Ctenocystoidea: New Class of Primitive Echinoderms

Abstract. *The oldest known "carpoids" of the echinoderm subphylum Homalozoa have been discovered in lower Middle Cambrian rocks of northern Utah. They were free-living benthonic animals characterized by a unique ctenoid feeding apparatus and flattened flexible theca with near bilateral symmetry. A new class, Ctenocystoidea, is proposed to include the new genus and new species,* Ctenocystis utahensis.

Several hundred tiny specimens of a single species of unusual free-living echinoderm have been discovered in the Spence Shale of northern Utah. They are known from three localities (*1*) in the Wasatch Mountains where they are associated with an abundant assemblage of early Middle Cambrian fossils (*2*). The specimens have a flattened, ovoid, flexible theca with double-layered marginal frame, near bilateral symmetry, peculiar ctenoid feeding apparatus, and mouth and anus at opposite body poles (Figs. 1 and 2). Lack of radial symmetry and presence of a marginal frame indicate a relation with "carpoids" of the subphylum Homalozoa (*3*). They differ from members of known homalozoan classes, however, by having better symmetry, a distinctly different feeding apparatus, and a double- rather than single-layered frame.

The echinoderms were prepared for study by dissolving calcareous skeletal plates from a hard noncalcareous matrix with hydrochloric acid. The resulting artificial molds were then cast with latex rubber to obtain detailed replicas of the original exterior morphology (Fig. 1).

Basic morphology of the new echinoderm is sufficiently different to warrant erection of a new class, which here is named Ctenocystoidea. Its concept is based on one known genus, *Ctenocystis*, from which it takes its name. The new class is diagnosed as follows:

Mobile benthonic Homalozoa with flattened, ovoid, near bilaterally symmetrical skeleton composed of theca and anterior ctenoid feeding apparatus. Brachial (aulacophore) and peduncular (stele) appendages are absent. Theca bounded by double-layered overlapping frame of larger marginal plates that encloses flexible upper and lower surfaces composed of distinctly smaller plates. Ctenoid apparatus partly encloses a central mouth and two lateral food grooves. Mouth and anus at opposite body poles.

Three "carpoid" classes, Stylophora, Homoiostelea, and Homostelea, previously have been assigned to the sub-

