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[Because the statements published in the paper in the American Geologist, April-December, 1890, clearly indicate publication subsequent to 1889 (MILLER's *North American Geology* and *Paleontology* containing provisional outline of families, p. 214-215), definitive first publication is evidently that in the American Geologist, p. 275-286, 340-357.

MILLER's paper in the Indiana 16th annual Report, p. 302-326, is identical with paper in the American Geologist and patently printed subsequent to December, 1890. This part of the Indiana 16th Report indicated as 1889 should be indicated as actually 1891. Pages noted in margin of the Indiana version are those of the American Geologist reference, which are taken to have precedence as definitive first references. —R. C. MOORE.]

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ADDENDUM TO SUBPHYLUM HOMALOZOA

CTENOCYSTOIDS

By James Sprinkle and R. A. Robison
[University of Texas at Austin and University of Kansas]

The following account of the Class Ctenocystoidea (Robison & Sprinkle, 1969) supplements coverage of the subphylum Homalozoa in *Treatise* Part S (1967).

Class CTENOCYSTOIDEA Robison & Sprinkle, 1969

[Ctenocystoidea Robison & Sprinkle, 1969, p. 1512]

Small, flattened echinoderms bearing a double-layered marginal frame surrounding two flexibly plated central areas; ovoid theca shows near perfect bilateral symmetry with mouth and anus at opposite body poles; no aulacophore, stele, or arm appendages present; seven marginal plates in each layer of frame alternate across knife-edge contact; dorsal centrals tiny and polygonal, ventral centrals tiny oval- or spear-shaped plates in aligned rows; grill-like array of 18 to 20 blade-shaped ctenoid plates attached to dorsal anterior of theca and apparently covering central mouth and two lateral food grooves; anal pyramid between layers of marginal frame at rear of theca. *M.Cam. (Glossopleura Assemblage-zone).*

Ctenocystoids are now known to occur in the Spence Tongue of the Lead Bell Shale at eight localities in northern Utah and southeastern Idaho. Nearly 1,000 specimens of the single described genus and species have been found at these localities in association with several trilobite genera of the *Glossopleura* Assemblage-zone, the eocrinoids *Gogia granulosa, G. palmeri, G.* n. sp., an undescribed stylophoran, inarticulate brachiopods, hyolithids, sponges, and rare annelids. Some beds in the Spence Tongue are packed with complete ctenocystoids jumbled together in all orientations; one example of this type of preservation is shown in Figure 617. Disarticulated ctenocystoid plates are also found in some beds, but complete specimens are usually more common.

Because of their flattened thecal shape, differentiation into marginal frame and enclosed central areas, and lack of radial symmetry, ctenocystoids belong in the echinoderm subphylum Homalozoa ("carpoids"). However, they differ from the other three homalozoan classes in several important respects. They are the only group that completely lacks appendages such as aulacophore, stele, or arms. Ctenocystoids are smaller, more bilaterally symmetrical, and better streamlined than other homalozoans, probably implying a more active mode of life. Other differences include the double-layered marginal frame and the grill-like array of ctenoid plates along the anterior thecal margin.

Ubaghs (1971) has suggested that ctenocystoids are most closely related to members of the homalozoan class Stylophora. Ctenocystoids and cornute stylophorans like *Phyllocystis* (U.Cam.-L.Ord.) both have well-developed bilateral symmetry, mouth and anus at opposite body poles, a marginal frame strongly differentiated from two tiny-plated central areas, and no tail-like peduncular appendage. However, ctenocystoids lack the typical stylophoran aulacophore appendage attached to the anterior end of the theca over the mouth, and instead have a grill-like array of ctenoid plates covering two lateral ambulacra along the anterior margin. If this inferred relationship between ctenocystoids and stylophorans is correct, then the marginal ctenoid grill may be homologous to all or part of the erect stylophoran aulacophore, even though these structures differ greatly in appearance and in their method of food gathering. It is interesting to note that ctenocystoids occur in the Spence Tongue

FIG. 617. Latex cast of bedding surface with several representative specimens of *Ctenocystis utahensis* ROBISON & SPRINKLE. Material from the Spence Tongue, Lead Bell Shale (lower Middle Cambrian, *Glossopleura* Assemblage-zone), Utah, ×3.5 (Sprinkle & Robison, n, USNM 163253).

