IOWA GEOLOGICAL SURVEY IOWA CITY, IOWA

H. GARLAND HERSHEY, Director and State Geologist

REPORT OF INVESTIGATIONS 5

A New Upper Devonian Cystoid

Attached To A Discontinuity Surface

by

DONALD L. KOCH HARRELL L. STRIMPLE

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A NEW UPPER DEVONIAN CYSTOID ATTACHED TO A DISCONTINUITY SURFACE

by

DONALD L. KOCH and HARRELL L. STRIMPLE

ABSTRACT

Adocetocystis williamsi Strimple and Koch 1968, n. gen., n. sp., constitutes the third described genus of Callocystitidae bearing a double hydropore. Only Lipsanocystis Ehlers and Leighly and Strobilocystites White previously were known. Adocetocystis williamsi is further characterized by an ovate theca, four unbranched ambulacra which are apical over most of their length, and an apical mouth, double hydropore and gonopore. The relatively few brachioles of A. williamsi, in comparison with Lipsanocystis and Strobilocystites, are compensated for by their great length.

Adocetocystis williamsi is part of a biocoenose composed dominantly of echinoderms (cystoids and edrioasteroids) and corals (mostly Aulopora). The organisms of this community are attached to a prominent but laterally restricted discontinuity surface. Features which characterize the discontinuity surface are: (1) an irregular upper surface with rounded limestone knobs; (2) prominent borings (post-lithification); (3) a conspicuous zone of pyrite impregnation; and (4) pebbles of the same bore-marked limestone in channelways between the limestone knobs. The origin and form of the discontinuity surface might have been organically controlled but, more likely, the surface was produced by subaerial erosion.

It is supposed that Adocetocystis williamsi lived in an environment of shallow water with at least moderate current activity. The length of stem developed on any individual was dependent upon the position of attachment in relation to the shape and relief of a limestone knob. Strobilocystites calvini, a cystoid with short brachioles, is found in the same environment as Adocetocystis williamsi, which has long brachioles.

INTRODUCTION

Recent collecting in north-central Iowa has revealed a remarkably fine echinoderm fauna. The single collecting locality was discovered by Koch while conducting research on the stratigraphy of the Shell Rock Formation. The members of the formation in ascending order are, Mason City, Rock Grove and Nora (Belanski, 1927; fig. 1). The echinoderm zone occurs near

	Calvin 1897		Fenton & Fenton 1924		Belanski 1927, 1928			Stainbrook 1935			IGS Present report 1968				
			Owen	UPPER	ту	Owen	ER.	ту	Owen		Creek	Owen			Owen
		Creek			Hackber	Cerro Gordo		Hackber	Cerro Gordo			Cerro Gordo		Creek	Cerro Gordo
		Lime	berry			Shef- field		Juniper Hill		PER	Lime	Juniper Hill	YER .	Lime	Juniper Hill
AN	ш								Nora	٩U	5	Nora	٩ ٩	\Box	Nora
DEVON			Cedar			Cedar		Rock	Rock Grove		Rock	Rock Grove		Rock	Rock Grove
		Valley	MIDDLE		Valley		Shell F	Mason City		Shell F	Mason City		Shell	Mason City	
							MIDDLE	Cedar Valley				Cedar Valley	MIDDLE		Cedar Valley

Figure 1. Nomenclature and usage of Upper and Middle Devonian Series in north-central Iowa.

the middle of the Mason City Member. Earlier authors included the Shell Rock in the Middle Devonian (Givetian) but the results of biostratigraphic and lithostratigraphic investigations (Belanski, 1927, 1928, and Koch, 1967, respectively) have demonstrated an Upper Devonian (Frasnian) age. Conodonts support the assignment of the Shell Rock to the Manticoceras Zone. Thomas (1949) listed Ancyrodella buckeyenis and Anderson (1966) noted the presence of Ancyrodella gigas (from the Rock Grove Member) and Polygnathus cf. P. angustidisca (from the Mason City Member).

This significant echinoderm fauna presents a biocoenose of cystoids (Adocetocystis williamsi Strimple and Koch, n. gen., n. sp., and Strobilocystites calvini White) and edrioasteroids (Agelacrinites hanoveri). Associated with these echinoderms are worm tubes (Spirorbis), tabulate corals (Aulopora), scarce rugose corals (Pachyphyllum and Smithiphyllum), bryozoans (Hernodia) and a few small subspherical stromatoporoids. All but the stromatoporoids attached themselves to the rounded, knobby surfaces of a lithified, highly bored fine-grained lime-stone. The irregular surface of attachment represents a prominent discontinuity surface (See origin and morphology of the discontinuity surface, p. 6).

Thirty cystoids have been recovered from the argillaceous dolomitic matrix which surrounds the irregular limestone knobs. A number of the cystoids are complete with anchored terminal attachment processes and long brachioles. Other specimens no doubt had complete stems and brachioles but these were not recovered in the field. Although most are adult (possibly gerontic) specimens, a few medium and very small-sized individuals are in our Shell Rock collection.

To our knowledge there has been no earlier publication on a colony of cystoids in which individuals unequivocally were preserved in their attached living position. The closest analogous situation was presented by Kesling (1961) in his review of the Ordovician (Richmondian) cystoid, Lepadocystis moorei. Thecae of L. moorei, some with attached stems and lobate terminal attachment processes, occur in limestone with disarticulated cystoid plates, branching bryozoan fragments, a few edrioasteroids (Carnyella) and other fossil debris. Kesling could only conjecture as to whether the cystoids were attached to living or

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dead bryozoans. The specimens in our collection clearly are preserved in their normal living position, showing only minor deformation which resulted from compaction of the sediment that apparently suffocated this biocoenose.

Occurrences of Upper Devonian cystoids are uncommon. The unique preservation of our new cystoid and the associated edrioasteroids presents a truly rare opportunity to add to our fragmentary knowledge of the morphology and ecology of these pelmatozoans — it is a fascinating ecologic niche!

ACKNOWLEDGMENTS

Several individuals merit recognition for their roles in realizing the completion of this work. Mr. Thomas Williams, on whose property the specimens were collected and in honor of whom the species was named, has always been most cordial and allowed ready access to his quarry for collecting. Jean Cutler Prior (Iowa Geological Survey) and Brian F. Glenister and William M. Furnish (University of Iowa) offered valuable technical advice during the preparation of the diagrammatic reconstruction of the faunal environment by Koch (pl. 1).

