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CARDIOCYSTELLA, A NEW CORNUTE STYLOPHORAN FROM THE UPPER CAMBRIAN WHIPPLE CAVE FORMATION, EASTERN NEVADA, USA

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INTRODUCTION

TWO NEW well-preserved cornute stylophorans from the Upper Cambrian Whipple Cave Formation represent a new genus and species assigned here to *Cardiocystella prolixora*. These nearly complete specimens contain morphological information not available from other cornute specimens previously collected from this formation. Both specimens are preserved with superior faces exposed. One specimen contains a nearly complete theca but a somewhat disrupted aulacophore, whereas the other theca has been partially damaged by burrows but has a nearly complete but moderately eroded aulacophore. *Cardiocystella prolixora* exhibits wide marginals, abundant supracentral platelets, and an aulacophore with cover plates. Supracentral platelets cover much of the interior regions of the theca, which lacks a visible zygal bar in both specimens. In holotype 1791TX13, a bulge in the superior face of the theca likely shows the zygal bar position. The wide marginals of these new specimens resemble those of a specimen previously described from a partial theca and aulacophore assigned to *Archaeocothurnus* species indeterminate (Sumrall et al., 1997); however, the specimens described here are heart-shaped rather than boot-shaped. The placement of this specimen in a new genus and species is based on its unique marginal shape and arrangement.

PREVIOUS WORK

Echinoderm members of the Cambrian Evolutionary Fauna, such as cornute stylophorans, eocrinoids, homoiosteleans, and edrioasteroids, are major contributors to skeletal concentrations in Upper Cambrian strata of the Great Basin (Sumrall et al., 1997). However, articulated specimens are rarely found. Recent fieldwork in the Upper Cambrian Whipple Cave Formation (Fig. 1) yielded two exceptionally-preserved cornute stylophorans. These specimens are nearly complete and contain morphological information that has not been preserved in cornute specimens previously collected from the Whipple Cave Formation.

Stylophorans, which comprise the Cornuta and Mitrata, are an enigmatic extinct clade of echinoderms that appeared during Middle Cambrian time and persisted until the Pennsylvanian (Late Carboniferous) (Kolata et al., 1991). Much research on stylophorans has focused on determining whether: 1) these organisms represent an extinct clade of echinoderms or basal chordates (Jefferies, 1986, 1997; Philip, 1979; Parsley, 1997; Lefebvre, 2000; David et al., 2000; Clausen and Smith, 2005); 2) intraclade relationships and homology (Parsley, 1997, 1998; Lefebvre et al., 1998; Lefebvre and Vizcaino, 1999; Lee et al., 2005, 2006; Lefebvre and David, 2001; Ruta, 1999, 2003; Parsley and Sumrall, 2007; Sumrall and Wray, 2007); as well as 3) understanding their paleoecology (e.g., Sumrall et al., 1997; Sumrall and Sprinkle, 1999) and functional morphology (Parsley, 1998; Sutcliffe et al., 2000; Lefebvre and David, 2001; Lefebvre, 2003).

Late Cambrian cornute stylophorans of the western United States are known from only a handful of specimens (e.g., Ubaghs, 1963; Sumrall et al., 1997), and the same pattern persists globally (Smith and Jell, 1990; Ubaghs, 1998; Lee et al., 2005). Most of the cornutes described are ~1 cm long, boot-shaped, and only rarely articulated. The abundance of echinoderm debris in Upper Cambrian strata of the western United States suggests that echinoderms were at times abundant; however, their paleoenvironmental preference (e.g., Lefebvre and Fatka, 2003) may not have been conducive to the preservation of whole specimens. Because they are so rarely preserved as articulated individuals, the preservation and environmental context of these specimens provide valuable information on the life-habit and substrate preference of cornutes; such information is important for understanding the ecology of echinoderm members of the Cambrian Evolutionary Fauna in light of the critical role which life-habit and substrate played in the subsequent radiation of echinoderm members of the Paleozoic Evolutionary Fauna (Guensburg and Sprinkle, 2000) during the Ordovician radiation.

