

PALEONTOLOGICAL CONTRIBUTIONS

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Paper 120

HOMALOZOAN ECHINODERMS OF THE WHEELER
FORMATION (MIDDLE CAMBRIAN)
OF WESTERN UTAH¹

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Abstract.—Three new species, representing three of the four homalozoan classes, are described from the upper Wheeler Formation of middle Middle Cambrian age in west-central Utah. *Ctenocystis colodon* n. sp. is only the fifth species of Ctenocystoidea to be described. The new order Ctenocystida is defined. The solutan *Castericystis? sprinklei* n. sp. is the fifth species of Homoiostealea to be reported from Cambrian strata. The cornute *Cothurnocystis? bifida* n. sp. is the fifth species of Stylophora to be reported from Middle Cambrian strata worldwide and only the second from North America. This homalozoan fauna is among the most diverse known from any Cambrian formation.

AMONG ECHINODERMS, homalozoans are unusual in their complete lack of radial symmetry. Representatives are relatively rare, especially in Cambrian strata. Three new Cambrian species, which represent three of the four homalozoan classes, are described here. All are from the upper Wheeler Formation of west-central Utah and include the ctenocystoid *Ctenocystis colodon* from the Drum Mountains, the homoiostelean *Castericystis? sprinklei* from the

House Range, and the stylophoran *Cothurnocystis? bifida* from the House Range.

Each homalozoan species in the Wheeler Formation is from a different locality. Such low diversity is typical of most Cambrian echinoderm faunas, although locally each species may be represented by numerous individuals.

For several years, knowledge of the class Ctenocystoidea was limited to the single species *Ctenocystis utahensis* Robison and Sprinkle, 1969, which is locally abundant in the Spence Shale of northern Utah and southern Idaho. The

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Spence fauna is of early Middle Cambrian age. Recently, the observed geographic distribution of ctenocystoids was vastly broadened by the description of the new species *Etoctenocystis bohémica* Fatka and Kordule, 1985, from Czechoslovakia, *Ctenocystis jagoi* Jell, Burrett, and Banks, 1985, from Australia, and *Ctenocystis smithi* Ubaghs, 1987, from France. Of these latter three species, *C. smithi* is the youngest, and it extends the observed stratigraphic range of the class to the upper Middle Cambrian. The description here of *C. colodon* n. sp. demonstrates that ctenocystoids have a modest stratigraphic range and some diversity in the Middle Cambrian of western North America. Discovery of more representatives is to be expected.

Cambrian representatives of the class Homoiostelea are known only from the United States. Moreover, the only well-known species is the solutan *Castericystis vali* Ubaghs and Robison, 1985, which is from the Marjum Formation of late Middle Cambrian age and, like most of the specimens described here, is from the House Range of Utah. Two fragmentary specimens of an unnamed solutan have been described from the Weeks Formation of latest Middle Cambrian age, also from the House Range (Ubaghs and Robison, 1985), and a single unnamed solutan stele has been described from the Whipple Cave Formation of late Late Cambrian age in Nevada (Ubaghs, 1963; Parsley and Caster, 1965). Additionally, undescribed solutans have been reported from the Lower Cambrian of Pennsylvania (Derstler, 1975, 1981; Paul and Smith, 1984) and the lower Upper Cambrian of Alabama (Bell and Sprinkle, 1980). Solutan specimens described here from the Wheeler Formation add significantly to this meager record of Cambrian homoiosteles.

Stylophora are equally rare in Cambrian strata. In North America, an undescribed cornute species has been reported from the Spence Shale of Utah (Robison and Sprinkle, 1969; Sprinkle, 1976; Sprinkle and Robison, 1978) and two cornutes, *Nevadaecystis americana* Ubaghs, 1963, and *Phyllocystis* sp., have been described from the Whipple Cave Formation (upper Upper Cambrian) of Nevada (Ubaghs, 1963, 1968). In Europe, only three cornute species have been described: *Ceratocystis perneri*

Jaekel, 1901, from the middle Middle Cambrian of Czechoslovakia (Jaekel, 1901; Bather, 1913; Ubaghs, 1967; Jefferies, 1969), *C. vizcainoi* Ubaghs, 1987, from the upper Middle Cambrian of France, and *Protocystites menevenis* Hicks, 1872, from the middle Middle Cambrian of Wales (Jefferies, Lewis, and Donovan, 1987). Additionally, *Ceratocystis* probably is represented in the lower Middle Cambrian of Sweden (Christina Franzén-Bengtson, cited by Berg-Madsen, 1986:67), and dissociated plates of an unidentified cornute have been reported from the Middle Cambrian of Bornholm, Denmark (Berg-Madsen, 1981:223; 1985:23; 1986:73). Thus, the new cornute *Cothurnocystis?* *bifida*, described here, is a significant addition to the meager record of Cambrian stylophorans.

Repository.—All homalozoan specimens described in this paper are deposited with collections of the U.S. National Museum of Natural History (USNM) in Washington, D.C. Illustrated specimens have separate USNM numbers (see figure captions). The remaining ctenocystoids have been assigned USNM catalog number 432875a-j, the remaining homoiosteles are cataloged under USNM accession number 369516, and the remaining stylophorans and associated fossils are cataloged under USNM accession number 368342.

Terminology.—Morphological terms used in this paper are defined in parts S (Ubaghs, 1968; Caster, 1968) and T (Sprinkle and Robison, 1978) of the *Treatise on Invertebrate Paleontology*.

Acknowledgments.—This study would not have been possible without the generous contributions and aid of others. We are especially indebted to Lloyd and Val Gunther, who discovered all of the homalozoa-bearing beds on which the study is based and who made the initial collections. Subsequently, Lloyd Gunther, Metta Gunther, Frieda Gunther, Val Gunther, and Phillip Reese worked long and hard to collect many more specimens. Funds to defray costs of collecting at the homoiostelean and stylophoran localities were provided by the Smithsonian Institution through arrangements made by I. G. Macintyre and F. J. Collier. Murielle Demaret-Fairon and Roger Fontaine did most of the photography, and Marie Masson aided in preparation of the line drawings. A preliminary draft of this paper was improved by helpful suggestions from R. L. Kaesler and

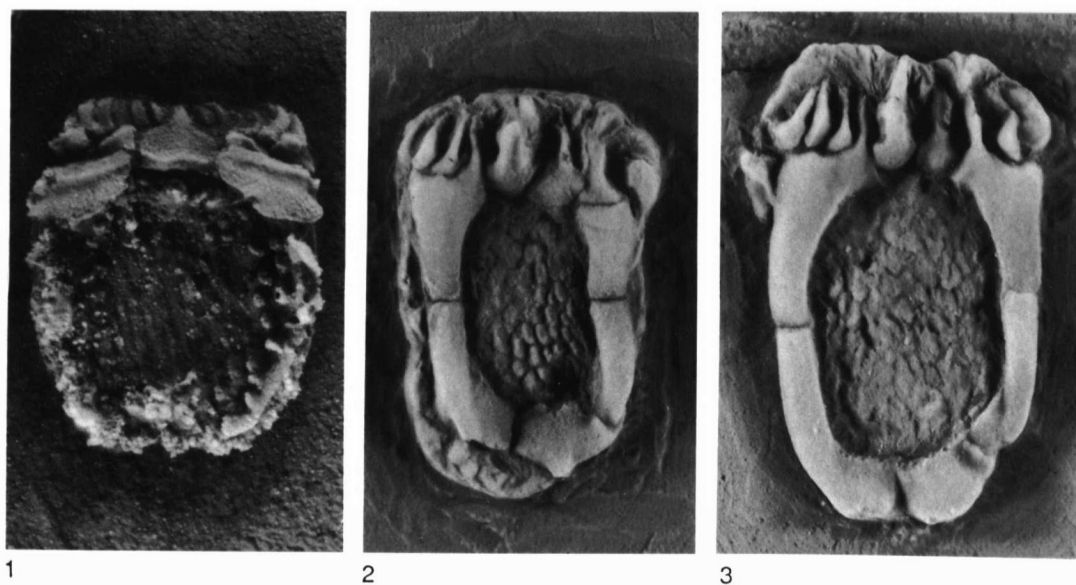


Fig. 1. *Ctenocystis colodon* n. sp. from upper Wheeler Formation, Drum Mountains.—1. Latex cast of superior surface, USNM 423872, $\times 12$.—2. Inferior surface, USNM 423873, $\times 11$.—3. Holotype, inferior surface, USNM 423874, $\times 10$.