H. Garland Hershey (State Geologist and Director of the Iowa Geological Survey) approved the project for study and offered to publish the completed manuscript. His continued interest and direction of the work are greatly appreciated.

We are particularly grateful to Glenister and Furnish for helpful discussion related to the origin of the discontinuity surface. P. E. Playford (an officer of the Geological Survey of Western Australia) and John L. Wray (Marathon Oil Company, Denver Research Center) have been kind enough to examine the discontinuity surface in the field. Jack B. Hayes (University of Iowa) made X-ray analyses of certain material. One of the limestone knobs was examined by D. C. Rhoads (Yale University). C. R. C. Paul (University of Indiana, Gary) assisted in establishing familial relationships of *Adocetocystis*. Richard Davis (University of Iowa) photographed specimens used for stereo-pairs (pl. 9). Mary C. Parker and Jean Cutler Prior (Iowa Geological Survey) carefully edited the manuscript.

Authors names are listed alphabetically in the title of this work and both authors share equal responsibility for all material presented in the study. Koch made the initial discovery of the edrioasteroids and a cystoid. However, the experience of Strimple in collecting echinoderms, and his knowledge of the nature of their usual gregarious habit resulted in the search for a colony of cystoids. Koch is responsible for stratigraphic control and is largely accountable for discussion of the origin of the discontinuity surface. Both authors are responsible for the cystoid systematics and preparation of the photographic plates and both are accountable for the paleoecological conclusions.

The laboratory facilities of The University of Iowa Geology Department were used in the preparation of study material. The authors shared in the time-consuming work of collecting and preparing specimens for study.

PREVIOUS WORK

Strobilocystites is the only cystoid previously reported from the Iowa Devonian. Thomas (1920) in his excellent report on the echinoderms of the Devonian of Iowa compared descriptions of S. calvini and S. polleyi with his new species, S. schucherti. Although nearly all of the strobilocystitids were recovered from the Cedar Valley (Middle Devonian) Thomas added that "... in some earthy dolomitic beds in the Shell Rock limestone in the vicinity of Nora Springs occur abundant internal molds of a Strobilocystites, presumably of this species [S. calvini] . . ." This horizon referred to by him is in the dolomitc beds at the top of the Rock Grove Member (fig. 1). The then new species S. schucherti was described upon one specimen from the Cedar Valley of Johnson County, Iowa, and two specimens from the Mason City Member of the Shell Rock Formation, at or slightly above the horizon of our present cystoid discovery.

Thomas also made the observation that "... the reduction of ambulacral branches in this species [S. schucherti] appears to be one of the indications of the extreme specialization attained by the genus before the disappearance of the rhomb-bearing cystids of which it is one of the last, if not the last represen-

tative." Although branching of the ambulacra was reduced in S. schucherti the ambulacra still were extended nearly to the base of the theca. Specimens of our new genus, Adocetocystis, exhibit ambulacra which are apical over most of their surface, extending only as far as the adapical margin of the lateral plates in mature individuals. The brachioles measure only about 2 mm in length in Strobilocystites (Stainbrook, 1941, p. 97) compared to a near-maximum of 44 mm in Adocetocystis (pl. 2, fig. 1; pl. 3, fig. 1). It is interesting to note that not one specimen of Adocetocystis previously was found in association with Strobilocystites schucherti or S. calvini in the Shell Rock.

Stainbrook (1941), in describing features of S. calvini from additional specimens collected from the Cedar Valley Limestone near Palo, Iowa, stated ". . . specimens mentioned by Thomas at the end of his description of S. calvini as occurring in the Shell Rock limestone, seem surely to be S. schucherti." Stainbrook's questioning of this identification was reasonable because the specimens mentioned are all internal thecal molds. However, four specimens of the cystoids in our Shell Rock collection are definitely allied to S. calvini (pl. 4, fig. 3). The relatively few strobilocystitids amid the more numerous individuals of Adocetocystis suggest that indeed the strobilocystitids may have diminished in number in early Late Devonian time. This decrease might have been related to the more efficient foodgathering system of Adocetocystis in an environment where intense competition for available food meant the sure demise of the less efficient feeders.

ORIGIN AND MORPHOLOGY OF THE DISCONTINUITY SURFACE

The lateral extent of the discontinuity surface is unknown but the surface is present in all exposed faces of the Williams Quarry which covers an area of approximately 95,000 square feet. The relief from the floor of the channelways to the upper surfaces of the limestone knobs is only 0.2 foot at the northern end of the quarry and increases to 0.7 foot toward the south. The argillaceous dolomite which covers the knobs has a level upper surface and ranges in thickness from 0.2 foot at the northern end of the quarry to 0.5 foot at the southern end (figs. 2, 3). A sharp downwarp in the beds at the north end carries

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Figure 2. Photographs of east face of Williams Quarry showing limestone knobs with pedestal-like supports surrounded and covered by dolomite silt. Head of hammer lies about 0.2 foot below top of dolomite silt. A distinct parting is present at base of limestone knobs; another parting is present about 0.3 foot lower.

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Figure 3. Photographs of east face of Williams Quarry showing additional shapes of limestone knobs. Dark, semi-continuous rim around knobs is zone of pyrite impregnation. Head of hammer lies at top of dolomite silt.

this zone below the quarry floor; however, reduction in the relief on the surface to the north and the thinning of the dolomite cover suggest that, at least megascopically, the discontinuity surface might not be recognizable much farther north. Also, it apparently is absent or is represented by the upper surface of a biostrome of subspherical stromatoporoids at an exposure approximately 700 feet south of the quarry. Edrioasteroids (*Agelacrinites hanoveri*) have been found attached to the stromatoporoids at the top of this biostrome (Belanski, 1927).

Two possibilities have been considered for the origin of the surface to which the organisms of this community are attached. The first is that the surface may represent a fairly extensive mat of knobby algal mounds. The second is that the surface represents one of erosional development. In either case, this horizon marks a discontinuity surface for which apparently no major time break is involved but a definite break in sedimentation is evident.