LOCATION AND STRATIGRAPHY

The Whipple Cave Formation (Kellogg, 1963) is uppermost Cambrian (Sunwaptan) in age; it is underlain by the Dunderberg Shale Member of the Nopah Formation and overlain by the Lower Ordovician House Formation (Taylor et al., 1989). Specimens of *Cardiocystella prolixora* n. gen. and sp. were recovered from outcrops of the Upper Member of the Whipple Cave Formation exposed in Sawmill Canyon, approximately 10 km northeast of the town of Lund in White Pine County, eastern Nevada (Fig. 1; see Taylor et al., 1989 for precise directions). At Sawmill Canyon, this unit consists of medium to thick-bedded carbonate mudstones, wackestones, and dolostones with thin, sparsely distributed packstones and grainstones. Large (3–5 m) microbial buildups also occur in at least two horizons, and microbial textures are common in many beds. This suite of features is interpreted to represent subtidal deposition on a gently dipping carbonate ramp (Cook and Taylor, 1975; Taylor et al., 1989).

PALEOENVIRONMENT AND TAPHONOMY

Both specimens of *Cardiocystella prolixora* n. gen. and sp. (1791TX13 and 1791TX14) were found on carbonate mudstone bedding planes, and were associated with disarticulated trilobite debris and moderate bioturbation (ii2-3; Droser and Bottjer, 1986). The interior portion of the theca and the thecal opening of the paratype specimen were disturbed by burrows. The burrows consisted primarily of horizontal tubes that penetrated shallowly into the sediment (<0.5 cm). The disruption of this specimen by burrows suggests that the substrate on which it was preserved was soft to firm, but not a hardground. The holotype specimen showed no internal disturbance from burrows, although a portion of the aulacophore was displaced. Articulation of these specimens, and specifically the abundance of preserved supracentral platelets, suggests these organisms were buried rapidly, perhaps at the time of death, prior to disarticulation or scavenging.

The nature of this substrate provides important paleoecological and taphonomic information. Many of the early echinoderms were specially adapted to hard substrates such as hardgrounds, flat-pebble conglomerates, and microbial build-ups by attaching to the sediment (Sumrall et al., 1997). Cornute stylophorans, however,

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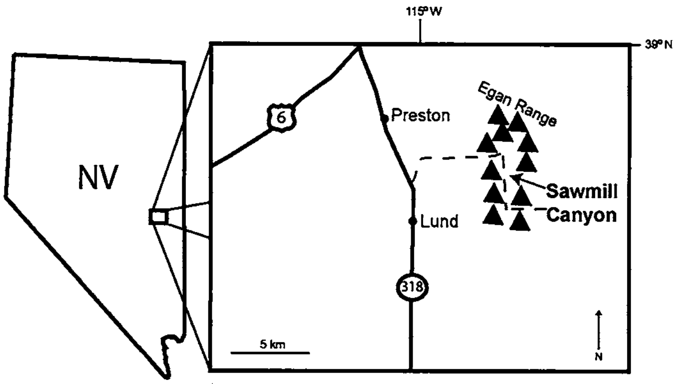

FIGURE *1*—Locality map of the Upper Cambrian Whipple Cave Formation, Sawmill Canyon, White Pine County, eastern Nevada. Specimens were found on north side of canyon wall on a bedding plane.

are not thought to have attached the substrate but rather lived as vagile deposit feeders (e.g., Guensburg and Sprinkle, 2000). These organisms likely lived in quiet-water environments on soft to firm substrates that were occasionally bioturbated and periodically subject to storm events. The lack of a robust skeleton, loose articulation of skeletal elements, and the inability to attach to the substrate may explain why fully articulated specimens have only rarely been found.

SYSTEMATIC PALEONTOLOGY

Class STYLOPHORA Gill and Caster, 1960
Order CORNUTA Jaekel, 1901
Suborder COTHURNOCYSTIDA (Bather, 1913)
Family COTHURNOCYSTIDAE Bather, 1913
Genus CARDIOCYSTELLA new genus

Type species.—*Cardiocystella prolixora* n. gen. and sp.

Diagnosis.—Corthurnocystid with heart-shaped theca lacking spines and marginal processes, complete zygal bar and M5/M′5 bar inferred, and two adorals and small centralia present.

