of the thecal wall with a coelomic canal running between them. This coelomic canal enters the theca through a separate opening distal to the peristome (Guensburg and Sprinkle, 2007, 2009; Guensburg et al., 2010). Later crinoids lose the floor plates and the arm lumen has no skeletal expression except for the large size of the food groove that carries the coelomic canal beneath it.

The upper surface of the paired ambulacral floor plates of *Maennilia* bears a shallow, featureless, but well-developed food groove. There are no impressions or other convincing evidence for a water vascular system traversing the length of the structure (Sprinkle, 1973; Parsley and Zhao, 2006; see Kolata et al., 1977 for a different interpretation). Directly paired with the ambulacral floor plates are tall over-arching blastozoan-like cover plates similar to those on many early eocrinoids (Sprinkle, 1973; Parsley and Zhao, 2006). They are oriented such that their distal ends interdigitate, zipper-like, along the entire length of the structure (Fig. 3.1, 3.7, 3.10).

The ambulacrum of *Maennilia* bears about 42 to 50 segments in mature specimens (Fig. 3.1) and is unusually long when compared to other solutes. In the proximal third approximately 14 to 17 segments the floor plates are as much as twice as tall as the cover plates, and up to 2.4 times taller than ambulacrals in the distal two thirds of the ambulacrum (Fig. 3.7). This distinct, tall, proximal section in *Maennilia* seems restricted to this genus and is not observed in other genera.

The tunnel is oval in the proximal part of the ambulacrum with its vertical axis approximately 3.4 times taller than its width (Fig. 3.9). In the distal part of the ambulacrum, the ambulacral floor plates and cover plates are nearly the same height and width and the tunnel is essentially circular. The proximal articulating surface on each pair of floor plates and covering plates is convex and is correspondingly concave on the distal sides of the plates. The combined articulatory surface at each end of the segment is oval. The distal end of each floor plate pair is enlarged and flared out to increase the size and flexibility of the articulatory surface (Fig. 3.7, 3.9). This flaring occurs for several segments past the proximal enlarged section. There is a distinct possibility that the cover plates on the most proximal segments of the ambulacrum did not open and their edges were part of the articulating surface that moved the structure back and forth.

Distally, the ambulacrum is more tubular, and tapers rather abruptly along the ventral side from the enlarged proximal section towards the distal section. The distal portion of the ambulacrum tapers gradually and ends in an acutely rounded point.

Functional morphology.—The ambulacrum is unusually long in *Maennilia* and the large tunnel within the floor plates is proportionately very large compared to other solutes. There is a strong possibility that additional turgor, in part, resulted from hydrostatic pressure of coelomic fluids within the lumen. The theca has a pressure valve type of anal opening and quite possibly the internal thecal pressure was above ambient. Pressurization may have aided the circulation of body fluids for more efficient respiratory exchange (Sumrall and Parsley, 2003; Parsley and Zhao, 2006). A pressurized feeding structure would facilitate greater length and reduced muscular development along its length.

Movement of the erect ambulacrum appears to be predominately lateral based on the oval cross-section (especially proximally) and the flared lateral articulating surfaces at the distal ends of the ambulacral plates. It was a structure that probably could move from side to side through a fairly wide angle. The sleeve plates may have been instrumental in lifting the erect ambulacrum so that when feeding at higher levels above the substrate it moved side to side at an acute angle over the substrate (see Rozhnov and Jefferies, 1996, p. 97; Fig. 4). The narrow reentrant in the marginals on the left side of the theca kept the narrow cross-section constrained so that the long cross-sectional axis remained essentially vertical and the cover plates directed upwards. The inflated articulation surfaces on the proximal ends of floor plates precluded rotation of the structure into a horizontal posture in the living animal. In many homoiostelean genera, including *Maennilia*, the erect ambulacrum is commonly preserved lying on its side. This probably results from taphonomic compression from overlying sediments.