In most instances, the first impression of an observer is that because of the rounded knobs and the many examples of a pedestal-like base (pl. 1; figs. 2, 3), the surface is surely related to an organic mode of origin, probably algal. Pursuing an algal origin, such mounds may have been formed within the intertidal zone by accretion of carbonate material, both organic and inorganic, into the filamentous algal framework. Similar algal mounds are being formed along modern coastlines (Logan, 1961). Tidal or current activity could have maintained irregular open scour channels which prevented large-scale coalescing of the mounds. Continued wetting and drying of the mounds in the intertidal zone would result in firm and probably partially lithified structures. With slight submergence algal growth would cease and the surfaces of the mounds would be attacked by boring animals and encrusted by organisms favoring the new milieu.

As indicated above, the rounded form of the linestone knobs appears to be the only indication of a possible algal origin for this discontinuity surface. Irregular, rounded knobs (some with pedestal-like supports and others with more massive attachment to the substrate), broad, flat, table-top forms and still other, more bizarre forms are present (pl. 1; figs. 2, 3). Laminations marking textural or compositional differences are completely

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lacking and there is no color banding. In addition, thin-section examination reveals no apparent morphologic elements of algal structure other than a few fossil fragments with thin algal encrustations. John L. Wray (written communication, Dec. 5, 1967) has concluded that the composition and nonlaminated character of the limestone knobs rules out an algal origin *per se*. Using Folk's classification (1965) the rock would be termed a micrite. Scattered fragmented fossils within the micrite include stromatoporoids, bryozoans, corals, gastropods, ostracods, and brachiopods.

It is perhaps more likely that this discontinuity surface was produced by erosion, probably subaerial. Such an origin required regression of shallow water from a nearly level plain of carbonate sediments. As indicated above, the lateral limits of this surface are not definitely known. If the surface could be identified in other exposures or in drill cuttings and cores (the surface might not be as pronounced at other locations), the areal distribution in a paleogeographic sense might indicate an irregular coast-line with islands and peninsulas. Similar features are discussed by Jaanusson (1961, p. 232-236) in comparing ancient and Recent discontinuity surfaces.

If the surface represents one developed by subaerial erosion, at least partial lithification of the exposed sediment could have been effected in a relatively short time by a precipitation of interstitial calcium carbonate, just as similar phenomena occur in tropical and subtropical regions today (Ginsburg, 1953, p. 95-96; Emery, Tracy & Ladd, 1954, p. 44-47). The exposed beach as well as the bottom of the ancient sea probably had only a very gentle slope, and consequently there existed a small vertical distance between the exposed land area and the base level of erosion. Most of the erosion of the lithified or partially lithified sediment probably was accomplished by sheet erosion and corrosion, possibly assisted by rill current activity if all or part of the area was within the limits of the intertidal zone. Development of this surface by submarine erosion of soft calcareous mud does not appear tenable because broadly overhanging knobs would not have been formed (pl. 1; fig. 2).

Slight submergence of this rough surface followed the period of subaerial exposure. Minor submarine scour could have effected further smoothing of the knobby forms. Boring animals

attacked the knobby surfaces advancing the borings from the top, sides and undersurfaces of the knobs (overhanging knobs in the latter case). The length of the borings rarely exceeds 20 mm and more commonly they are 5-10 mm in length (pl. 1). Some of the boring activity was contemporaneous with the encrustation and growth of the edrioasteroids, cystoids and associated organisms, but much of it was completed prior to encrustation. Thin sections and polished cross sections of edrioasteroids demonstrate that, in most instances, the borings do not pass through the thecal plates of the edrioasteroids, but rather that they start at the rock surface immediately beneath the thecae.

Pyrite is a conspicuous feature of the limestone knobs and is concentrated at and adjacent to their surfaces (top, sides and undersurfaces). It varies within a single knob from a thin, discontinuous rim to a prominent band as much as 8 mm in thickness (pl. 1; figs. 2, 3). There appears to be no relationship between the thickness of a pyrite band and the relief on the surface of a knob. Borings entering the knobs are rimmed with pyrite but usually the pyrite concentration is very low or even absent near the terminal parts of the borings. This pyritic zone is an excellent example of a zone of impregnation (Orviku, 1940) which is characteristic of many discontinuity surfaces (Stauffer, 1925). Although a phosphatic stain often is associated with discontinuity surfaces, X-ray analysis showed no indication of the presence of phosphate within the zone of pyrite impregnation (J. B. Hayes, personal communication, Nov. 1967).

Small pebbles of the same bore-marked and pyrite-bearing limestone that make up the discontinuity surface occur on the floors of the channelways between knobs and within the channelways as high as the general upper level of the discontinuity surface. Most of the pebbles are more highly bored than the larger limestone knobs and some are completely impregnated with pyrite. Although there is no prominent conglomeratic structure, these pebbles represent further erosion of the discontinuity surface, probably produced during submergence.

In summary, the rough surface with its irregular, rounded, limestone knobs, the prominent borings which are filled with material from the superjacent bed, the conspicuous rims of pyrite impregnation, and the pebbles of identical limestone within the channelways are features which have been ascribed to discontinuity surfaces (Orviku, 1940; Jaanusson, 1961). There is no evidence a priori of an algal origin. Most of the features described suggest an erosional development. This surface marks a distinct break in sediment deposition from the time of initial emergence to the period of influx of carbonate material which ended the growth of the encrusting organisms. No major hiatus is involved and the length of time needed to develop the surface is probably comparable to that represented by other breaks above and below this zone. A planar pyritic surface is present two feet above this horizon and two planar zones, with a concentration of bituminous or carbonaceous material (figs. 2, 3) occur below. The surface described here is all the more spectacular because of the remarkably fine fauna which has been preserved.

PALEOECOLOGY

Favorable environmental conditions existed long enough to enable the organisms in this assemblage to develop into a thriving community. Retention of articulated plates in the echinoderms, especially the terminal attachment processes of the cystoids, clearly illustrates that the faunal assemblage represents a biocoenose. Growth of the community required a continuous supply of food particles for these microphagous organisms. The concentration of disarticulated columnals and thecal plates on the floors of channelways between the limestone knobs suggests that many individuals had lived through their normal life cycle and expired. A few echinoderm fragments were lifted to the top surfaces of the knobs and were deposited in shallow depressions. Currents moved any finer debris or clastic material into deeper water (Koch, 1967).