Etymology.—*Cardiocystella* n. gen. is derived from the Latin word *cardio* meaning heart, and *cystella* meaning little sac, which describes the small heart-shaped theca.

Occurrence.—*Cardiocystella prolixora* n. gen. and sp. is known from two specimens from the Upper Cambrian Whipple Cave Formation, eastern Nevada.

Discussion.—*Cardiocystella* n. gen. is assigned to Cothurnocystidae based on the presence of an MC plate positioned between M2 and M3, and the apparent closure of the theca by an M5/M′5 bar on the posterior end of the theca. It differs from chauvelicystine cothurnocystids by bearing a posterior bar of M5 and M′5. It conforms well to other cothurnocystine cothurnocystids in terms of marginal plating, but differs from *Cothurnocystis* Bather and *Arauricystis* Lefebvre and Vizcaino by the digital and glossal enclosing the posterior end of the theca. The similarly shaped *Phyllocystis* Thoral can be easily distinguished by the absence of digital and glossal plates.

CARDIOCYSTELLA PROLIXORA new species
Figures 2–5

Diagnosis.—As *Cardiocystella* is monotypic, generic and specific taxobases are the same.

Description.—Cornute with small, heart-shaped theca, slightly longer than wide with closed posterior frame margin, holotype theca 8.8 mm long and 7.7 mm wide, and paratype theca 7.4 mm long and 6.3 mm wide (Figs. 2, 3); marginal frame known only from dorsal surface, consists of 11 elements including digital, glossal, and zygal plates, theca heart-shaped with slight anterior invagination where aulacophore inserted; right thecal corner along M2 extends somewhat more anterior than left corner along M′1