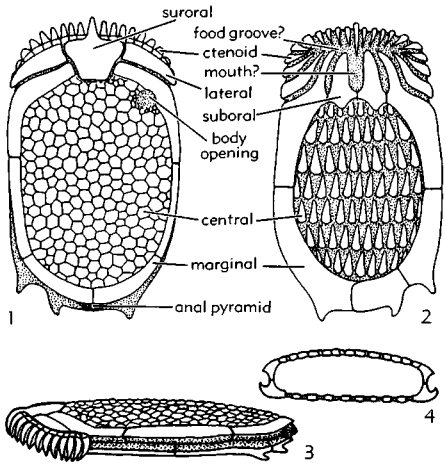

FIG. 618. Morphological features of Ctenocystoidea, based on *Ctenocystis utahensis* ROBISON & SPRINKLE, Middle Cambrian, Utah.——*1-4*, dorsal, ventral, side, and cross-sectional views of reconstructed specimen, ×5 (*1,2*, after Robison & Sprinkle, 1969, by permission of R. A. Robison and James Sprinkle, and *Science*, v. 166, p. 1512-1514, 19 December, 1969, copyright 1969 by American Association for the Advancement of Science; *3,4*, Sprinkle & Robison, n).

with a rare cornute stylophoran similar to *Phyllocystis*; these two forms now are among the earliest known homalozoans in the fossil record (early Middle Cambrian).

Although an average ctenocystoid is only about 6 mm. long and 4 mm. wide, at least 210 plates are present in four major body regions: the marginal frame, the anterior food-gathering ctenoid grill, and the two central areas. The marginal frame is composed of 14 medium-sized, mostly elongate, curved plates. These **marginals** are arranged in two series of seven plates each on the dorsal (superior) and ventral (inferior) surfaces, joined together along a knife-edge hinge line (see Fig. 618,*3,4*) that extends around the lateral and posterior margins of the theca. The anterior-most plate on the dorsal side, called the **suroral,** has a distinctive trapezoidal shape and a large central tooth-like process (Fig. 619, *1a,c,e*), resembling the other ctenoids on this margin. This suroral process fits into a groove between two symmetrically arranged small frame plates, called **suborals,** on the ventral surface (Fig. 619,*1a*). The mouth was probably located at the center of the anterior margin below the suroral and just above and between the two suborals.

The anterior margin of the theca bears a grill-like array of 18 to 20 **ctenoid plates** articulated either with the suroral, with two wedge-shaped plates called **laterals** lying beside it, or with the edges of the two other anterior supermarginals (Fig. 619,*1c*). These ctenoid plates intermesh ventrally with two suborals or projections from the two anterior infermarginals (Fig. 619,*1a*). Each ctenoid is a curved, tooth- or blade-shaped plate ranging from 0.5 to 1.2 mm. long, increasing in size from the center of the anterior margin beneath the suroral toward both sides. New ctenoid plates may have been added beneath the suroral, because one well-preserved specimen (Fig. 619,*1a*) shows a tiny plate inserted here. If true, the number of ctenoids probably increased during thecal growth to an observed maximum of 20.

Several specimens have the ctenoid plates slightly open, revealing two shallow grooves running along the anterior margin (Fig. 619,*1d*). These probably represent short ambulacral food grooves leading to the central mouth. The larger lateral ctenoids close off the ends of these grooves from the rest of the thecal margin, which also bears a shallow groove but without any kind of cover plates (Fig. 618,*3*).

Within the marginal frame on the dorsal and ventral thecal surface are central areas covered with flexible membranes bearing tiny plates **(centrals).** The dorsal central area is slightly domed and somewhat larger than the nearly flat ventral one (see Fig. 618,*1,2,4*), probably because the ventral marginals are wider and flat. The dorsal central areas contains approximately 100 to 110 tiny polygonal centrals (Fig. 619,*1c*), whereas the ventral area contains 50 to 60 tiny elongate oval or spear-shaped centrals that do not appear to be tightly sutured, but partially arranged in rows (Fig. 619,*1f*). The ventral centrals appear to be about twice as large as the dorsal centrals (0.5-0.6 mm. long vs. 0.2-0.3 mm. long and wide).

Two of the posterior infermarginals apparently overlap along a slanting suture (Fig. 619,*1d*) instead of directly abutting.

This probably allowed the **anal pyramid,** which is a small cone-shaped structure with about 15 tiny plates located here in an elliptical area between the frame layers (Fig. 619,*1b*), to protrude for venting or pumping. At least two posterior infermarginals have short spines extending back from the theca (Fig. 619,*1c*).

A small groove or sulcus extends down the inner surface of the right anterior supermarginal (Fig. 619,*1e*), perhaps representing another body opening, such as a hydropore or gonopore.