Kolata, Strimple and Levorson, (1977) and Rozhnov and Jefferies (1996) orientated the homoiostelean animal with the food groove facing the substrate. This seems highly unlikely with the observed orientation in *Maennilia*. Furthermore, in this orientation, the domed hydropore/madreporite plate located next to the base of the erect ambulacrum would be buried in the substrate. Also, the cover plates seem to have opened distally rather widely and not narrowly (to facilitate a sieve-like food intake).

We suggest that feeding was in quiet water at the accumulation layer above the sediment-water interface with open cover plates helping to trap food as the ambulacrum was moved back and forth. Where currents were stronger and the accumulation layer was more dispersed the animal probably faced into the current, raised the feeding structure and created back eddies and swirls so that food was conducted to the food groove positioned on the down-current side, past the opened cover plates. Food was probably trapped by mucus and moved towards the mouth by cilia.

PHYLOGENIC POSITION

To help determine where *Maennilia* fits within Soluta and refine character polarity, this taxon was rescored for characters 8, 10, and 12 in the matrix presented by Parsley and Sumrall (2007) to incorporate new information (see Parsley, 1997 for character list). Character 8 reflects the differentiation of marginal plates and somatics. Characters 10 and 12 reflect the reinterpretation of the plating of the mesostele and distal stele. The new matrix (Appendix) was analyzed in PAUP* (Swoford, 2002) using maximum parsimony. All character states were equally weighted and treated as unordered. The matrix was polarized using the eocrinoid *Gogia* as outgroup.

The analysis recovered four equally most parsimonious trees with a length of 44 steps, RI=0.64, RC=0.75 (Fig. 5). The topology is fully congruent with that recovered by Parsley and Sumrall (2007) however a bootstrap analysis of 1,000 pseudoreplicate matricies shows very weak support for most of the nodes of the tree. The node placing *Coleicarpus* as sister taxon to all other solutes is well supported with a bootstrap proportion of 100 percent. High support was also recovered for the node placing *Castericystis* and *Minervacystis* as sister to more derived forms (85 percent) and *Iowacystis* as sister taxon to *Scalernocystis* (84 percent). Very weak support was found for *Myeinocystites* as sister to *Belemnocystites* (56 percent), the clade including *Syringocrinus*, *Myeinocystites*, *Belemnocystites*, *Iowacystis* and *Scalenocystites* (47 percent) and *Maennilia* as sister to *Heckerocystis* (41 percent). No other node was recovered in more than 40 percent of pseudoreplaicate matricies.

The low bootstrap support for the analysis shows considerable noise in the matrix. Many character states of *Maennilia* are found to be convergent with other taxa whereas the only synapomorphous character found to unite *Maennilia* and *Heckericystis* is the presence of multimerous rings in the proxistele.

SYSTEMATIC PALEONTOLOGY

Class HOMOIOSTELEA Gill and Caster, 1960
Order SOLUTA JAEKEL, 1901
Family MANNILIIDAE Rozhnov and Jefferies 1996

Discussion.—Rozhnov and Jefferies, 1996 included the genera *Maennilia* and *Heckericystis* in the original family grouping. We place *Heckericystis* in the Dendrocystitidae Bassler, 1938 where it was originally placed by Caster, 1968. The principal character that defines the Manniliidae is the presence of a narrow band of fused marginal plates that is differentiated from the tessellated somatic plates that make up both upper and lower surfaces, and the large blunt aboral lobe at the anterior end of the animal. *Heckericystis* lacks these features and is otherwise clearly closely related to the dendrocystitids.

Genus MAENNILIA Rozhnov and Jefferies, 1996

Type species.—*Maennilia estonica* Rozhnov and Jefferies, 1996.

Diagnosis.—*Maennilia* is monospecific therefore generic diagnosis is redundant with species diagnosis.