Literally thousands of edrioasteroids (Agelacrinites hanoveri) grew on the upper surfaces and on the sloping sides of the limestone knobs (pl. 1). A 4x4 inch surface may have as many as 125 edrioasteroids, depending upon their size. Growth stages are represented by very young specimens which show faint ambulacral development, half-grown specimens on which the

ambulacra begin to curve and adult individuals with fully curved ambulacra (pl. 1; pl. 5, fig. 3; pl. 6, fig. 1). Morphologic variations from the typical form which possesses two solar and three contrasolar rays are to be found. For example, a number of specimens exhibit six ambulacra, two solar and four contrasolar, wherein the additional ray is derived by a division of anterior ray III (pl. 5, fig. 3). One specimen possesses three solar and two contrasolar ambulacra. Another species grew commensally on living cystoid thecae (pl. 8, figs. 1, 3, 5). Intense crowding is evidenced by many examples where the theca of one individual expanded onto and sometimes over the rim of its neighbor. There is no preferred orientation of the thecae with respect to positioning of the interradius containing the anal pyramid (pl. 1; pl. 5, fig. 3; pl. 6, fig. 1). Thus, orientation of the edrioasteroids offers no clue to the prevailing current direction, although it has been suggested (Bather, 1915, p. 260) that a healthy pelmatozoic mode of life would be effected by an orientation which allowed the anal stream to be swept away without passing over either the mouth or any considerable part of the food-grooves.

The irregular, rounded limestone knobs also provided a secure habitat for the cystoids. Re-entrants, undersurfaces of overhanging knobs and shallow depressions on the surfaces of the knobs were the favored locations for attachment and growth, and probably offered optimum protection to the organisms (pls. 1-3; pl. 6, fig. 1; pl. 7, fig. 5). Apparently most of the cystoids were in a sub-horizontal attitude when withdrawn into a re-entrant or when withdrawn beneath an overhanging knob, but straightening of the stem allowed a near-vertical orientation. Even where individuals attached their stems at the base of shallow depressions on the upper surface of the knobs the brachioles extended but a short distance above the general level of the knobs.

We suppose that the water was shallow during the development of this community and was subjected to at least moderate current or eddy activity, possibly tidal. The longest stem of the specimens of *Adocetocystis*, including the terminal attachment processes, is only 35 mm in length (table 1; pl. 5, fig. 2). The stems of the specimens of Strobilocystites have a maximum length of only 16 mm (pl. 4, fig. 3). Strobilocystites is known from the Cedar Valley Limestone in which the preserved portion of the stem measures 6 cm in length; these longer stems are no doubt the response to a different environment. The short stems of Adocetocystis and Strobilocystites from the Shell Rock collection would have allowed more stability of the organisms while being subjected to current motion. In addition the water surface might have been only inches above the level of the knobs resulting in the development of very short stems that would maintain the thecae and brachioles below the level of the water. A few specimens show addition of secondary supports higher on the stem, a feature which would further serve to stabilize the column. Some other structural and functional aspects of the stem which may be applicable to Adocetocystis (the latitude of movement of columnals in turning the angle of the theca, the nature of the musculature in the proximal part of the column, for example) have been presented by Kesling (1961, p. 137-139) for Lepadocystis.

Restriction of ambulacral grooves to the upper portion of the theca and the unusually long brachioles provided a distinct advantage for *Adocetocystis*. Full extension of the brachioles yielded a large collecting area for filtering the food particles supplied by currents. Distal brachiole segments that were accidentally broken off apparently were regenerated to assure maximum food-gathering capacity (pls. 1-3).

Ultimately an influx of calcareous mud smothered the living community. The mud filled in the channelways between the limestone knobs and then encroached upon the upper surfaces of the knobs. The low-lying edrioasteroids, corals, bryozoans and worm tubes were the first to be covered and finally the cystoids succumbed. Continued catastrophic deposition resulted in a thin blanket-like layer of mud above the knobs which prevented disarticulation and/or destruction of the organisms by scavengers.

Cystoids have been uncovered which possess all the brachioles and their cover plates (pls. 2, 3). In other specimens distal portions of some brachioles were lost prior to burial. Later compaction of the enclosing sediment caused only minor damage to some specimens, either by off-setting a segment of the stem or by partially crushing the theca. Sediment was squeezed into the thecal cavity in cases where the anal pyramid collapsed or where sutures between the thecal plates were opened. Undamaged tests are filled with calcite.

The occurrence and preservation of this fauna is truly unique and the abundance of all forms in association with each other leaves little to be desired for study material. There is no need to surmise regarding the nature of attachment of the cystoids and edrioasteroids. The physical evidence is straightforward. Less fortunate was Bather (1915, p. 261) when, in his study of the Edrioasteroidea he remarked, "Here, as in so many similar cases, the field collector and observers have not supplied the laboratory worker with the desired evidence."

RELATIONSHIPS OF ADOCETOCYSTIS

We are grateful to C. R. C. Paul, who is currently engaged in an evolutionary study of the Callocystitidae (personal communication, Jan. 17, 1967), for his advice in establishing relationships of Adocetocystis. The genus Tetracystis Schuchert (1904) (Upper Silurian-Lower Devonian) is thought to be ancestral to Lipsanocystis Ehlers and Leighly (1922) (Middle Devonian Traverse Group of Michigan) and to Strobilocustites White (1876) (Middle and Upper Devonian of Iowa). Adocetocustis is apparently derived from a form like Lipsanocystis. Knowledge of an anal pyramid surrounded by small bordering plates in Lipsanocystis was not known originally but was illustrated by Stumm (1955). All four forms under discussion have this feature. Lipsanocystis, Strobilocystitcs and Adocetocystis have a double hydropore, and one specimen of Tetracystis which normally appears to have a single hydropore has been found to have a double hydropore (Paul, personal communication, Jan. 17, 1967). Tetracystis has long ambulacra which extend over most of the length of the theca, and Lipsanocystis typically has long ambulacra; however, somewhat shortened grooves were reported by Stumm (1955, pl. 1, figs. 12-15) for L. rugosus Stumm (1955). Ehlers and Leighly (1922, p. 156) quoted an

opinion from Schuchert that Lipsanocystis was ". . . a changed Apiocystites, having become more depressed and therefore has changed somewhat the arrangement of the plates . . ." Paul (1967) has divided the Callocystitidae between those forms having two to four strongly protruding ambulacra developed on smooth bands on the theca (Staurocystinae Jaekel, 1899) and those forms with four or five ambulacra developed in shallow grooves in thecal plates, not strongly protruding (Apiocystitinae Jaekel, 1899). According to Paul Apiocystites belongs to the latter subfamily and Lipsanocystis to the former subfamily. Ehlers and Leighly (1922, p. 156) noted the pectinirhombs somewhat resembled those of Tetracystis chrysalis Schuchert but that Lipsanocystis differed from it and all other genera of the family in having the periproct almost entirely enclosed by plate L5. This was true of the holotype which was monotypic but Paul (1967a, p. 210, figs. 3-6) figured other specimens of L. traversensis which have one to four plates around the periproct.