James Sprinkle. Additional support was provided by the National Science Foundation under grant number EAR-8519324.

GEOLOGY AND PALEONTOLOGY

The Wheeler Formation in the House Range and Drum Mountains of west-central Utah is composed of an upward-shallowing sequence of marine shale and limestone. Thickness of the formation ranges from as little as 128 m in the House Range to as much as 304 m in the Drum Mountains. Rocks of the Wheeler Formation record the early infilling of the House Range embayment, which was a broad asymmetrical trough that deepened and widened as it extended westward for some 400 km across the Middle Cambrian shelf of western North America (Rees, 1986). Evidence that the embayment was produced by a northeastward-striking, high-angle fault has been presented by Rees (1986), who also described the lithofacies of the embayment and interpreted their depositional environments.

Homalozoans have been found only in the

upper Wheeler Formation. They are preserved in a thin-bedded limestone and shale lithofacies, which has been interpreted to represent mostly pelagic settling of fine-grained sediment in a deep-ramp environment (Rees, 1986:1060–1061). Rare beds with common to abundant homalozoans suggest that these animals were gregarious and lived in small, discrete patches on the seafloor. Little evidence of decay and disarticulation prior to burial suggests that they were overwhelmed and buried alive, perhaps by episodic storm deposits.

The Wheeler Formation contains a diverse biota. Trilobites are the most commonly preserved fossils (Robison, 1964, 1971, 1984), but rare noncalcareous algae and soft-bodied animals (e.g., Conway Morris and Robison, in press) indicate the original presence of a community much like that of the celebrated Burgess shale (Conway Morris, 1979, 1986; Whittington, 1985). Agnostoid trilobites of the upper Wheeler Formation are characteristic of the upper *Ptychagnostus atavus* Interval-zone of middle Middle Cambrian age (Robison, 1984).

SYSTEMATIC DESCRIPTIONS

Subphylum HOMALOZOA

Whitehouse, 1941

Class CTENOCYSTOIDEA Robison
and Sprinkle, 1969Order CTENOCYSTIDA Ubaghs
and Robison, new

Description.—Characters of class (Sprinkle and Robison, 1978:T998-T1001).

Discussion.—This taxon is established to complete the taxonomic hierarchy to which described ctenocystoid species are assigned.

Family CTENOCYSTIDAE Sprinkle
and Robison, 1978Genus CTENOCYSTIS Robison
and Sprinkle, 1969

CTENOCYSTIS COLODON new species

Figures 1, 2

Holotype.—USNM 423874 (Figs. 1,3; 2,1).

Etymology.—From Greek *kolos*, shortened, and *odon*, tooth; in reference to the short anterior process on each of the two anterolateral inframarginal plates.

Material.—Twenty-seven specimens are preserved in medium-gray lime mudstone. All are complete and most are well preserved, but the limy matrix is difficult to remove from the tiny calcitic skeletons. Marginal frame plates are best exposed on three specimens, one showing the superior surface (Fig. 1,1) and two showing the inferior surface (Fig. 1,2,3). Small plates of the central areas (centralia) are not well exposed on any specimen.

Diagnosis.—*Ctenocystis* with relatively short anterior process on anterolateral inframarginal plates. Suboral plates with little or no posterior projection over infracentralia. Suroral plate relatively short.

Discussion.—Specimens of *C. colodon* most closely resemble those of *C. utahensis*, differing most noticeably in the shape and shorter anterior process of the anterolateral inframarginal plates (Fig. 2). Also, two shallowly scalloped spaces along the anterior edge of a prominent shoulder on these plates appear to conform to the ends of two anteriorly adjacent ctenoid plates (Fig. 1,2,3), whereas a less broad shoulder

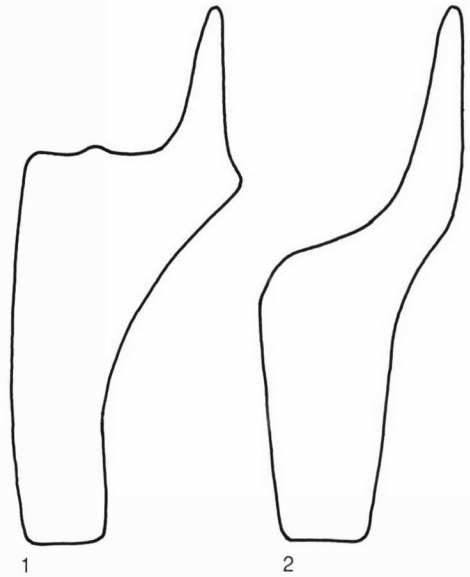


Fig. 2. Shape of anterolateral inframarginal plates in two species of *Ctenocystis*.—1. *C. colodon* n. sp.; based on holotype, compare Fig. 1,3.—2. *C. utahensis*; based on specimen illustrated by Robison and Sprinkle, 1969, fig. 1E.

on plates of *C. utahensis* is flanked by only one ctenoid plate (Robison and Sprinkle, 1969, fig. 1A,D,E). The suroral plate of *C. utahensis* is variable in shape, but on average its main part is longer than that of *C. colodon* (Fig. 1,1). Other exposed plates of *C. colodon* do not appear to differ significantly from those of *C. utahensis*; however, some details were inadvertently obliterated during preparation and others remain obscure. For this reason, neither a detailed description nor a reconstruction of *C. colodon* is attempted here.

C. colodon differs from all other described ctenocystoid species in the lack of conspicuous rearward extension of the two suboral plates.

Occurrence.—All specimens are from a single bed about five meters below the top of the Wheeler Formation in the Drum Mountains. The locality is on a north-facing slope in the SW NE sec. 20, T. 15 S., R. 10 W., of the Drum Mts. Well Quadrangle (7.5 minute topographic map, U.S. Geological Survey, 1971).