MAENNILIA ESTONICA Rozhnov and Jefferies, 1996
Figures 1, 3.1–3.11, 4

Diagnosis.—Dendrocystitid with flattened biconvex tessellated theca with weak but distinct marginal frame that does not extend significantly onto either surface; aboral lobe prominent; ambulacral structure long, freestanding, biserial ambulacral series with small sleeve plates between it and the oral frame, with well-defined tunnel piercing ambulacrals and opening directly into body cavity; tall arching cover plates over shallow food groove; proxistele composed of polyplated rings, short sharply tapering mesistele, and dististele composed of alternating pentagonal to rectangular plates.

Description.—Theca essentially bilaterally symmetrical; symmetry primarily disrupted by broadly rounded aboral lobe, protuberant at (distal) anterior right side of theca (Fig. 3.3–3.5); anal (left proximal) lobe of theca inflated and broadly rounded at proximal angle; adanal (right proximal) lobe less inflated and proximal angle rather acute (Fig. 3.3); erect ambulacrum extends from upper margin of theca at bottom of U-shaped, forward facing reentrant of marginal plates located on left thecal margin about one-third the distance posteriorly from anterior end of theca (Fig. 3.1); proxistele fits into a shallow embayment of slightly enlarged marginals (adsteleals) located approximately mid-width along proximal margin (Fig. 3.2, 3.3, 3.11); in contrast to most solutans no clearly differentiated marginal plate pattern in adstelial embayment evident (Fig. 3.2, 3.11); in cross-section theca slightly biconvex, especially adjacent to union with proxistele; narrow band of tightly sutured plates form marginal band around entire theca; marginal band in cross-section forms folded structure composed of two to four irregularly shaped plates that produce rounded rim; no extension of marginals across either dorsal or ventral surfaces exists; tight suturing of marginal platelets appears more robust