Four ambulacra are present in Tetracystis, Lipsanocystis, Strobilocystites and Adocetocystis. The grooves of Tetracystis pass down the sides of the theca to near the column and typically do the same in Lipsanocystis, although some species of the latter have shortened ambulacra which apparently leads to the short grooves of Adocetocystis. Strobilocystites retains the elongated ambulacra and in addition branches several times in mature individuals. There are many brachioles in mature Strobilocystites which provide an appreciable food-gathering area although the brachioles are very short. Conversely the sharp reduction in the number of brachioles of Adocetocystis is compensated for by greatly increased length of the brachioles. Young specimens of Adocetocystis have fewer brachioles than older specimens which is also known to be the case in Strobilocystites. The facets are more widely spaced in Adocetocystis than in other members of the family.

Tetracystis, Lipsanocystis, Strobilocystites and Adocetocystis all have pectinirhombs B2:IL2, L1:R5, and L4:R3.

Paul (1967, p. 310) has suggested that an apical cone of collection is formed by the brachioles (with food grooves on

the adoral side) of *Glansicystis*, and possibly also *Prunocystites* (known only from small [immature?] specimens), wherein the brachioles are grouped about the mouth and the food grooves on the theca are short. It was his opinion that this type of construction was more advantageous for securing falling food particles in a relatively still sea. It appears that he considered other Callocystitidae to be ". . . better adapted to take advantage of currents in a relatively agitated sea." This would be those forms which have long food grooves on the theca with many short brachioles. In our present study there are forms within the same habitat that possess long brachioles (*Adocetocystis*) and forms with short brachioles (*Strobilocystites*) although the former are more numerous.

SYSTEMATIC DESCRIPTION

Super family GLYPTOCYSTITIDA Bather Family CALLOCYSTITIDAE Bernard Subfamily STAUROCYSTINAE Jaekel Genus ADOCETOCYSTIS Strimple and Koch 1968,

new genus

Type species.—Adocetocystis williamsi Strimple and Koch, 1968, new species.

Diagnosis.—A callocystitid cystoid with ovate theca, four unbranched ambulacra, elongated brachioles with interlocking brachiolars which number as many as 57 pairs in mature or gerontic individuals, double hydropore, and a variable number of plates surrounding the periproct.

Previously, Lipsanocystis Ehlers and Leighly and Strobilocystites White were the only described genera of Callocystitidae bearing a double hydropore.

Description.-The theca is ovate, longer than wide. Four undivided ambulacra are present in the apical region and extend a short distance onto the lateral sides of the theca. A double hydropore, gonopore and mouth are apical and the periproct is lateral. Three pectinirhombs are distributed B2:IL2, L1:R5, L4:R3 and are widely disjunct. Vestibule rims are present on each half-rhomb. The slits are depressed below the normal surface of the theca on the side where the ridges are more pronounced (half-rhombs IL2, L1, and L4). Sinclair (1948, p. 307) suggested that such a system (montidisjunct) in *Glyptocystites* served to direct a stream of water emerging from the rhomb, and so preventing to some extent wasteful reuse. The brachioles are elongated and composed of interlocking pairs of plates. Food grooves on the brachioles are covered by minute, interlocking cover plates. The stem is of moderate length, tapers rapidly for a short distance but thereafter remains constant to the termination where an irregular attachment process is present.

Remarks.-Relationship of the genus has been discussed in the previous section (p. 15). Generic name derived from the Greek word, *adoketos*, meaning unexpected.

Occurrence.--Upper Devonian; North America.

ADOCETOCYSTIS WILLIAMSI Strimple and Koch, 1968, new species

Plates 1-9

Text-figures 4-9

Description.—The theca is ovate with the height reaching slightly greater than ¼ times more than the diameter (table 1). There are four undivided ambulacra which extend only a short distance below the apical region. The mouth, double hydropore, and gonopore are apical; the anus is lateral. A complete stem is present, including an anchored terminal attachment process.

There are 26 thecal plates consisting of 4BB, 5ILL, 5LL, 5RR and 7OO. Slight variations in the length and slope of suture lines in different specimens reflect various growth stages. Figure 4A illustrates the arrangement of the first four circlets in the holotype. One specimen in our collection is unique in that the position of the usual IL4 is occupied by two plates and B1 is modified accordingly (fig. 4B). Also, this specimen appears to possess a definite additional ambulacrum (III) which follows the suture between O3 and O4 and terminates in a single brachiole facet on the adapical margin of R3. Ambulacrum II is displaced

TABLE I

Measurements of Selected Specimens o	Adocetocystis williamsi	Strimple and Koch
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				Stem					Number
SUI No.	The	ca	Diam	eter	Length		of		
	Diameter	Height	Proximal	Distal		B2:1L2*	L1:R5*	L4:R3*	Brachioles
32293	16.9mm	22.3mm	6.0mm	N		6.9; 32	9.3; 40	10.8:46	15
32294	16.5mm	21.2mm	6.9mm	N		5.7; 24	7.3; 30	6.8; 28	12?
32295	16.1mm	21.7mm	6.9mm	3.1mm	27 mm	P	7.9; 30	P	14?
32296	15.5mm	21.0mm	5.9mm	2.3mm	20mm	Р	7.9; 30	P	11?
32297	15.4mm	20.3mm	6.5mm	3.0mm	26mm	4.8; 22	P	P	12?
32308	15.3mm	20.2mm	5.6mm	N		4.9; 20	6.6; 26	7.0; 30	13
32298	14.9mm	19 . 4mm	5.9mm	2.9mm	21 mm	6.8; 30	P	8.8; 38	14
32292	14.8mm	19.5mm	6.8mm	3.1mm	27mm	6.2; 26	7.2; 32	8.2; 34	12
32299	14.7mm	19.2mm	5.2mm	И		P	Р	10.0; 40	12?
32300	14.1mm	18.0mm	6.0mm	2.5mm	35mm	4.2; 16	5.2; 22	P	11
32309	13 . 8mm	17.7mm	5.9mm	N		6.4; 26	P	7.9; 34	13?
32301	13.5mm	17.4mm	5.6mm	2,7mm	20mm	P	P	7.3; 32	10?
32302	12.9mm	17.0mm	5.3mm	N		5.9; 26	7.7; 32	8.6; 36	10
32303	11 . 5mm	13.1mm	4.5mm	2.8mm	1 <i>5</i> mm	P	P	7.4; 29	13
32304	11 . 1mm	14.5mm	4.9mm	N		4.0; 16	6.0; 24	6.6; 28	Ν
32305	6.9mm	8.0mm	3.3mm	2.3mm	7+mm	P	2.6; 13	3.0; 14	11
32306	5.8mm	7.1mm	2.5mm	N		2.0; 7	P	2,9; 12	5?
32307	2.4mm	3.3mm	1.3mm	N		very weakly developed			3?