Ctenocystoids show a high degree of bilateral symmetry, deviating from this primarily in the slightly off-center arrangement of the posterior infermarginals and their spines (Fig. 618,*2*). This strongly developed symmetry along with their small size, streamlined airfoil shape, and mouth and anus at opposite body poles all point to an active mobile (probably swimming) mode of life. Using their flexible central areas and hinged marginals in a bellows-like manner, ctenocystoids could have drawn sea water into a cloaca-like structure just inside the posterior anal pyramid, extended the pyramid, and jetted this water back out, propelling the animal forward for a short distance along or above the sea bottom. The elongate ventral centrals and the posterior infermarginal spines would have prevented lateral drift of the animal during movements of this type. Ubaghs (1968) has proposed a similar type of movement for stylophorans but ctenocystoids were probably more mobile because of their smaller size, better symmetry, and lack of appendages.

The feeding apparatus of ctenocystoids does not seem to be comparable to food-gathering structures found in any other homalozoan class. The ctenoid plates may possibly represent greatly modified ambulacral cover plates that have become reduced to only one series of enlarged, blade-shaped plates articulated dorsally. The arrangement and articulation of ctenoid (and lateral) plates suggest that they were probably used for digging or sifting through fine-particulate material, implying that ctenocystoids were most likely detritus-feeders living on the surface or in the top few mm. of sediment. Mucus secretion,

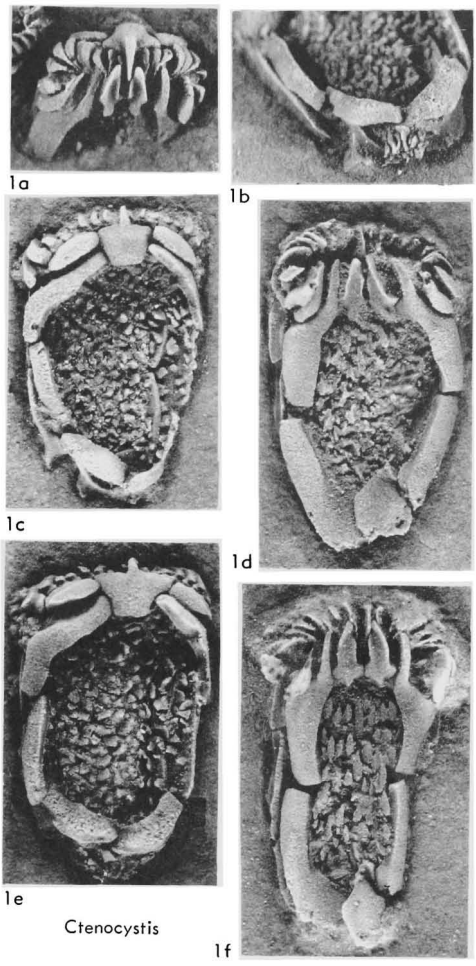

Fig. 619. Ctenocystidae (photos by courtesy of R. A. Robison and James Sprinkle, from *Science,* v. 166, p. 1512-1514, 19 December, 1969, copyright 1969 by American Association for the Advancement of Science) (p. *T*1001).

ciliary currents, or both would have aided in collecting microscopic food particles from the fine detrital sediment and transporting them to the central mouth. No evidence for ambulacral tube feet has been observed.

Family CTENOCYSTIDAE
Sprinkle & Robison, new family

Characters of class. *M.Cam.(Glossopleura Assemblage-zone).*

Ctenocystis Robison & Sprinkle, 1969, p. 1513 [**C. utahensis*; OD]. Theca small, flattened, ovoid, nearly bilaterally symmetrical; marginal

frame double-layered, each layer consisting of seven plates that alternate across a hinge line; central areas flexibly plated with tiny polygonal plates dorsally and rows of tiny oval or spear-shaped plates ventrally; anterior grill of blade-shaped ctenoid plates apparently covers central mouth and two lateral food grooves; anal pyramid between marginal layers at opposite thecal pole; posterior infermarginals bear short spines; third opening present on edge of right anterior supermarginal. *M.Cam.(Glossopleura Assemblage-zone)*, USA(Utah-Idaho).——FIG. 619,*1*. *C. utahensis*, Utah; *1a*, ant. view showing well-preserved ctenoid series, ×6; *1b*, post. view with anal pyramid between marginal layers, ×6; *1c,e*, dorsal views of two specimens (*1c* is holotype); note shape of suroral and posterior spines, ×6; *1d,f*, ventral views showing suborals and spear-shaped centrals, ×6 (from Robison & Sprinkle, 1969; courtesy R. A. Robison and James Sprinkle, and *Science*, v. 166, p. 1512-1514, 19 December, 1969, copyright 1969 by American Association for the Advancement of Science).

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