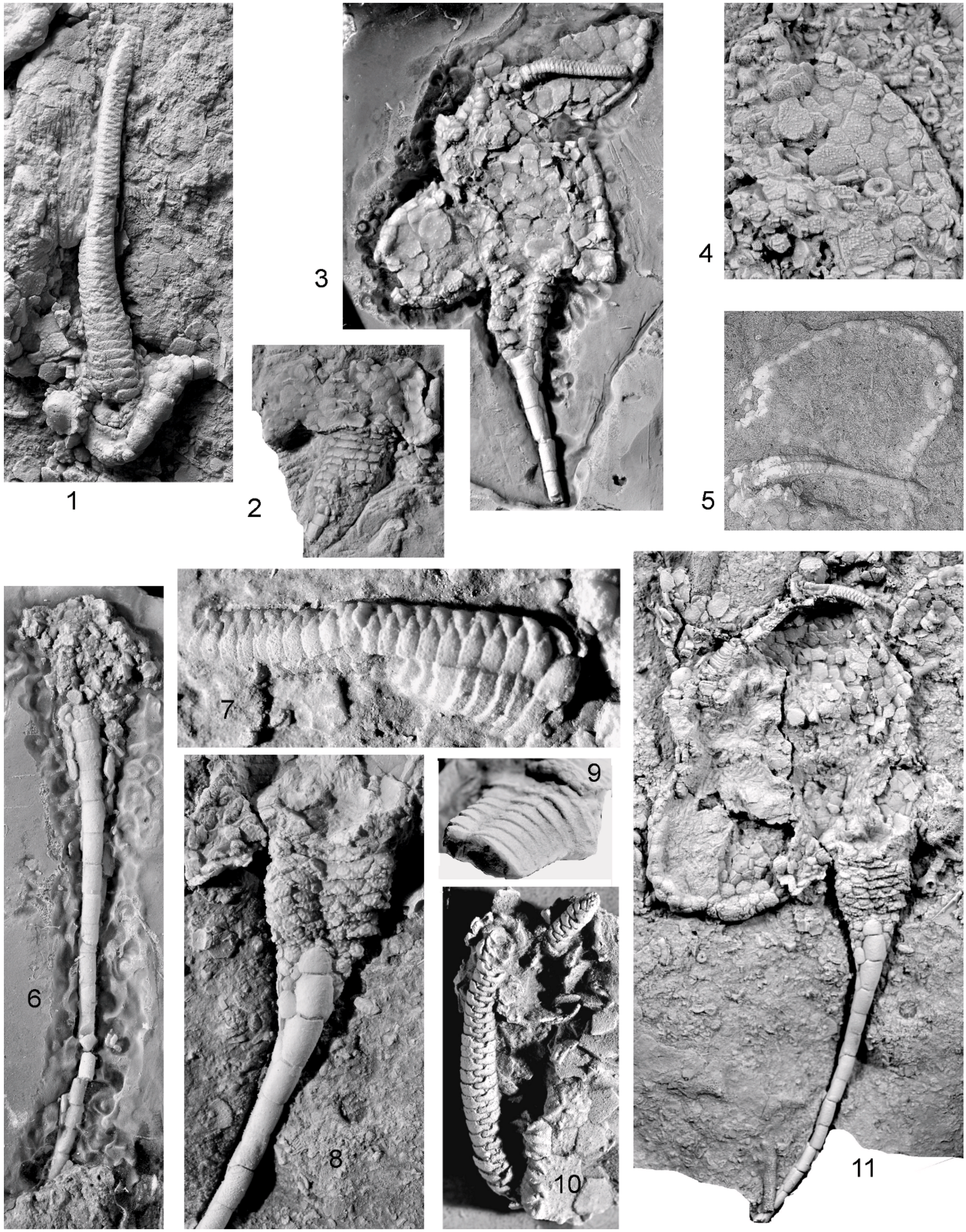

FIGURE 3—Specimens of *Maennilia estonica* Rozhnov and Jefferies 1996. All specimens are from the Upper Ordovician Vazalemma Formation in a working quarry near Vazalemma, Estonia. All specimens are whitened with a heated sublimate of NH_4Cl. Specimens are in the collections of the Paleontological Museum, Russian Academy of Science, Moscow (PIN) or the Institute of Geology, Talinn University of Technology, Estonia (GIT). *1,*