* First value, width of rhomb measured along the plate suture; second value, number of dichopores

N Not recovered

P Not exposed

? Apical surface incompletely exposed (generally obscured by brachioles and matrix)





Figure 4. Sketch of the arrangement of thecal plates of the first four circlets of Adocetocystis williamsi Strimple and Koch. A. Holotype, SUI 32292. B. Paratype, SUI 32308. BB1-4, basals; ILL1-5, infralaterals; I.L1-5, laterals; RR1-5, radials. Circles and half-circle pairs mark positions of last-formed brachiole facets on ambulacra.

anteriorly so that the last-formed brachiole facet is on R2. Unfortunately, the right-lateral and apical areas are somewhat crushed and corroded making more exact determinations difficult. The significance of this morphologic variant has not been realized, but such a condition may represent regression.

Ornamentation of thecal plates is moderate and consists of irregular ridges and weak tubercles. A prominent ridge parallels the suture lines on each plate and one or two less well-developed ridges occur toward the centers of the plates. Irregular, weak, radiating ridges may be developed. Low tubercles adorn the remaining surface area of the plates (pls. 1-9).

Considerable variation exists in the arrangement of the plates around the periproct. L5 forms the major portion of the adoral boundary (pl. 5, fig. 1; pl. 8, fig. 3). IL5, IL4 and L4 form various combinations with L5 in enclosing the aboral boundary (fig. 5). Paul (1967a, p. 210, figs. 3-6) illustrated similar variation in the arrangement of the thecal plates surrounding the periproct in *Lipsanocystis* Ehlers and Leighly (1922). L5 completely surrounds the periproct in one specimen of *Lipsanocystis*. Considering the variation shown for *Adocetocystis*, it appears that L5 conceivably could surround the periproct, but this condition has not been observed in the specimens collected to date.

There are three disjunct pectinirhombs as follows: B2:IL2, LI:R5 and L4:R3 (fig. 4; pl. 7, figs. 1, 3, 4). Specimens of nearly equal size show considerable variation in the number of dichopores. Smaller specimens may have more dichopores than larger individuals (table 1). Half-rhombs IL2, L1 and L4 are deeply depressed and exhibit high, closed vestibule rims. Halfrhombs B2, R5 and R3 are longer, not depressed, have lower, unclosed vestibule rims and often exhibit two more slits than are visible in the adjoining half-rhombs.

The mouth is apical and has an elongated oval outline. Figure θ shows the position of the mouth in association with seven oral plates. The orals present a series of slightly elevated plates with the upper surface at or slightly above the level of the mouth and the adoral portions of the primary food grooves. Ornamentation is very weak on the orals.









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Figure 5. Sketches showing the variation in the arrangement of plates around the periproct in Adocetocystis williamsi. A. Two plates around the periproct in Paratype SUI 32311. B, C and D. Variations with three plates around the periproct (Paratypes SUI 32295 and SUI 32303 and Holotype, SUI 32292 respectively). E and F. Four plates around the periproct in Paratypes SUI 32293 and SUI 32308. ILLA-5, infralaterals; LLA-5, laterals; Pe, periproct; IV and V, ambulacra IV and V.

Reconstruction of Shallow Sea Bottom in North-central Iowa During Upper Devonian Time

Limestone knobs with pedestal-like supports and others with more massive attachment to the substrate are depicted (see also figs. 2, 3). The scale applies to the knob and the attached organisms in the center foreground.

The right side of the drawing represents a cross section through two of the limestone knobs and shows the nature of the borings. A prominent semi-continuous band or rim of pyrite (black) forms a zone of impregnation around the outer surfaces of the knobs and lines the walls of the borings. The depth of pyrite penetration is variable. Although the pyrite stain is shown in this illustration, it probably was formed after burial of this surface.

Attachment positions of all organisms shown are based on actual specimens. Edrioasteroids (Agelacrinites hanoveri) are randomly oriented with respect to positioning of the interradius containing the anal pyramid. They attached and grew on the upper surfaces and steeply sloping sides of the limestone knobs. Another edrioasteroid species grew commensally on the sides of cystoid thecae (not shown-see pl. 8, figs. 1, 3, 5). Pachyphyllum and Aulopora are shown on the knob in the foreground. The former are rare in occurrence, while the latter are common. Like the edrioasteroids, Aulopora grew on the upper surfaces and on steeply sloping sides of limestone knobs. Individuals of Adocetocystis williamsi are attached to undersides of overhanging knobs and in shallow re-entrants in the knobs. Various growth stages are represented. The short stems allowed partial withdrawal of the thecae for protection against predators or during periods of strong current activity. The long brachioles and the flexibility of the stem in turning the angle of the theca gave A. williamsi a distinct feeding advantage over the low-lying edrioasteroids and corals. Disarticulated plates of individuals that lived through their normal life cycle were concentrated on the floors of channelways between limestone knobs. Only a small amount of this debris is shown in the drawing.

PLATE 1

Reconstruction of Shallow Sea Bottom in North-central Iowa During Upper Devonian Time

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Figure 6. Camera lucida drawings (x6) of the apical region of Adocetocystis williamsi showing the arrangement of oral plates. The complete ambulacra are shown along with the position and size-relationships of brachiole facets. A. Holotype, SUI 32292; B. Paratype, SUI 32303. G, gonopore; H, hydropore; OO1-7, orals. I^1 , I^2 , facets of ambulacrum I; II¹, II², etc., facets of ambulacrum II, etc.