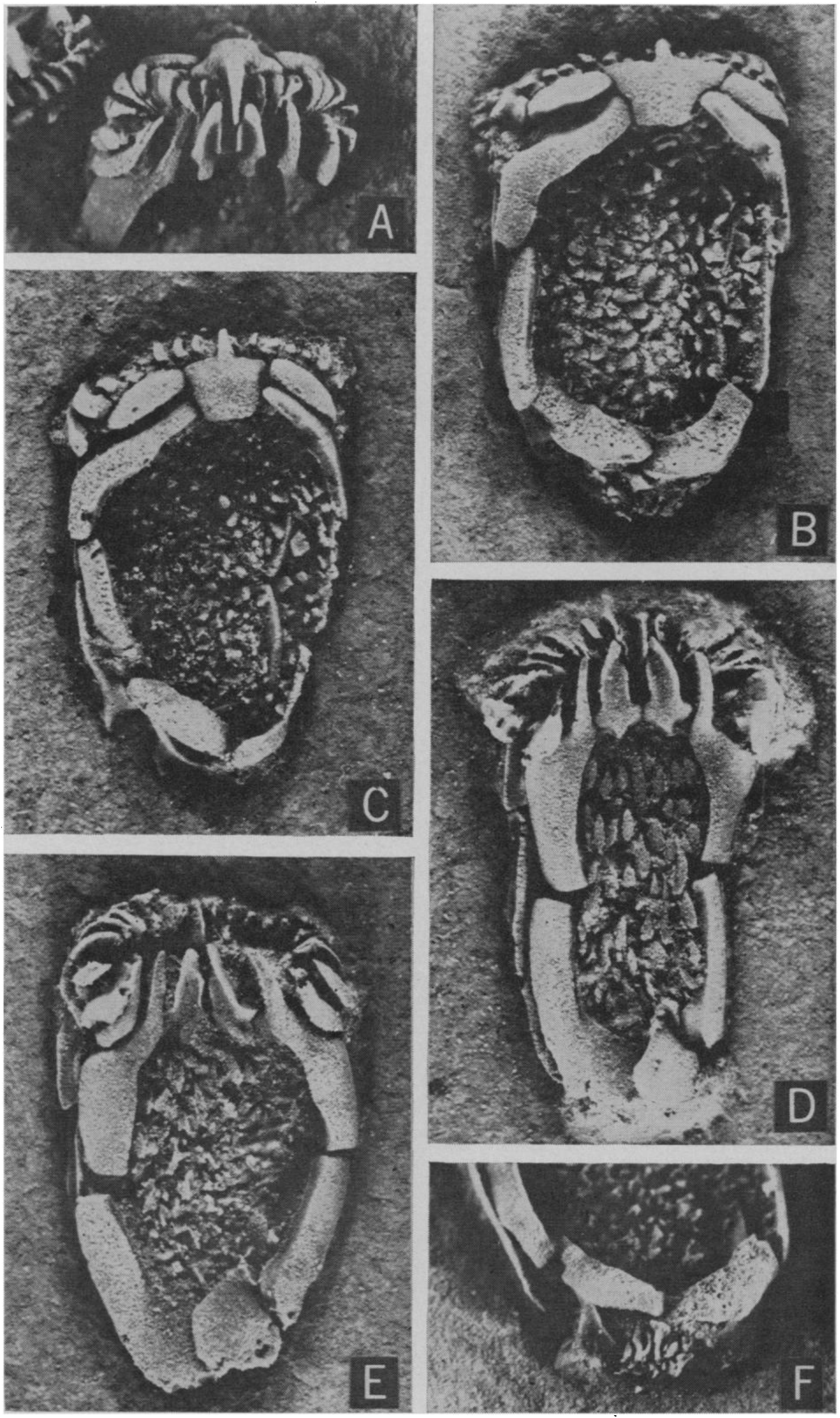

Fig. 1. *Ctenocystis utahensis*, new genus and new species. (A) Anterior view of ctenoid feeding apparatus (USNM 163253) (× 10). (B) Superior surface of holotype (USNM 163252); note sulcus on right anterolateral marginal (× 10). (C) Superior surface of paratype (USNM 163254) (× 10). (D) Inferior surface of constricted paratype (USNM 163255) showing elongate central plates (× 10). (E) Inferior surface with indication of anterior submarginal food grooves (USNM 163256) (× 10). (F) Posterior view of specimen with anal pyramid extended (USNM 163257) (× 10). All species are latex casts.

phylum Homalozoa. Major similarities and differences between the new class Ctenocystoidea and those three classes are summarized in Table 1.

Morphology of ctenocystoids (Fig. 2) gives clues concerning their mode of life. Absence of a peduncular organ, near bilateral symmetry, a horizontally flattened skeleton, and an oral opening on the anteroventral midline all are characteristics of mobile benthonic organisms.

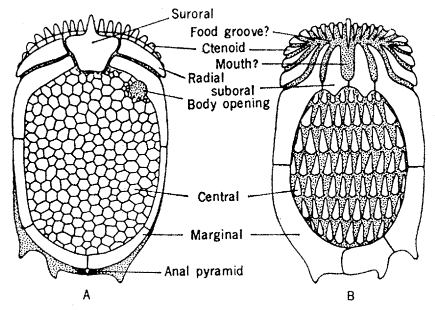

Fig. 2. Reconstruction and morphology of *Ctenocystis utahensis*, new genus and new species. (A) Superior surface. (B) Inferior surface.

Locomotion may have been achieved by periodic rapid expulsion of water from the anal pyramid. Rhythmical expansion and contraction of the flexibly plated superior and inferior body walls, hinged along thin sutures between superior and inferior marginals, would produce a bellows-like pumping action. Overlapping expansible infermarginals beneath the anal pyramid (Fig. 1, D and E) suggest a flexible periproct capable of being protruded when water was jetted. The problem of gyration induced by forcible expulsion of water appears partly to have been remedied by anterior-posterior elongation of the inferior centralia (Fig. 1D), which would act as multiple keels to impede lateral drift of the body. Three posteriorly directed spines on infermarginal plates in the anal region also would exert a stabilizing influence and impede lateral and posterior motion of the body. The concave inferior body surface may have functioned like an airfoil to enable the animal to glide on a cushion of water just above the sea floor.

The method of locomotion suggested here is somewhat similar to that postulated by Ubaghs (*4*) for stylophorans. More obvious streamlining and better bilateral symmetry exhibited by ctenocystoids, however, indicate that they were more mobile than stylophorans.