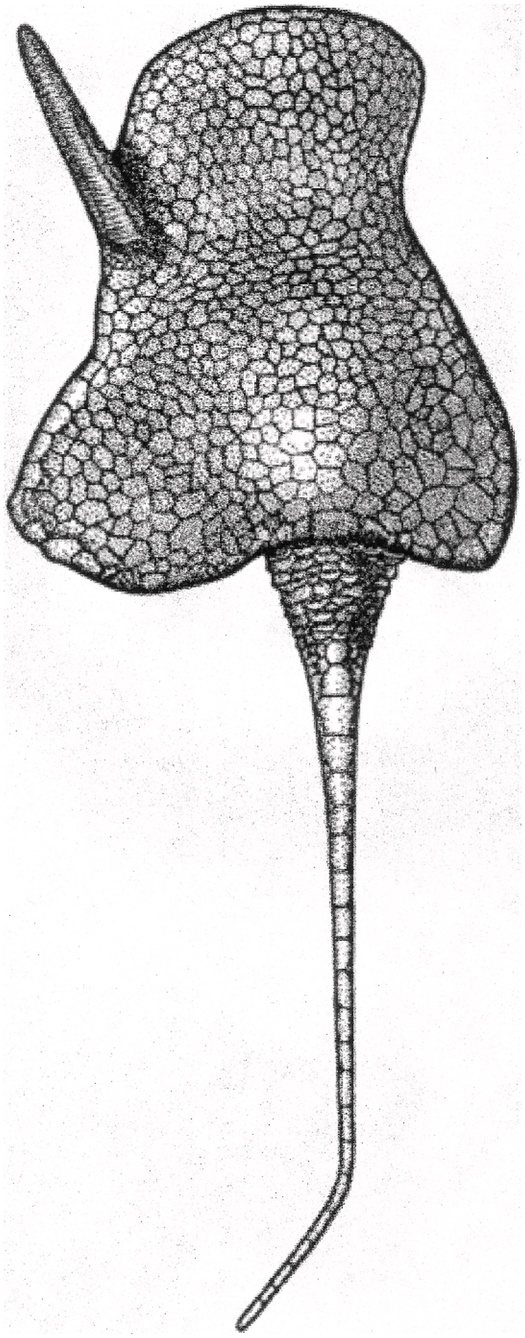

FIGURE *4*—Reconstruction of the dorsal surface of *Maennilia estonica.*

on left side of theca than right and especially in U-shaped reentrant area into which feeding structure is inserted (Fig. 3.1, 3.3, 3.11); both surfaces covered with polygonal tessellated platelets with pustulose ornament (Fig. 3.4, 3.11); more mature marginal and somatic plates develop radiating ridges that extend from near plate center to plate angles; dorsal platelets in anal lobe near proximal angle appear to be tightly sutured and form near smooth surface (Fig. 3.2, 3.3).

Peristomial opening at bottom of U-shaped reentrant of marginals, circular, in alignment with large lumen in exothecal floor plates of erect ambulacrum; food groove on top surface of floor plates; cover plates tall, evenly paired with ambulacrals forming arched vault over food groove (Fig. 3.7, 3.9), distal ends pointed forming zigzag (zipper-like) perradial suture (Fig. 3.10); floor plates and cover plates separated from theca by narrow sleeve of three or four circlets of small platelets apparently embedded in folds of dense tissue; anal area poorly preserved in all specimens, adjacent to proximal angle on ventral face, appears to be composed of a flattened "sugar-loaf" plate surrounded by circlet of sub rectangular anal valve plates (Fig. 3.11); hydropore opening located on inflated large madreporeite-like plate on lateral margin close to the oral opening; opening appears as several small circular intake pores on top of pustular-shaped plate; stele as described in Rozhnov and Jefferies, 1996 (Fig. 3.8).

Discussion.—Maennilia has the simplest and most primitive pattern of solutan marginal plates. Simple enlargement and tight suturing produces a narrow rim. The construction of this margin is morphologically dissimilar to those found in Middle and Upper Ordovician genera from Laurentia. In those Laurentian genera, marginal plates extend well onto the lower surface and less so on the upper. In contrast, marginal development *Maennilia* is restricted to a narrow marginal band of fused small platelets that does not extend over either surface.

Degree of fusion in marginal plate suturing and robustness also varies in *Maennilia.* The anterior side, right lateral side and abanal lobe marginals appear to grade directly into the somatics with little differentiation. However, the left margin, especially in the re-entrant enclosing the base of the erect ambulacrum, and along the anal lobe, the marginals appear to be thicker, probably stood a little taller above the somatics, and are more rigidly sutured. This differentiation is clearly manifest in preservation. There is a clear majority of fragments from the left side of the theca especially along the base of the erect ambulacrum and most of the anal lobe.

Maennilia is unusually large for a solute. The holotype (Fig. 3.11) has a thecal length of 60 mm when measured from anal lobe to anterior end of the theca. With the addition of the stele gives a total length of approximately 120 mm. Most specimens in the study collection are large and mature and there are virtually no remains of juvenile individuals. This suggests that size sorting took place in the deposition processes. The lack of distortion in the somatic plates suggests that the animal was rather thin in life. The thin somatic plates that form flexible central pavements along with the lack of marginal rigidity in these large animals lead to post mortem fragmentation. Ambulacra and steles are the exception and tend to preserve relatively intact.