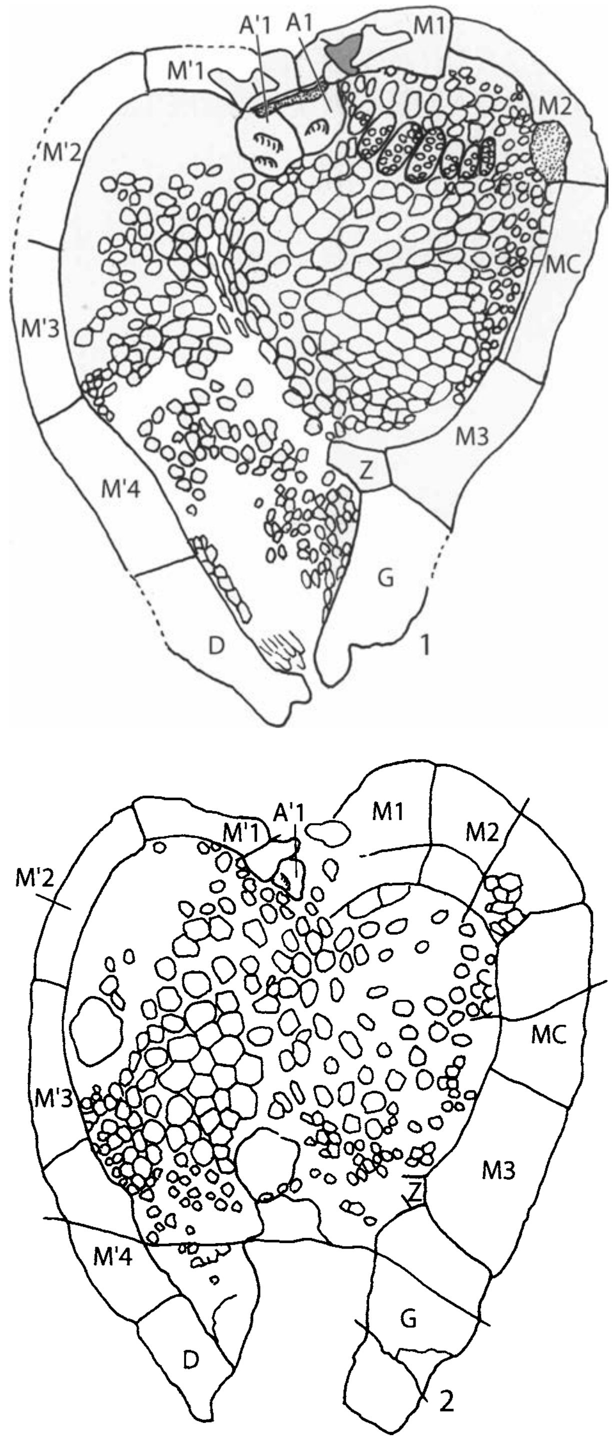

FIGURE 2—Thecal drawings for each specimen of *Cardiocystella prolixora* n. gen. and sp. *1*, holotype showing superior face. Two adorals are shifted slightly left and the cothurnopores are covered by small platelets, ×10; *2*, paratype showing partly weathered through superior face with incomplete posterior margin, ×12; A = adoral; C = cothurnopores; D = digital; G = glossal; M = marginal; P = periproct; Z = zygal.

and M′2 suture; theca reaches maximum width along suture between M2 and M3 on right and M′3 on left; theca narrows posteriorly with gently rounded left margin and essentially straight right margin that is slightly inset at zygal in holotype; posterior corner sharp, formed at junction between digital and glossal plates; right margin formed from five plates, M1 relatively large, sharply curved, indented along midline where aulacophore inserts,

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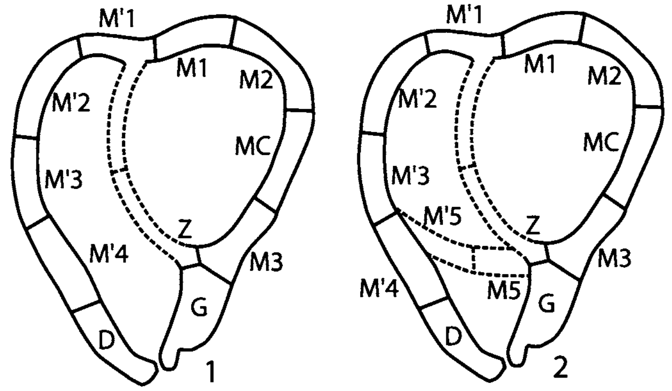


FIGURE 3—Alternate interpretations of the marginalia of *Cardiocystella prolixora* n. gen. and sp. based on disruption patterns of the centralia; *1*, marginals based on holotype with inferred zygal bar; *2*, marginals with inferred zygal bar and M5/M'5 bar. Number 2 is the preferred interpretation.

narrowly expressed along anterior margin of dorsal surface, apparently with much wider expression on ventral surface (Figs. 2.3, 3.2); inner side of plates hollowed out and bearing poorly developed apophyses; large scutulae present on each plate marking attachment points of adorals; scutulae connected by low transverse ridge extending along posterior margins of apophyses (Fig. 2.1); oblique anterior groove present along edge of right scutula and transverse anterior groove present posterior to low transverse ridge; M2 long curved forming anterior right corner of theca, with narrow expression on dorsal surface that becomes wider with proximity to MC suture, and apparently wider expression on ventral surface. MC long, straight, with wide flange along outer margin. M3, long nearly straight with wide flange on outer margin, linear margin curves toward thecal interior where plate sutures to zygal; glossal poorly preserved in both specimens, apparently long, straight, with very wide flange along outer margin, suture with digital not preserved; left margin formed from five plates, ventral surface information lacking in available material; M'1 relatively large, equal in size to M1, sharply curved, indented along midline where aulacophore inserts, process extending towards center of theca forming portion of zygal bar; M'2 long, evenly curved, forms proximal left corner of theca, narrowly exposed on dorsal surface; M'3 long, gradually curved, narrowly exposed on dorsal surface; M'4 long, nearly straight, narrowly exposed on dorsal surface; digital long, slightly curved especially at posterior point where may form distal point on thecal margin, narrowly exposed on dorsal surface; zygal bar poorly constrained; zygal plate apparent on both specimens along M3/glossal suture; zygal passes under dorsal centralia integument near margin but is apparent in gently curved ark from zygal to M'1 where centralia disrupted (Figs. 2.9, 4); second M5/M'5 bar apparently connecting M'4 to zygal and glossal, placement suggested where centralia disturbed in posterior portion of theca, poorly constrained (Figs. 2.9, 4). Two adoral plates present, each about 0.7 mm wide; A1 large triangular, with deep pit in surface; A'1 large round, with two pits in surface; A0 apparently not present in taxon; adorals articulate to processes on M1 and M'1 framing aulacophore insertion point; internal details of M1/M'1 symphasis exposed in holotype; aulacophore attaches to deeply depressed area along suture about 0.45 mm wide; lateral edges formed from tall triangular processes on M1 and M'1; adorals (displaced in holotype) articulate to processes forming the dorsal margin of anterior thecal opening. Dorsal integument formed from numerous small adjacent centrals; centrals polygonal, generally hexagonal, equant, largest in holotype where 0.4 mm just posterior to cothurnopores, generally smaller toward marginal frame and left side of theca where typical plate 0.15–0.25 mm (Figs. 2.3, 2.9, 3); ventral integument not seen in available material; cothurnopores position