There are four unbranched ambulacra of which ambulacrum II is the longest in the holotype (figs. 6A, 7A; pl. 7, fig. 2). Ambulacrum I apparently is the longest in gerontic (?) specimens and possesses five brachiole facets in SUI 32292 (fig. 8). Extension of ambulacrum IV is limited by its encroachment on the posterior edge of pectinirhomb L4:R3 and the adapical margin of the periproct. Extension of ambulacrum V is limited by its encroachment on the adapical margin of the periproct. Extension of ambulacrum V is limited by its encroachment on the adapical margin of pectinirhomb L1:R5 (pl. 7, fig. 2).



Figure 7. Camera lucida drawing (x6) of ambulacrum II (A) and the traces of the ambulacral flooring plates on the thecal plates (B) in Adocetocystis williamsi. Holotype, SUI 32292. I, II, ambulacra I and II. OO2-3, orals; MFG, main food groove; LFG, lateral food groove; F, facet; SA, secondary ambulacral flooring plate; PA, primary flooring plate.

The primary food groove is about 1 mm wide apically and diminishes to about 0.5 mm in width distally. Interlocking cover plates on the primary food groove are about 0.25 mm in width, and they form a steeply sloping angular roof covering the groove (pl. 4, fig. 2; pl. 6, fig. 1; pl. 7, fig. 2). The lateral food grooves are 0.4-0.5 mm wide, possess cover plates, and terminate in prominent circular facets. These facets are de-



Figure 8. Camera lucida drawing (x6) of ambulacrum I (A) and the traces of the ambulacral flooring plates on the thecal plates (B) in Adocetocystis williamsi. Paratype, SUI 32293. II, IV, V, ambulacra II, IV and V. OO1-2, orals. Remaining symbols as in figure 7.

veloped on a pair of flooring plates, one primary and one secondary (Paul, 1967a, p. 212), the latter forming the adoral portion (figs. 7B, 8B). The first-formed facet in each ambulacrum is branched off to the left of the ambulacrum as viewed from the apex to the tip. Successive facets alternate from right to left. The flat crest of the first facet on ambulacrum II in the holotype is about 1.7 mm in diameter and the most distal facet surface is 1.2 mm in diameter. Maximum crest diameter of the first-formed facets in other mature or gerontic specimens is about 2 mm.

Brachioles are attached to the brachiole facets and taper to a fine point. They are composed of interlocking pairs of brachi-

olars which possess cover plates. Only one brachiole was recovered on the holotype but other specimens show all the brachioles, many extending the full length to their termination points (pl. 3, fig. 1; pl. 8, fig. 4). There are numerous examples of what apparently represent regeneration of broken ends of brachioles. For example, a brachiole tapers uniformly along the series of brachiolars, suddenly decreases sharply in diameter, and then tapers uniformly again to a fine point along the series of smaller brachiolars (pl. 3, fig. 1; pl. 6, fig. 1; fig. 9). The most distal brachiole in the series on any ambulaerum normally is the shortest and smallest in diameter. First-formed brachioles in mature (gerontic?) specimens possess as many as 57 brachiolars and measure as long as 45 mm in length.

The periproct is covered by a series of triangular pyramidal plates and a circlet of subrectangular auxiliaries. These plates are not preserved in the holotype. Usually, the anal pyramid is composed of six plates but the number ranges from five to seven (pl. 8, figs. 3, 5). The auxiliaries, of which the aboral plates are largest, range from eight to ten in number. Encroachment of L5 may partially conceal the much smaller adoral plates. Ornamentation on plates covering the periproct is minimal.

Terminology used in description of the hydropore and gonopore follows that of Paul (1967a, p. 214). The hydropore opens as two sub-oval structures on O1 and O7. Each has a strongly elevated perimeter and each contains numerous (as many as 75) perforations. The gonopore is a small circular opening situated across the suture between O1 and O7 (pl. 4, fig. 2; pl. 7, fig. 2; fig. 6). Three (?) small gonals were preserved on one specimen but were lost during final cleaning of the oral surface.

The complete stem is present and terminates distad in a root-like attachment process which is firmly cemented to the underside of a limestone knob (pl. 5, fig. 2; pl. 9, fig. 1). For the first 8-10 mm of length the stem decreases in size until its diameter is slightly greater than one-half that of the proximal diameter and then maintains a nearly constant diameter for the remaining length. It is approximately at this point where the smaller, nearly hidden inner stem segments cease to be present between the larger, aborally flanged outer segments.



Figure 9. Camera lucida drawings (x6) of two of the longest brachioles in a specimen of Adoctocystis williamsi. Paratype, SUI 32298. A. Aborallateral view of brachiole II¹ showing point of reduction in diameter of brachiolars (arrow); there are 55 pairs of brachiolars (23 proximal brachiolars are not shown). B. Lateral view (slightly twisted) of brachiole V¹ showing cover plates and point of reduction in diameter of brachiolars (arrow); there are 57 pairs of brachiolars (19 proximal brachiolars are not shown). Brachiole II¹ possesses only 12 brachiolars beyond the point of reduced diameter while brachiole V¹ has 24.

Ultimately, the length of the stem on any individual was dependent upon the position of attachment in relationship to the relief on a limestone knob or the degree of overhang on a knob. Individuals that attached their stems in low depressions on the upper surfaces of knobs developed shorter stems (pl. 6, fig. 1). The articulating surface between adjacent segments is smooth externally but internally there is a series of low crenulations which extend a short distance outward from the lumen. The lumen is approximately equal to half the stem diameter.

Types.—Holotype, SUI 32292. Paratypes, SUI 32293-32313. Reposited in Department of Geology, The University of Iowa, Iowa City.

Material available .-- Thirty specimens.

Horizon.-Mason City Member, Shell Rock Formation.

Locality.—Thomas William Quarry, NW⁴, SW⁴, sec. 28, T. 96 N., R. 18 W., Floyd County, Iowa, U. S. A.

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PLATES

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . . 17

Fig. 1. Block containing four complete specimens. View is vertical, looking down on natural surface of knobby limestone. Cystoids are attached near base of limestone ridge which separates upper two specimens from lower two. Note preservation of long brachioles; decrease in diameter near ends of many brachioles suggests regeneration of broken tips. *Aulopora* and numerous individuals of *Agelacrinites hanoveri* are attached to limestone surface. Pattern on left side of block due to marks of mechanical chisel on partially excavated dolomite silt. Paratypes: upper left, SUI 32301; upper right, SUI 32298; lower left, SUI 32297; lower right, 32295. x0.8.