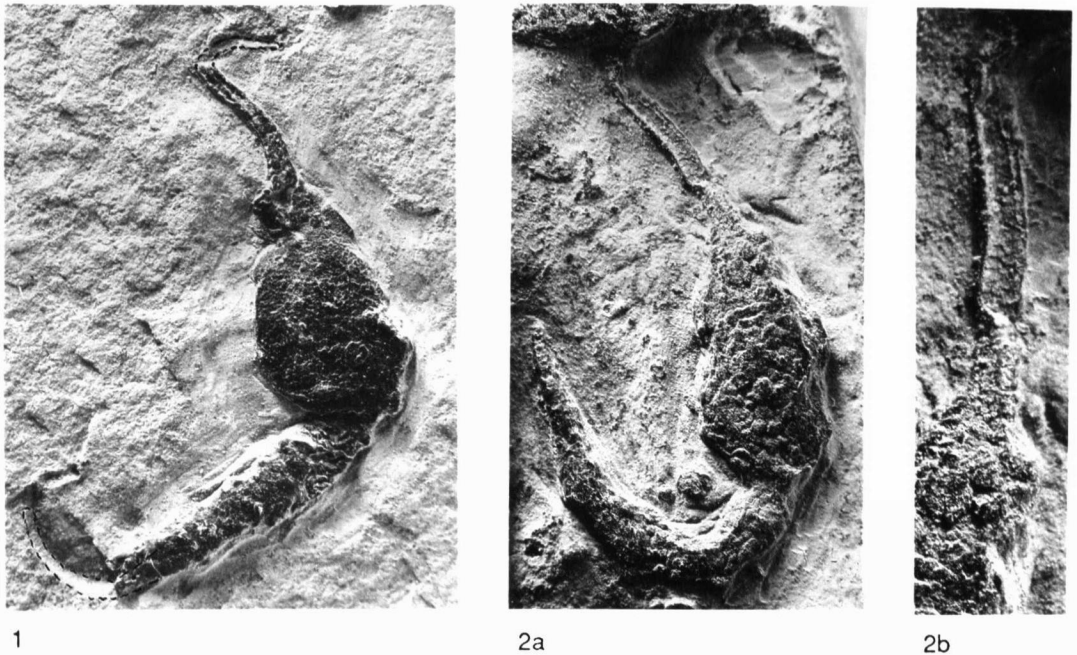


Fig. 3. *Castericystis? sprinklei* n. sp. from upper Wheeler Formation, House Range. —1. Specimen encrusted with calcite, complete except for tips of arm and stele (molds outlined by dashed lines); USNM 423876, $\times 3$. —2. Holotype with arm showing oral groove, theca and stele encrusted with calcite, USNM 423877; a, $\times 3$; b, alternating brachial plates of arm, $\times 6$.

Class HOMOIOSTELEA Gill and
Caster, 1960
Order SOLUTA Jaekel, 1901
Family undetermined
Genus CASTERICYSTIS Ubahgs
and Robison, 1985

CASTERICYSTIS? SPRINKLEI
new species

Figure 3

Holotype.—USNM 423877 (Figs. 3, 2a, b).

Etymology.—Named for James Sprinkle for his many contributions to the knowledge of early Paleozoic echinoderms.

Material.—More than 200 specimens are preserved in light-gray calcareous shale. Most are small calcite-encrusted masses of irregular shape. Some retain the general outline of the body, but only five or six specimens show a few thecal or arm plates and none shows stele plates.

Description.—The theca is elongate, probably pyriform, narrowest at the summit and widest slightly above the base (Fig. 3, 1, 2). In the best preserved specimens, it is about twice as long as wide, ranging from 8 to 11 mm in length and 4 to 6 mm in width. Although a weak proximal lobe may be present, it is not distinct. The arm and stele are at opposite ends of the theca, and both appear to be either axial or subaxial. Conditions of preservation do not allow recognition of an extensiplane, but a relatively high degree of bilateral symmetry is probable. No thecal opening has been observed.

Plates of the theca are polygonal and tessellated. The few that have been observed are large in comparison to thecal size, ranging from 1.3 to 2.5 mm in length and from 1.3 to 1.9 mm in width. External plate surface is smooth, flat or convex, and shows a regularly reticulated stereom of fine hexagonal mesh with openings that are 0.04 mm wide.

The arm is about as long as the theca. Its width decreases gradually in distal direction. Brachial plates are almost twice as wide as long; alternating, they number 4 per mm on each side of the proximal arm (Fig. 3,2*b*). The oral face has a hemicylindrical groove almost as wide as the arm itself, indicating the presence of a large lumen. Cover plates have not been observed; however, the oral groove of some specimens is partly filled with a segmented calcitic structure that probably is an internal mold of the brachial cavity, its shape suggesting that the oral covering of the arm was pointed like a roof.

The stele is about twice as long as the theca. In all available specimens its anatomy has been wholly obliterated by secondary crystallization. Even its division into regions is not clear.

Discussion.—Only two solutans of Middle Cambrian age have been reported, both being from the House Range of western Utah. *Castericystis vali* is from the Marjum Formation, and an unnamed genus and species is from the overlying Weeks Formation (Ubaghs and Robison, 1985). *C.?* *sprinklei* resembles *C. vali* in having an elongate theca without differentiated margins or conspicuous lobes, rather large and nonimbricate thecal plates, and an axial or subaxial arm and stele. It can be distinguished from *C. vali*, however, by its pyriform rather than ovoid thecal outline, a relatively longer arm, and probably fewer thecal plates. It can not be assigned to *Castericystis* with certainty because information is lacking about structure of the stele and position of the anus. It differs from the unnamed solutan in the Weeks Formation, which is poorly known, by having fewer thecal plates and probably a different thecal shape. The occurrence of these three distinct species in rocks of Middle Cambrian age indicates that the solutans were already well diversified at that time.

Occurrence.—About 200 solutans were collected from a single bedding surface in an abandoned commercial trilobite mine in the upper Wheeler Formation at its type locality in Wheeler Amphitheater of the central House Range. The mine is in the NE SE NW sec. 1, T. 17 S., R. 13 W., of the Marjum Pass Quadrangle (7.5 minute topographic map, U.S. Geological Survey, 1972). The fossiliferous bedding surface is probably between

10 and 20 m below the top of the formation and is about 0.5 m below a thin bed that has been mined for its abundant specimens of the trilobite *Elrathia kingii* (Meek). A few more solutans were collected from what is probably the same stratigraphic horizon but in another trilobite mine about 1.15 km to the west-southwest in the NW SE SE sec. 2 of the same township.

Class STYLOPHORA Gill and Caster, 1960

In the *Treatise on Invertebrate Paleontology*, the stylophoran carroids are interpreted as non-radial echinoderms, the skeleton of which is composed of a theca and a jointed appendage, termed an aulacophore, supporting an ambulacrum and serving as a single feeding organ (Ubaghs, 1961). A very different interpretation has been espoused by Jefferies in a series of papers since 1967 and in a recent book (1986). He called the group calcichordates and regarded them as primitive chordates from which arose the vertebrates and other living chordates. According to Jefferies (1986:192), they are provided with a locomotory chordate tail (corresponding to the aulacophore of Ubaghs) and a head (corresponding to the theca), with the "tail and head being accurately homologous with those of a tunicate tadpole and broadly homologous with those of other chordates." A third interpretation (Philip, 1979), while supporting the echinoderm assignment, rejected the identifications of the jointed appendage as either a feeding organ or a chordate tail, but considered it to be a stele homologous with that of other carroid echinoderms. Each of these conflicting interpretations has been accepted by some but rejected by others (as well summarized by Jefferies, 1986:351-358). Our purpose is not to evaluate these differing viewpoints but merely to describe one new species of these strange fossils, which we assign to the Stylophora.

Order CORNUTA Jaekel, 1901
Family COTHURNOCYSTIDAE
Bather, 1913

Genus COTHURNOCYSTIS Bather, 1913

Type species.—*Cothurnocystis elizae* Bather, 1913.

Emended diagnosis.—Theca boot-shaped in outline, with well-differentiated posterior lobe; spinal, glossal, and digital processes present. Knobs or spikes generally prominent on inferior face of some marginal plates. Integument within marginal frame ordinarily plated on both faces. Cothurnopores present.

Discussion.—The diagnosis of *Cothurnocystis* is slightly modified to include some peculiarities of the new species described here. These peculiarities are judged to be of no more than specific importance. Nevertheless, though similar in many respects to typical members of *Cothurnocystis*, this species is only provisionally assigned to the genus because of our incomplete knowledge of some morphological features, especially of the superior face of the theca.

Occurrence.—?Middle Cambrian, Lower-Upper Ordovician; Europe, ?North America (Utah).

COTHURNOCYSTIS? BIFIDA new species

Figures 4–10

Holotype.—USNM 415804 (Figs. 5, 1; 6, 3; 10, 3).

Etymology.—From Latin *bifidus*, split into two parts like a snake tongue; in reference to the forked tips of the cover plates.