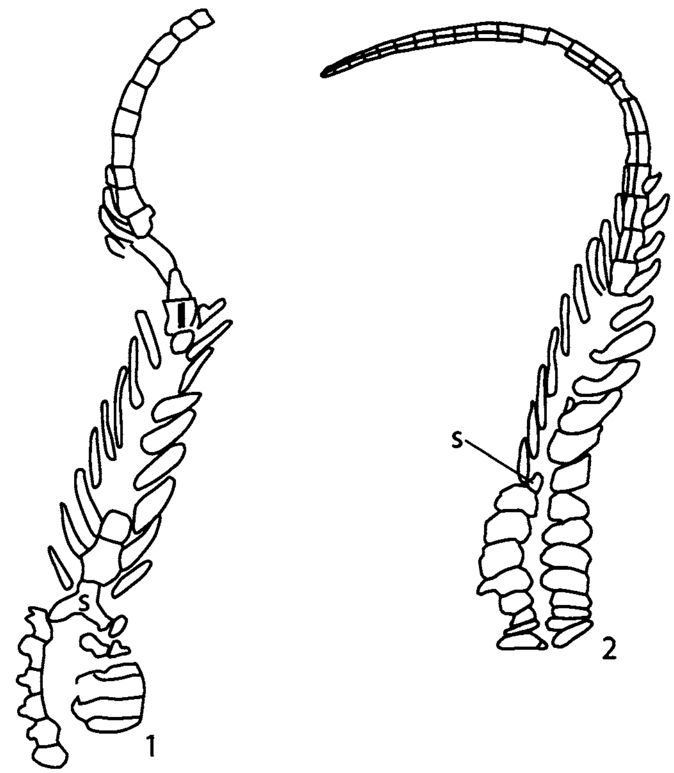
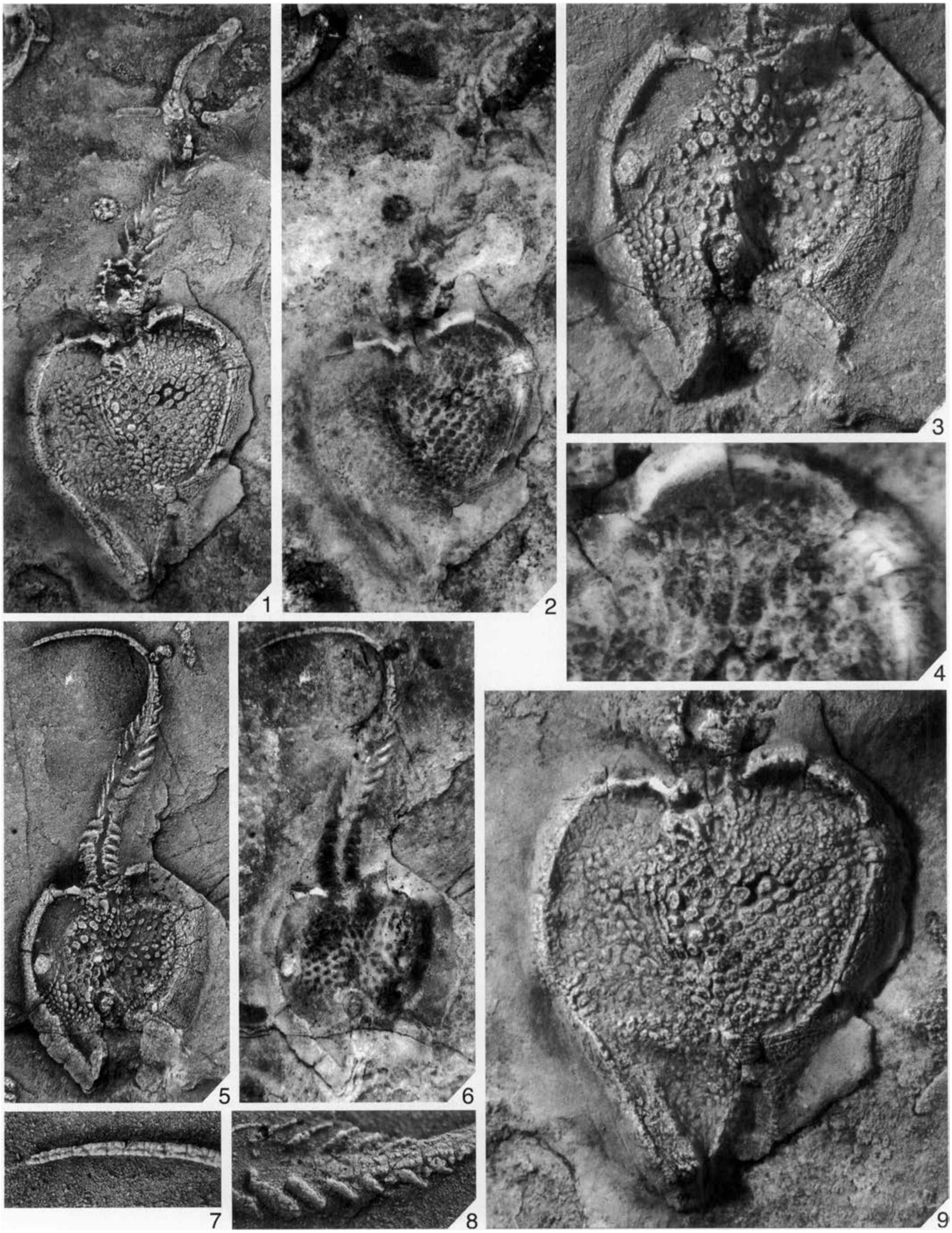