EXPLANATION OF PLATE 3

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . . 17

Fig. 1. Same block as illustrated in plate 2 with limestone ridge removed exposing complete length of stems. Note decrease in width of ridge with depth. All stems terminate in a root-like attachment process. Upper left, upper right and lower right specimens are attached beneath lip of ridge; specimen at lower left is attached below and to left of middle of theca. (See stereophoto, pl. 9, fig. 3.) Paratypes: upper left, SUI 32301; upper right, SUI 32298; lower left, SUI 32297; lower right, SUI 32295, x0.8. 36 A NEW UPPER DEVONIAN CYSTOID



PLATE 2



PLATE 3

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . . 17

- Fig. 1. Right lateral showing detail of rhomb L4:R3 with strong vestibule rim on L4 and much lower rim on R3. Last-formed brachiole facet on ambulacrum II encroaches on rim of half-rhomb R3. Note ornamentation on thecal plates. Paratype, SUI 32293. x1.4.
- Fig. 2. Detail of apical area showing double hydroporc, gonopore, mouth and primary and secondary food grooves with cover plates. Paratype, SUI 32293. x1.4.
- Fig. 3. Specimen of Strobilocystites calvini in same habitat as Adocetocystis williamsi and attached to limestone knob in living position. Note bulbous attachment process. Fracture across theca occasioned while cleaning specimen. L, limestone knob; D, dolomite silt. SUI 32314. x1.4.



(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. .. 17

- Fig. 1. Posterior-lateral view showing periproct surrounded by IL4, IL5 and L5. Lowest brachiole facet on ambulacrum V is on posterior adoral edge of half-rhomb L4. Note ornamentation on thecal plates. Holotype, SUI 32292. x1.4.
- Fig. 2. Posterior-lateral view of theca with complete stem. Terminal attachment process is slightly damaged. Holotype, SUI 32292. x1.4.
- Fig. 3. Vertical view, looking down on natural surface of a limestone knob containing many specimens of Agelacrinites hanoveri at various growth stages. Note random orientation of interradius containing anal pyramid. Large specimen near bottom center (anal pyramid toward left) possesses six rays. Brachioles of a withdrawn specimen of Adocetocystis williamsi are visible at lower left. L, limestone knob; D, dolomite silt. Paratype, SUI 32312. x1.4.



PLATE 5

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . . 17

Fig. 1. Vertical view looking down on natural surface of a limestone knob. Specimen of *A. williamsi* positioned in shallow depression on limestone knob; stem and terminal attachment process are present but not visible. Note attached *Pachyphyllum* and numerous small *Agelacrinites hanoveri* on limestone surface. Paratype, SUI 32303. x1.4.

ATTACHED TO A DISCONTINUITY SURFACE 43



PLATE 6

A NEW UPPER DEVONIAN CYSTOID

EXPLANATION OF PLATE 7

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . 17

- Fig. 1. Left-lateral view showing detail of rhomb L1:R5. Holotype, SUI 32292. x1.4.
- Fig. 2. Apical surface showing double hydropore (damaged), gonopore, mouth and primary and secondary food grooves with cover plates. Holotype, SUI 32292. x1.4.
- Fig. 3. Right-lateral view showing detail of rhomb L4:R3. Last-formed brachiole facet on ambulacrum II encroaches on anterior edge of R3; last-formed brachiole on ambulacrum IV encroaches on posterior edge of L4. Holotype, SUI 32292. x1.4.
- Fig. 4. Anterior-lateral view showing detail of rhomb B2:IL2. Holotype, SUI 32292. x1.4.
- Fig. 5. Right-lateral view of specimen protruding from reentrant in limestone knob. View is vertical looking down on natural surface of limestone knob. Note numerous individuals of Agelacrinites hanoveri. Triangular patch to left of cystoid due to chip broken off of limestone knob. L, limestone; D, dolomite silt. Paratype, SUI 32313. x0.6.

ATTACHED TO A DISCONTINUITY SURFACE 45



PLATE 7

A NEW UPPER DEVONIAN CYSTOID

EXPLANATION OF PLATE 8

(all specimens coated with ammonium chloride sublimate)

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Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. .. 17

- Fig. 1. Left-lateral view of specimen with edrioasteroid attached to theca and covering area between rhombs B2:IL2 and L1:R5. Paratype, SUI 32293. x1.4.
- Fig. 2. Right-lateral view of specimen with nearly complete stem attached to underside of overhanging limestone knob (attachment process not recovered). Height of distal stem segments is about twice as great as those of all other specimens. Paratype, SUI 32310. x1.4.
- Fig. 3. Detail of periproct showing anal pyramid and auxiliary circlet. Periproct surrounded by L4, IL4, IL5 and L5. Note side view of edrioasteroid on right-lateral side of theca. Paratype, SUI 32293. x1.4.
- Fig. 4. Left-lateral view of slightly crushed specimen showing long brachioles. Terminal attachment process of stem is hidden beneath lower right. (See pl. 9, fig. 2.) Paratype, SUI 32296. x1.4.
- Fig. 5. Specimen with edrioasteroid attached near posteriorright-lateral margin; another edrioasteroid (not shown) is attached to left-lateral side. Brachioles are present in unexcavated area at top. Paratype, SUI 32294. x1.4.



PLATE 8

(all specimens coated with ammonium chloride sublimate)

Page

Adocetocystis williamsi Strimple and Koch, n. gen., n. sp. . . 17

- Fig. 1. Stereophoto of specimen illustrated in pl. 5, fig. 2 at different angle showing terminal attachment process of stem. Holotype, SUI 32292. x0.7.
- Fig. 2. Stereophoto of specimen illustrated in pl. 8, fig. 4 showing terminal attachment process of stem. Paratype, SUI 32296. x0.7.
- Fig. 3. Stereophoto of block containing four attached specimens (See pl. 3, fig. 1.) Paratypes: upper left, SUI 32301; upper right, SUI 32298; lower left, SUI 32297; lower right, SUI 32295. x0.5.

ATTACHED TO A DISCONTINUITY SURFACE 49



PLATE 9