Material.—About 100 specimens are preserved in soft, argillaceous, lime mudstone. Approximately two-thirds of the specimens expose the inferior face—that is, the face upon which the animals are thought to have rested in life. Many specimens are covered with a thick crust of secondary calcite. Usually, however, the large spinal process projecting from the right posterior corner of the theca is exposed. Rarely, parts of the thecal frame, glossal process, and digital process are exposed. Parts of the inferior face, including the aulacophore, are free of incrustation in a few specimens. No specimens have the superior face free, and most of its features remain unknown. Many specimens retain the glossal process and at least part of the aulacophore (including cover plates), which suggests rapid burial at or near the place where the animals lived.

Diagnosis.—Theca having very elongate posterior lobe; inferior face of right and left anterior marginal plates with simple denticulate thickenings (no spikes); spinal process large,

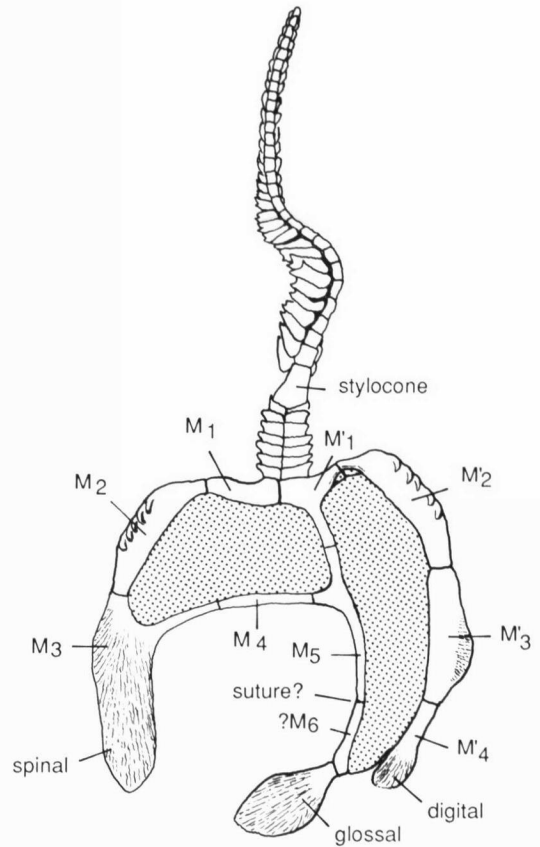
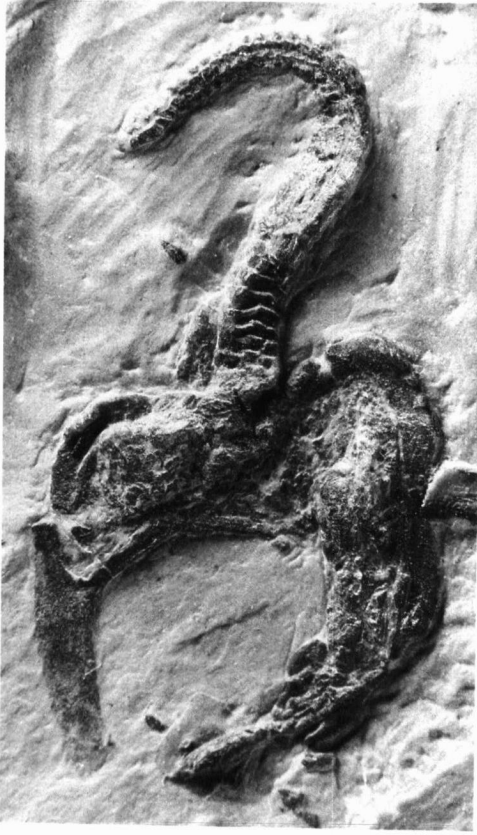


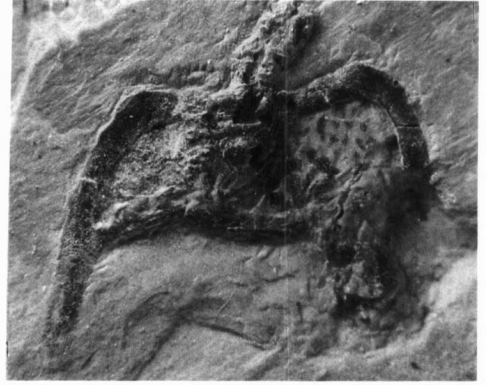
Fig. 4. Reconstruction of *Cothurnocystis? bifida* n. sp. as viewed from the inferior side; M₁–M₆ are marginal plates of the right side, M'₁–M'₄ are marginals of the left side.

glossal moderately large, digital small, a mere outgrowth of left posterior marginal; integument within marginal frame of inferior thecal face a nonplated sheet of extremely thin retiform stereom; adoral plates two or, more likely, three; cothurnopores probably present. Aulacophore about one-third longer than theca; proximal region having 8 rings; inferior face of ossicles in distal region flat or slightly concave; cover plates with forked tips.

Description.—The flattened theca, boot-shaped in outline, has a large spinal process and a long posterior lobe that commonly is curved toward the main axis of the body and prolonged into a well-developed glossal and a smaller



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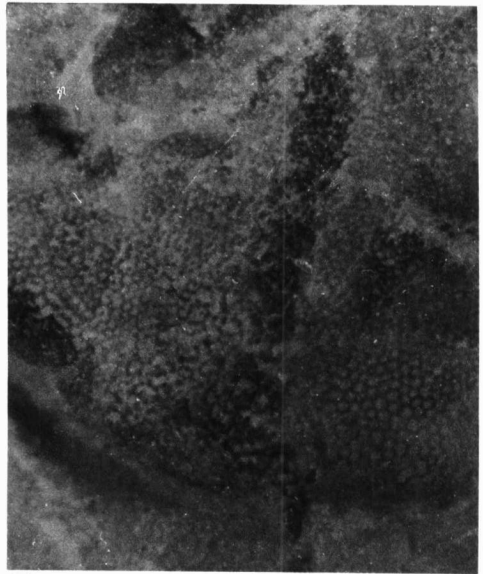
2a



2b



3a



3b

Fig. 5. (Explanation on facing page.)