FIGURE 4—Drawing of the plating of the aulacophore of *Cardiocystella prolixora* n. gen. and sp., both ×10. *1*, holotype showing weathered through proximal aulacophore, weathered stylocone and somewhat incomplete distal aulacophore; *2*, paratype 1791TX14 with mostly complete proximal aulacophore, slight exposure of the stylocone and a nearly complete distal aulacophore with the cover plates weathered away distally. Note that in both specimens the distal aulacophore is preserved with the cover plates open.

in anterior right edge of dorsal integument in arc concave anteriorly (Figs. 2.4, 3.1), minimally seven in holotype where right edge not preserved, but number likely eight or nine; cothurnopores oval, anterior-posteriorly elongate forming a sweeping pattern, largest positioned centrally, 0.8 mm high 0.25 mm wide in holotype, decreasing in size laterally; cothurnopores covered by integument of extremely small platelets that hint of close packed placement in alternating rows of two-three plates, equant, 0.06–0.08 mm across; anal opening possibly marked by somewhat lathe-shaped plates at extreme posterior margin, but plates very poorly preserved here in holotype (Figs. 2.9, 3.1); inferior surface unknown except for trace of zygal and potentially M5/M'5 bar where supracentrals disrupted. Complete aulacophore one and one half times length of theca (Fig. 2.5, 2.6); complete aulacophore in paratype 11.8 mm long; proximal aulacophore poorly preserved in both specimens with up to eight telescopic flexible rings formed from paired tectals and paired inferolaterals; lumen relatively large; stylocone known from poorly preserved holotype, conical, 0.6 mm long, 0.7mm wide; distal aulacophore composed of small hemicylindrical ossicles (brachials) and elongate cover plates; 29 preserved segments in paratype and perhaps two more apparent as node where weathered away at tip, gradually tapers distally; brachials 1.5 times as long as wide, upper surface with median groove bounded by raised lip otherwise poorly preserved (Fig. 2.7), cover plates poorly preserved, two per brachial, preserved open in both specimens exposing median groove (Figs. 2.1, 2.5, 2.8, 5); lower surface unknown.