The feeding apparatus possessed by ctenocystoids is unique among known echinoderms and probably was used for detritus or filter feeding. It apparently involved a series of 18 movable ctenoid plates, two elongate lateral plates, and at least parts of one superior and four inferior marginal plates. Preservation of some specimens (Fig. 1E) suggests that two lateral submarginal food grooves could be opened between some of the ctenoid and adjacent infermarginal plates. The grill-like array of ctenoid plates (Fig. 1A) most likely was used for digging, sifting, or filtering out small food particles, perhaps aided by mucus secretion or ciliary currents, or both.

Ceratocystis perneri Jaekel, a stylophoran from the late Middle Cambrian of Czechoslovakia (*5*), is the oldest previously known homalozoan. The ctenocystoid described here, and an associated undescribed stylophoran, extend the known stratigraphic range of Homalozoa back to the early Middle Cambrian. This early association of a ctenocystoid and a stylophoran, both of which appear relatively specialized and quite distinct, indicates considerable prior evolution. Therefore, the search for ancestral homalozoans should be extended to include rocks at least as old as Early Cambrian.

Ctenocystis, new genus

Type: Ctenocystis utahensis Robison and Sprinkle, new species.

Diagnosis: Small flattened echinoderms; observed length ranges from 3 to 9 mm, and averages about 6 mm; observed width ranges from 2 to 6 mm, and averages about 4 mm. Each layer (superior and inferior) of marginal frame composed of seven plates (marginals) that overlap with

Table 1. Comparison of major characteristics of homalozoan classes.

Character	Stylophora	Homoiostelea	Homostelea	Ctenocystoidea, new class
Degree of asymmetry	Strong to moderate	Strong to moderate	Moderate	Slight
Thecal outline	Much variation	Much variation	Circular, oval, pyriform, and triangular	Oval
Feeding apparatus	One aulacophore differentiated into three regions with single ambulacrum protected by cover plates	One tetramerous and undifferentiated arm with ambulacrum and cover plates	Two epithecal marginal grooves with cover plates	Eighteen movable ctenoid, two lateral, and five modified marginal plates
Stele or peduncle	Absent	Present	Present	Absent
Marginal frame	One layer with 10 to 12 plates	Usually not differentiated; plates irregular in number	One layer with 10 to 12 plates	Two layers with seven plates in each layer
Centralia	Usually distinctly differentiated from marginal frame	Usually not differentiated from marginal frame	Distinctly differentiated from marginal frame	Distinctly differentiated from marginal frame
Mouth	Intrathecal at or near proximal end of aulacophore	Intrathecal, probably near proximal end of arm	Small orifice on right anterolateral margin	On medial inferior surface near anterior margin
Anus	On superior surface at opposite (posterior) pole from mouth	Commonly near left posterolateral margin	On superior surface near anterior midline; covered by large operculum	Between layers of marginal frame near posterior midline
Alimentary tract	Probably untwisted	Probably untwisted	Twisted	Probably untwisted

plates of opposing layer. Short blunt spine projects backward from each of three posterior-most infermarginals. Mouth probably located above and between anterior processes of anterocentral infermarginals (suborals). Feeding apparatus includes grill-like series of movable (ctenoid) plates that surround anterior thecal margin. Vertical blade-like process on lower side of anterocentral supermarginal (suroral) separates two lateral series of nine ctenoids. Upper part of each ctenoid articulates either with suroral or one of two thin, flat, narrow (lateral) plates that extend outward from suroral across superior surface. Anal pyramid composed of elongate, radially arranged, small plates located between layers of marginal frame near posterior midline. Apparent overlapping of infermarginals beneath anal pyramid probably allowed thecal expansion. Inner surface of right anterolateral supermarginal has prominent sulcus that may have partly enclosed a hydropore or other body opening. Plates of superior and inferior central surfaces (centralia) flexibly arranged and distinctly smaller in size than marginals. Superior centralia cover slightly larger area than inferior centralia, and are composed of tiny polygonal plates. Inferior centralia are roughly aligned elongate plates of slightly larger size than superior centralia.

Etymology: From Greek *ktenos*, a comb, and *kystis*, a sac.

Ctenocystis utahensis, new species

Holotype: (Fig. 1B) USNM 163252 (*6*).

Description: Because *Ctenocystis* is monotypic at present, characteristics of the species are the same as those given in the generic diagnosis. The species is named for the state of Utah where it was discovered.