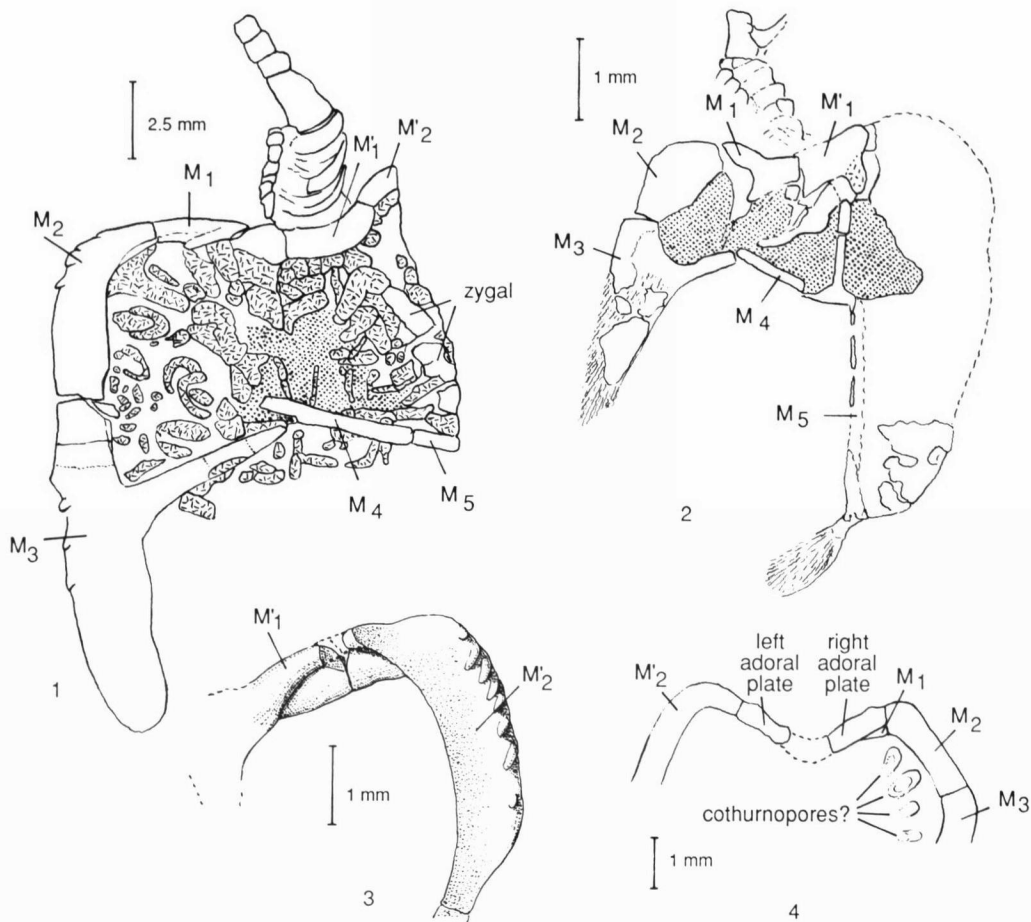


Fig. 6. Theca of *Cothurnocystis? bifida* n. sp.—1. Part of theca and aulacophore, inferior face partly encrusted with secondary calcite, showing remnants of integument (stippled), USNM 415823.—2. Theca and part of aulacophore, inferior face, with integument (stippled) partly preserved (compare Fig. 5, 3a).—3. Holotype, left anterior corner of theca, inferior face (compare Fig. 5, 1).—4. Anterior part of frame, superior face, USNM 415815. See Fig. 4 for explanation of symbols for marginal plates.

digital process (Fig. 4). The anterior margin on the lower side is slightly concave; on the upper side, it has a moderately deep median hollow that houses the aulacophore (Fig. 6, 4). The right anterior corner bends smoothly toward the rear at an obtuse angle, whereas the somewhat salient left corner curves more sharply. It

is on these greatly thickened corners that, in life, the anterior part of the theca was supported. Rearward, the theca becomes much thinner and more even, so that most of the posterior part probably rested on the seafloor.

The theca of the holotype is 10.0 mm long and 8.9 mm wide. That of the largest paratype

Fig. 5. Inferior surfaces of *Cothurnocystis? bifida* n. sp.—1. Holotype (compare Figs. 6, 3; 10, 3), USNM 415804, $\times 6.4$.—2. USNM 415805; a, $\times 6$; b, left anterior portion showing nonplated integument with short irregularly placed spots of darker calcite, possibly representing remains of stiffening rods, $\times 15$.—3. USNM 415827; a, $\times 10.8$ (compare Fig. 6, 2); b, stereom meshwork of integument on both sides of zygag bar (darker median area), $\times 55$.

is 11 mm long and 10 mm wide. That of the smallest paratype is 3.0 mm long and 2.3 mm wide. The ratio of thecal length to width ranges from 1.0 to 1.3.

The thecal frame comprises at least eight, but possibly more, elongate marginal plates, the evidence being unclear about the structure of the posterior region of the theca (Fig. 4). The M_1 is short and slightly curved, widening and bulging in the area of aulacophore insertion. The M_2 is thick and relatively long and wide, except at each end where it narrows and thins; its strongly thickened outer lower edge carries up to eight small knobs that, in many specimens, look like little hooks directed in and back (Fig. 6, 1). The M_3 is forked, with the short anterior branch meeting the M_2 and the much longer and narrower branch forming part of the posterior thecal margin. Where its branches meet, the M_3 expands into a large, almost flat, variably shaped, fixed spinal process, which is more or less posteriorly directed and becomes very thin distally (Fig. 6, 1, 2). The abaxial edge of the spinal is sharp and, in some specimens, serrate; the adaxial edge is thicker and rounded (Fig. 7). The M_4 is a narrow, relatively short, straight or slightly bent plate, with the concave side outward. Whether it is separated from the next marginal plate by a suture or a fracture is not clear, but in all available specimens a discontinuity is evident on the frame. It is followed by a triradiate plate, here designated M_5 , of which one short branch meets the M_4 , another branch runs forward to form the posterior part of the zygial bar, and the third branch runs back along the adaxial edge of the posterior lobe. Whether the rear branch of the M_5 supports the glossal blade directly or whether a short marginal plate, M_6 , intervenes between the M_5 and the glossal, as suggested by some specimens (Fig. 8, 1, 3), remains uncertain.

The glossal process is lanceolate or leaf-shaped, longer than wide, and ordinarily turned toward the main axis of the body (Figs. 5, 1, 3a; 8). It is rather thin, with a sharp adaxial edge and a somewhat thicker and rounded opposite edge. How it fits into the marginal frame is not quite clear, but it looks more like a distinct plate, as in typical species of *Cothurnocystis*, than an outgrowth of the posteriormost right marginal plate, as in species of *Chauvelicystis*.

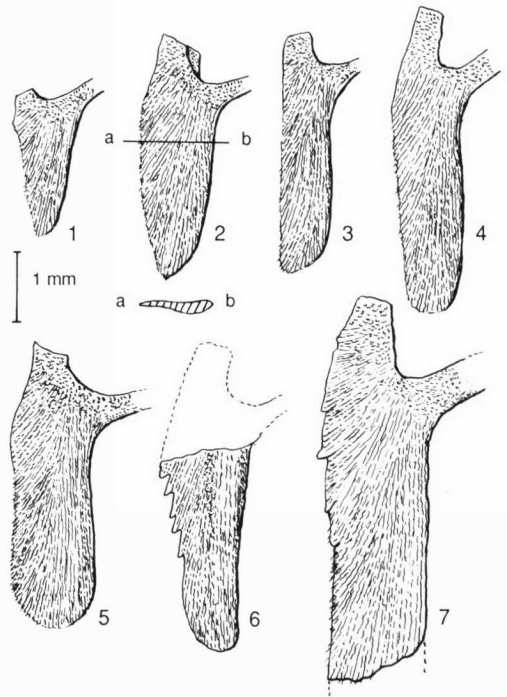


Fig. 7. Spinal process of *Cothurnocystis? bifida* n. sp.—1. USNM 415810.—2. USNM 415811, with cross section below.—3. USNM 415812.—4. USNM 415813.—5. USNM 415814.—6. USNM 415817.—7. USNM 415816; all at the same scale.