Material.—*Cardiocystella prolixora* n. gen. and sp. is known from two specimens, both of which preserve a nearly complete upper aspect. Holotype 1791TX13 was found by J. Adrain and later given to Sumrall for description (Figs. 2.1, 3.1). It is preserved with theca almost completely intact. Left thecal region is



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slightly depressed into the sediment relative to the right side. Some bulging of theca occurs over zygal bar. Left thecal region is partially eroded, but right thecal region preserves most if not all supracentral platelets. All marginalia are preserved as are adorals. Stylocone is preserved, but is slightly telescoped into the sediment. Proximal end of aulacophore is broken, but distal end of aulacophore is preserved somewhat displaced to the left. Paratype 1791TX14 was found by Pruss and Finnegan, is slightly weathered, disrupted, and covered by a few burrows (largest one removed), and the aulacophore is preserved slightly twisted but complete almost to the distal tip (Figs. 2.2, 3.2). Some disruption of interior of cornute caused by burrows. Paratype 1791TX14 was exposed on a limestone bedding plane that contained disarticulated trilobite debris and both horizontal and vertical burrows.

Occurrence.—Cardiocystella prolixora n. gen. and sp. is known only from the Upper Cambrian Whipple Cave Formation from the Sawmill Canyon locality, White Pine County, eastern Nevada.

Etymology.—Prolixora is a compound of the Latin prolixus (wide) and ora (rim), which refers to the diagnostic wide marginals around the edge of the theca.

Discussion.—The presence and trace of the zygal on the inferior surface can clearly be seen where plates are disrupted in the supracentral series (Fig. 3.1). However, a second zone of disruption on the holotype seems to connect the zygal to M′4. If this second trace reflects an underlying bar on the lower surface, it would most likely be M5 and M′5 (Fig. 3.2). Such a plating pattern would imply stronger cothurnocystine affinities than chauvelicystine affinities. The width of the marginals is poorly constrained because of weathering of the thin edges.

Cardiocystella prolixora n. gen. and sp. is clearly different from other specimens described from the Whipple Cave Formation. *Nevadaecystis americana* (Ubaghs) has large lateral processes on the marginals and large stellate supracentrals. *Archaeocothurnus* sp. (Ubaghs) has centralia nearly the same size but strongly differs in the curvature of M2 and M′2. *Scotiaecystis*? sp. (Sumrall et al., 1997) is a poorly preserved juvenile, with wide marginals and small centralia, but differs in the thin lamellipores and the unusual plate growth pattern.

Cardiocystella prolixora n. gen. and sp. differs from other North American Late Cambrian Stylophora by shape of the marginals. *Archaeocothurnus goshutensis* Sumrall et al. has a strongly curved MC (M3 in Sumrall et al., 1997) with a wide flange, and a differently shaped zygal. *Acuticarpus*? *republicensis* Sumrall et al. has different curvature of the M′2 plate, much larger centrals, and three adorals. Other North American species are too poorly preserved to warrant comparison.

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FIGURE 5—Photographs of specimens of *Cardiocystella prolixora* n. gen. and sp. *1, 2, 4, 9,* holotype 1791TX13. *1, 2,* whole specimen whitened and immersed, ×6; *4,* detail of the cothurnopores (dark ellipses) showing small platelets over the pores, ×17; *9,* detail of the theca, whitened, ×10. Note traces of zygal and M5/M′5 bars shown by disruption pattern of centralia, compare to Fig. *5.1*; *3, 5–8,* paratype 1791TX14; *3,* detail of the theca, whitened, ×10. Aboral theca (lower edge) damaged by large horizontal burrow (now removed), and centralia showing two small vertical burrows (lower center and left); *5, 6,* Whole specimen whitened and immersed, ×6; *7, 8,* distal and proximal portions of distal aulacophore, whitened, showing food groove with no cover plates and food groove with attached, open, cover plates, ×15.

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