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2. Some taxa have been described by C. D. Walcott, *U.S. Geol. Surv. Monogr. 51* (1912); *Smithsonian Inst. Misc. Collect* **64**, No. 5, 303 (1916); C. E. Resser, *ibid.* **97**, No. 12, 1 (193 → R. A. Robison, *J. Paleontol.* **39**, 355 (196 → *ibid.* **43**, 1169 (1969).
3. G. Ubaghs, in *Treatise on Invertebrate Paleontology, Echinodermata*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1967), part S, vol. 1, p. 51.
4. ———, in *ibid.*, p. 540.
5. ———, *Univ. Kans. Paleontol. Contrib. Pap. 22*, 1 (1967).
6. Holotype and illustrated paratypes are deposited with paleontological collections of U. S. National Museum (catalog Nos. USNM 163252–163257). Remainder of specimens are deposited with paleontological collections of Department of Geological and Geophysical Sciences, University of Utah (UU 100-102), and Museum of Comparative Zoology, Harvard University (MCZ 605).
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Choroid Plexus and Cerebrospinal Fluid Production

Abstract. *Acute progressive hydrocephalus occurred in 76 rhesus monkeys undergoing ventricular obstruction 2 to 6 months after choroid plexectomy and was only slightly less pronounced than in 73 nonplexectomized animals with similar ventricular obstructions. The composition of cerebrospinal fluid after choroid plexectomy was essentially normal. Experiments with ventricular perfusion techniques indicate only a slight reduction in cerebrospinal fluid production after choroid plexectomy. Thus, the choroid plexus is probably not the sole or even the major source of cerebrospinal fluid within the primate ventricular system.*

Since the experiments of Dandy and Blackfan (*1, 2*) it has been generally accepted that cerebrospinal fluid is secreted or otherwise formed within the cerebral ventricles by the choroid plexuses. Recent reports tend to support this view (*3*), but there is enough conflicting data (*4, 5*) to justify a review. Among the facts most difficult to reconcile with this theory is that, in the treatment of hydrocephalus, removal of the choroid plexus (choroid plexectomy) is rarely curative and is far less effective than might be anticipated.

In this report the consequences of ventricular obstruction in normal and choroid-plexectomized rhesus monkeys are examined, and composition and rates of production of cerebrospinal fluid in these two groups are reported. Because the validity of any study of the choroid plexus depends on the refinement of the experimental model, the technique of choroid plexectomy that was used is described.

The choroid plexus was removed from either one or both lateral ventricles of 76 rhesus monkeys through a small occipital burr hole. The ventricles were entered through a 0.5-cm cortical incision (Fig. 1A) with fine surgical instruments. After the ventricle was entered at the level of the trigone, the plexus was grasped with forceps just in front of the glomus and was stripped back gradually from the foramen of Monro. Similarly, the choroid plexus of the temporal horn was gently stripped back toward the glomus, where the entire structure was carefully removed in one piece (Fig. 1B). Retractors or other instruments were not used within the ventricular cavity, and bleeding was controlled with frequent saline irrigations rather than by electrocauterization or other hemostatic devices. Nevertheless, many failures occurred, and it was necessary to exclude a number of cases. In some instances, although it was believed that complete plexectomy had been performed, subsequent study revealed excessive scar formation in the operative area, unsatisfactory healing of the cortical incision, or residual tags of choroid plexus. Eventually, 35 animals with unilateral plexectomies and 41 animals with bilateral plexectomies were accumulated in which the operation was accomplished with what was believed to be a minimum of surgical trauma.

After choroid plexectomy, the animals were returned to their cages for 2 to 6 months. Thereafter, these animals and a group of normal rhesus monkeys were operated upon as follows. (i) In 6 unilaterally plexectomized animals, 35 bilaterally plexectomized animals, and 73 normal rhesus monkeys, the fourth ventricle was obstructed with an inflatable balloon (*6*). (ii) In ten cases of unilateral plexectomy and in six cases of bilateral plexectomy, the third ventricle (including both foramina of Monro) was obstructed by inserting cotton through a small opening in the corpus callosum. (iii) In 19 cases of unilateral plexectomy, the foramen of Monro on the same side was obstructed by simple scarification of the foraminal orifice (Fig. 1E). At selected intervals from 3 hours to 3 months after ventricular obstruction, the animals were killed and perfused with either glutaral-

Table 1. Cisternal cerebrospinal fluid. Data given in milligrams per 100 ml of cerebrospinal fluid.

Ion	Content in 14 normal animals	Content in 16 plexectomized animals
Na$^+$	158	156
K$^+$	2.8	2.7
Cl$^-$	132	129
Ca^{2+}	4.9	5.0
PO$_4^{2-}$	1.4	1.6
Mg^{2+}	3.5	3.8
Protein	18.1	18.2