Only four marginal plates are present on the left side of the theca. The M'_1 , which is short, sends a branch back to form the anterior part of the zygial bar; its adaxial bulging part houses half of the aulacophore insertion, the other half being housed by the M_1 . The M'_2 is very similar to the M_2 , though more strongly bent. Like the M_2 , the thickened lower outer edge of the M'_2 bears knobs or hooklike protuberances (Fig. 6, 3). At their junction, on the lower side, the M'_1 and M'_2 appear to be divided into a narrow rounded outer portion, which in life was external, and an inner semilunate area, which was internal (Figs. 5, 2b; 6, 3). The M'_3 is about as long as the M'_2 but much thinner; its slightly concave lower face is provided with a thin extension along part of its outer edge (Figs. 4; 5, 1). The M'_4 is short, widens distally, and ends in a flattened short outgrowth, which probably corresponds to the

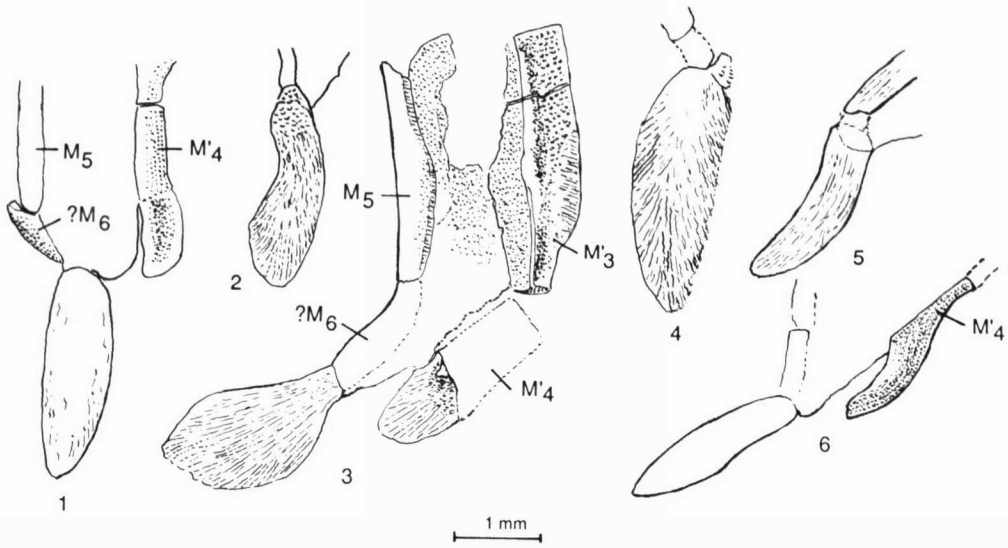


Fig. 8. Glossal and digital processes of *Cothurnocystis? bifida* n. sp.—1. Glossal and digital, USNM 415819.—2. Glossal, USNM 415820.—3. Glossal and digital, USNM 415821.—4. Glossal, USNM 415823.—5. Glossal, USNM 415822.—6. Glossal and digital of holotype (compare Fig. 5,1); all at the same scale.

digital process of previously described species of *Cothurnocystis*, though it is not a distinct appendage of the frame but an integral part of it (Figs. 4; 8,1,3,6).

No marginal plates have been observed between the left and right portions of the frame at the posterior end of the theca, which is poorly preserved in all available specimens. Therefore, it is not clear whether the frame was interrupted or closed at that place.

The external surface of the marginal plates is finely granular. The spinal (Fig. 7), the glossal, and the digital processes (Fig. 8), as well as the extension of the outer lower margin of the M'_3 plate (Fig. 4), are covered with tiny diverging ridges that give a finely striated appearance. These ridges on the spinal and glossal are parallel to the adaxial edge but oblique to the abaxial edge.

The zygial bar connecting the M'_1 and M_5 is composed of two subequal portions. It is straight, rather narrow, and its lower face is slightly concave.

Right and left, subrectangular, adoral plates are supported by the M_1 and M'_1 (Fig. 6,4). These plates are apparently too short to meet or to form an arched structure above the au-

lacophore insertion. Very likely, therefore, a third plate was present between them, but it has not been observed.

The covering of the superior thecal face remains unknown. That of the inferior face consists of a very thin (0.025 mm), smooth, probably supple, calcified integument of retiform stereom having mesh 0.02 to 0.03 mm wide (Fig. 5,3b). Irregularly arranged spots of darker calcite on the integument of some specimens (Fig. 5,2a, b) may represent short stiffening rods but they lack stereomic structure, possibly due to secondary crystallization.

No thecal openings have been clearly observed. When specimens are immersed in alcohol, however, four or five elliptical features appear faintly in the right anterior thecal area on the superior face of USNM 415815 (Fig. 6,4) and possibly USNM 415818. These features probably represent cothurnopores.

The aulacophore (Figs. 4; 5,1) is about one-third longer than the theca. The proximal region (Figs. 9,1; 10,1-3), which makes up one-fifth to one-sixth of the total length of the organ, contains eight distally imbricating endoskeletal rings. Each ring is composed of four plates, two smaller tectals on the upper side,

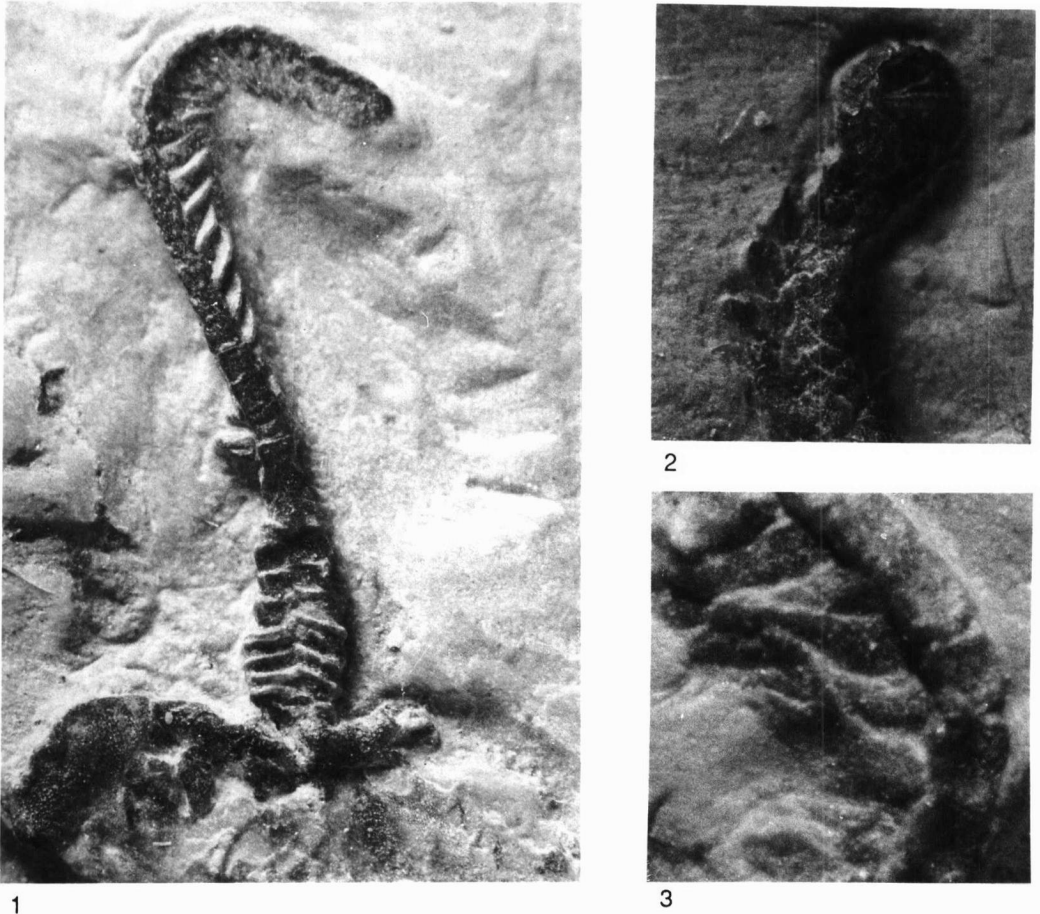


Fig. 9. Aulacophore of *Cothurnocystis? bifida* n. sp.—1. Complete aulacophore, inferior face (compare Fig. 10,1), USNM 415807, $\times 14.3$.—2. Coiled distal end of aulacophore (compare Fig. 10,4), USNM 415824, $\times 16$.—3. Cover plates showing forked tips (compare Fig. 10,5), USNM 415825, $\times 37$.

and two larger inferolaterals on the lateral and lower sides. The outer surface of the inferolaterals is smooth and concave with a slightly protruding distal margin (Fig. 10,1,2). The tectals are more flattened and are arranged like the symmetrical slopes of a pointed roof (Fig. 10,3).