Like most solutes, *Maennilia* has a large hydropore structure suggesting the presence of a large internal hydrocoel contained totally within the theca. In addition, for possible

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nearly complete specimen, holotype, PIN4125/1, ×1; *2,* nearly complete erect ambulacrum in marginal plates embayment, PIN4125/1, ×2; *3*, nearly complete specimen, anal and adoral lobes distorted somewhat by rotation, PIN4125/48, ×2; *4,* part of aboral lobe, pustulose ornament is well developed, PIN4125/26, ×2; *5,* aboral lobe with marginals well defined, GIT 609-1-1, ×2; *6*, nearly complete distal stele, PIN/47, ×3.3; *7,* expanded proximal ovoid part of the erect ambulacrum that tapers to the distal circular portion, zigzag dorsal contact of cover plates well developed, PIN4125/44, ×5.5, *8,* detail of proximal, mesi and proximal part of dististele, holotype, PIN 4125/1, ×2; *9,* proximal part of proximal ovoid erect ambulacrum, oval internal lumen visible in fractured end, PIN 4125/35, ×4.5; *10,* dorsal view of distal erect ambulacrum, zigzag pattern of closed cover plates and distal end well developed, PIN4125/21, ×5; *11*, nearly complete but distorted specimen, holotype, PIN 4125/1, ×1.

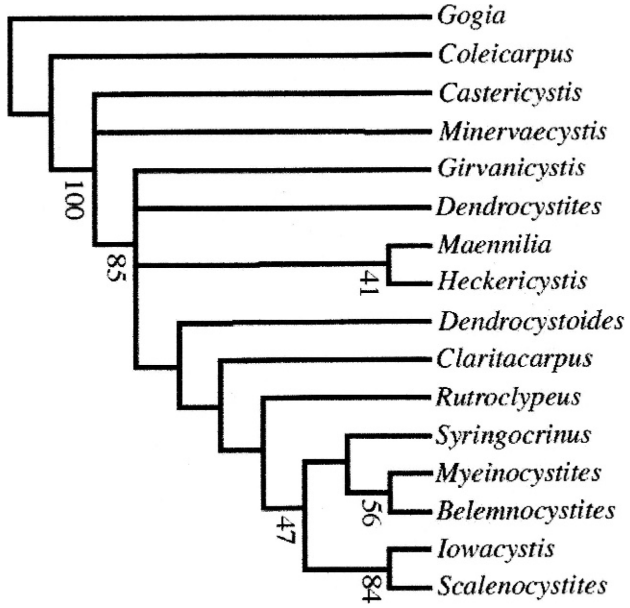

Figure 5—Revised cladogram of the Class Homoiostelea.

bolstering turgor to the erect ambulacrum, the internal body cavity may have added turgor to the tessellated somatic surfaces, which, bordered by a semi-rigid marginal plate frame, may have imparted a drum-head-like aspect to them.

ACKNOWLEDGMENTS

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APPENDIX *1*—Revised character matrix for the Homoiostelea, based on and modified from character set in Parsley (1997, p. 235, 241) and Parsley and Sumrall (2007, p. 1493).

	Characters																	
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Gogia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleicarpus	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Castericystis	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
Minervaecystis	1	1	2	0	0	1	0	0	2	1	1	1	1	0	1	0	0	0
Dendrocystites	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	1	0	1
Maennilia	1	1	2	1	1	1	1	1	1	2	1	2	1	1	0	0	1	1
Heckericystis	1	1	2	1	1	?	1	0	1	1	1	1	1	0	0	0	0	0
Dendrocystoides	1	1	2	1	1	1	1	0	2	1	1	1	1	1	0	1	0	1
Girvanicystis	1	1	1	1	1	2	1	0	2	3	1	3	1	0	0	0	1	0
Rutroclypeus	1	1	1	0	0	1	2	0	2	3	1	3	1	1	0	1	?	1
Syringocrinus	1	1	1	0	1	1	3	1	2	2	1	2	1	1	1	1	0	0
Iowacystis	1	1	1	0	1	1	3	1	2	2	1	2	1	1	0	0	1	1
Myeinocystites	1	1	1	0	1	1	3	2	2	?	1	?	1	1	0	1	0	0
Belemnocystites	1	1	1	0	1	1	3	2	2	?	1	?	1	1	0	1	0	0
Scalenocystites	1	1	1	0	1	1	3	1	2	2	1	2	1	1	0	0	1	1
Claritacarpus	1	1	2	1	1	?	?	?	2	2	1	2	?	1	0	1	0	?