The stylocone, which is a truncated conical ossicle, is barely half as long as the proximal region. The best preserved stylocone (Fig. 10,1) is 0.80 mm long, 0.45 mm wide proximally, and 0.35 mm wide distally (length to width ratio is 1.8). Its lower and lateral surfaces are rounded and finely granular. Its upper face,

which has not been observed, was protected by at least one pair of cover plates inserted near its distal end.

The distal region is about three times as long as the proximal one. It is composed of as many as 30 small ossicles (Figs. 9,1; 10,1,2,4-6). The inferior faces of these ossicles, slightly convex in those near the stylocone, become flat in those following distally, and then concave; their lateral faces are slightly convergent upward and their upper faces (as seen in cross section, Fig. 10,7) have a median groove. Their length and width, which are almost equal, decrease evenly in a distal direction. For

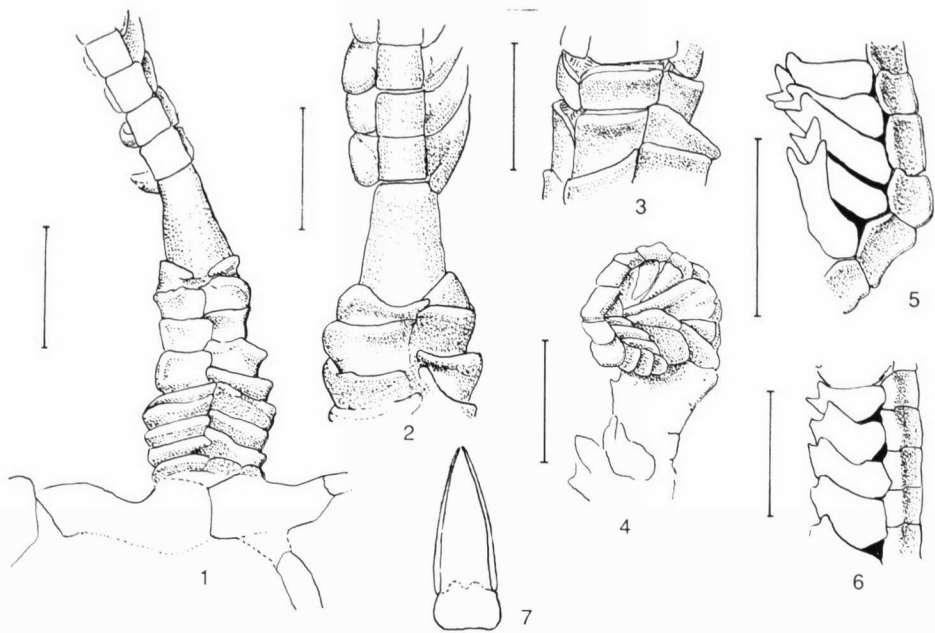


Fig. 10. Aulacophore of *Cothurnocystis? bifida* n. sp. (scale bars all 1 mm).—1. Proximal region, stylocone and part of distal region, inferior face (compare Fig. 9,1).—2. Stylocone and parts of distal and proximal regions, inferior face, USNM 415806.—3. Part of proximal region, superior face of holotype showing tectals (compare Fig. 5,1).—4. Coiled distal end of aulacophore (compare Fig. 9,2).—5. Cover plates (compare Fig. 9,3).—6. Cover plates, USNM 415826.—7. Diagrammatic cross section of distal region.

example, in USNM 415807 (Fig. 9,1) the length decreases from 0.30 mm in the five most proximal ossicles to 0.25 mm in the next five, and it is 0.20 mm in the fifteenth ossicle. The aulacophore does not end abruptly, as Jefferies (1973:416; 1981:498) supposed to be the case in all stylophorans, but narrows gradually and terminates distally in a blunt point.

The cover plates are inserted on the distal parts of the ossicles. They are remarkably high, being about five times higher than the lateral sides of the ossicles that carry them (as seen in cross section, Fig. 10,7). Their lateral margins are curved, and each one slightly overlaps the next one in distal direction. Their free end, which is very thin and rarely preserved, is divided into diverging tips, separated by a wide but moderately deep cleft (Figs. 9,3; 10,5,6). Somewhat similar cover plates are present in the eocrinoid *Kinzercystis durhami* Sprinkle, each having two small distal projections that overlap

into the next cover plate (Sprinkle, 1973:74, text-fig. 5A).

Although details of the articulation between ossicles of the distal region are unknown, the curved or even contorted positions of this part of the aulacophore, as preserved in many specimens, suggest a fair amount of flexibility. The terminal portion could even coil upon itself (Figs. 9,2; 10,4), which is a peculiarity not previously reported in other cornute stylophorans.

Discussion.—The cornute species described here is similar to such typical species of *Cothurnocystis* as *C. elizae* and *C. fellinensis* in having a theca with a distinctly boot-shaped outline and a well-differentiated posterior lobe, a narrow marginal frame within which stretches an integument (at least on the inferior face), a large spinal and two posterior processes (glossal and digital), and probably cothurnopores. It differs, however, from all or some described

species of *Cothurnocystis* in having small knobs instead of spikes on the thickened outer edges of its M_2 and M'_2 , a nonplated integument on the inferior thecal face, a marginal frame that may be interrupted at the posterior end of the theca, a spinal process borne on the third rather than fourth right-marginal plate of the theca, and possibly a marginal M_4 plate (Fig. 11,1).

The knobs on the lower outer margin of the M_2 and M'_2 are likely morphological equivalents of the spikes or protuberances on corresponding plates in, for example, *C. elizae* and *C. primaeva*, and are judged to be a species-level character.

Structure of the integument of the lower thecal face is diverse in described species of *Cothurnocystis*. Therefore, a continuous sheet of very thin retiform stereom in *C. ? bifida* rather than a plated and apparently flexible pavement is judged to be a species character, but it does not seem to warrant the assignment of this species to another genus.

Possible interruption in the posterior marginal frame may be taxonomically more significant, but evidence about this point is not clear. Posterior interruption of the marginal frame is a distinctive feature of the Amygdalothecidae (Fig. 11,9; Ubaghs, 1970; Jefferies and Prokop, 1972) and possibly the cothurnocystid *Chauvelicystis* (Fig. 11,6; Ubaghs, 1983). Our new species is not attributed to this genus for, among other features, it lacks characteristic marginal spines. Its thecal outline resembles that of the amygdalothecid *Galliaecystis* (Fig. 11,9), but there is no transverse bar on its superior face at the base of the posterior lobe (as established by exposing the inner face of the M_5 and M'_3 in USNM 415808), and its marginal frame lacks spikes on its lower face. Moreover, it possesses both a glossal and a digital process, a condition that has not been observed in *Galliaecystis*.

The location of the spinal process on the third instead of the fourth right-marginal plate of the theca is common to all described Cambrian species of Stylophora: *Ceratocystis perneri*, *C. vizcainoi*, *Protocystites menevensis*, *Nevadaecystis americana*, and seemingly the undescribed cornute from the Spence Shale figured by Sprinkle (1976, pl. 1, fig. 1). This probably primitive feature is retained in *Cothurnocystis primaeva* and *C. melchiori* (Fig. 11,5) from the Lower Ordovician, as well as in the

Scotiaecystidae (Fig. 11,7,8) and *Galliaecystis* of the Amygdalothecidae (Fig. 11,9). In all other Ordovician species of *Cothurnocystis*, including the type *C. elizae* (Fig. 11,4), and in *Chauvelicystis* (Fig. 11,6), the spinal process is borne by the fourth right-marginal plate. How the passage from one condition to the other was effected is not clear. It, however, does not seem to be of primary taxonomic importance because both conditions are present in *Cothurnocystis primaeva* (Jefferies, 1969:497).

A marginal M_4 , distinct from the following triradiate M_5 , is not present in typical species of *Cothurnocystis* (Fig. 11,4) but is present in *C. melchiori* (Fig. 11,5) and in all members of the Scotiaecystidae (Fig. 11,7,8). In thecal outline and frame structure, *C. melchiori* is more like species of the scotiaecystid *Bohemiaecystis* (Fig. 11,8) than, for example, *C. elizae* (Fig. 11,4). However, it possesses cothurnopores rather than lamellipores and for this reason was assigned to *Cothurnocystis* (Ubaghs, 1983). In *C. ? bifida*, the thecal outline is decidedly more cothurnocystid than scotiaecystid, and no character except the questionable M_4 suggests scotiaecystid affinities. This feature alone probably should not preclude assignment of this species to *Cothurnocystis*.

C. ? bifida is easily distinguished from all described Cambrian stylophorans. It differs from species of *Ceratocystis* (Fig. 11,2) in its more distinctly boot-shaped and transversely elongate thecal outline, long posterior lobe, narrow marginal frame, thin nonplated integument rather than a rigid pavement of large plates on the inferior thecal face, and well-differentiated zygial, spinal, glossal, and digital processes. It differs from *Nevadaecystis americana* (Fig. 11,3) in its thecal outline, absence of prominent spikes on some marginal plates, unplated and flexible inferior thecal face, and clearer differentiation of the zygial bar from adjoining integument. Many features of *C. ? bifida* are present in the undescribed early Middle Cambrian stylophoran of the Spence Shale (Sprinkle, 1976), but differences in thecal outline and shape of the marginal appendages are obvious.

C. ? bifida resembles *Protocystites menevensis* by its long posterior lobe and extremely thin integument of retiform stereom (Jefferies, Lewis, and Donovan, 1987). Also, in places the integument may have been stiffened by irregularly

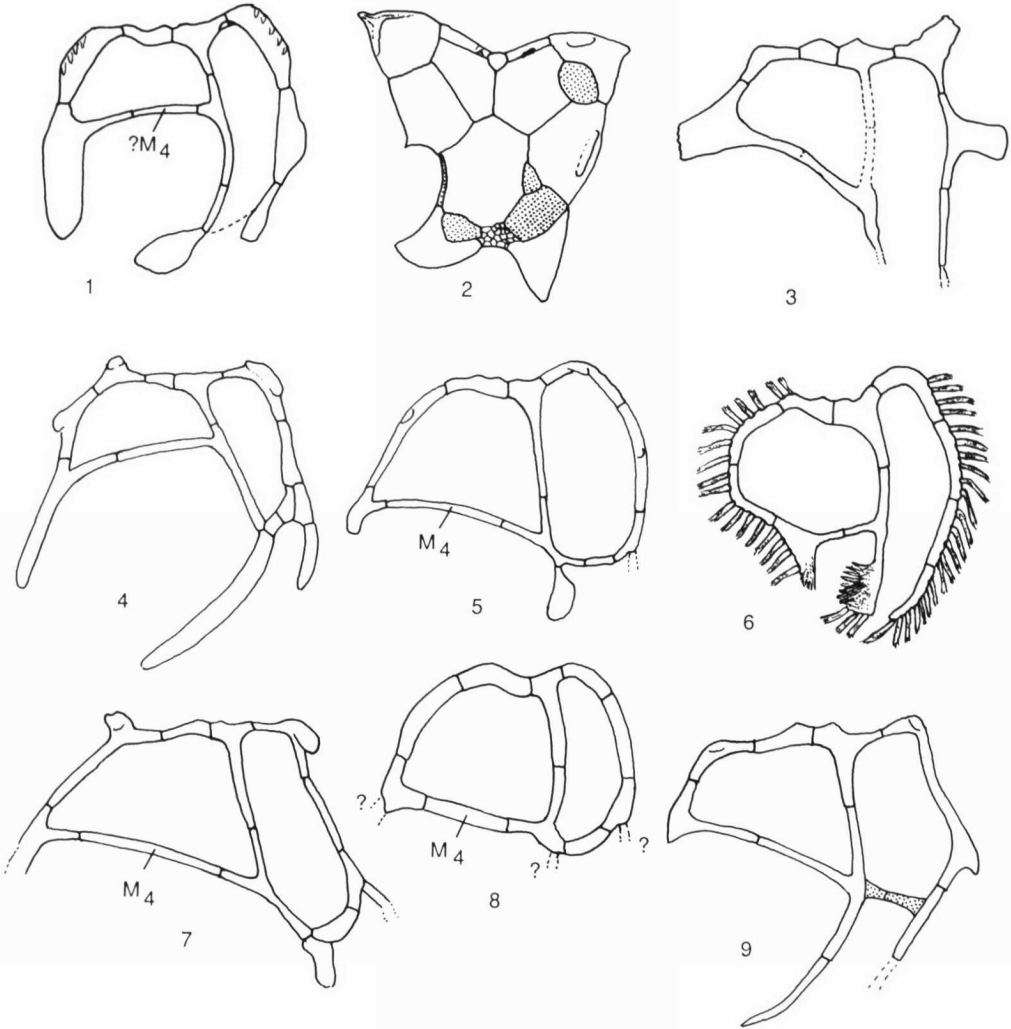


Fig. 11. Marginal frame, inferior face, among Cornuta (not to scale).—1. *Cothurnocystis? bifida*, Middle Cambrian, Utah.—2. *Ceratocystis perneri* (central plates stippled), Middle Cambrian, Bohemia.—3. *Nevadaecystis americana*, Upper Cambrian, Nevada.—4. *Cothurnocystis elizae*, Upper Ordovician, Scotland.—5. *Cothurnocystis melchiori*, Lower Ordovician, France.—6. *Chauvelicystis spinosa*, Lower Ordovician, France.—7. *Thoralicystis griffeti*, Lower Ordovician, France.—8. *Bohemiaecystis bouceki*, Middle Ordovician, Bohemia.—9. *Galliaecystis lignieresi* (bar of superior face, stippled), Lower Ordovician, France.

placed rodlike structures (Fig. 5,2a,b). Within the lower marginal frame, however, the integument of *C.?* *bifida* forms a continuous sheet rather than being divided into plates. *C.?* *bifida* further differs from *P. menevensis* in thecal outline and has a less robust skeleton, a better differentiated marginal frame, a clearly distinct zygial bar, and differently shaped spinal, glosal, and digital processes.

C.? *bifida* also closely resembles some incomplete specimens from the uppermost Cambrian of Nevada, which have been identified (possibly erroneously) as *Phyllocystis* sp. (Ubaghs, 1963). Similarities include a lack of spikes on the lower face of the M_2 and M'_2 plates and the presence of small knobs on the thickened lower outer margin of at least the M'_2 . Differences are the presence in the Nevada specimens of a plated

integument on the inferior thecal face and six rather than eight rings in the proximal region of the aulacophore.

Comparison of *C.?* *bifida* with the two described species of *Ceratocystis*, *Protocystites menevensis*, and the undescribed new cornute stylophoran from the Spence Shale of northern Utah (Sprinkle, 1976) demonstrates that by Middle Cambrian time the cornute stylophorans were already well diversified and variously specialized. This suggests a more remote origin for the stylophorans.

Occurrence.—The locality is just south of an unimproved road along the southern flank of Antelope Mountain in the central House Range, Utah. It is in the SE SE NE sec. 35 (unsurveyed), T. 17 S., R. 13 W., of the Marjum Pass Quadrangle (7.5 minute topographic map, U.S. Geological Survey, 1972). All stylophorans are from the surface of a single thin bed of soft, light-gray, argillaceous, lime mudstone. The stratigraphic position of the bed has not been precisely determined, but it probably is between 15 and 30 meters below the top of the Wheeler Formation.

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