THE CALCEOCRINID PUZZLE

BY

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Abstract — Calceocrinids are among the most enigmatic crinoids by having a highly modified, bilaterally symmetrical crown and a column that was prostrate along the sediment-water interface during life. Despite or perhaps because of this highly unusual morphology and paleoecology, the Calceocrinidae had the longest duration (~170 million years) of any well-defined crinoid family. Many ideas have been proposed for the paleoecology of calceocrinids, with the runner model favored in recent years. Two questions remain, did calceocrinids have both muscles and ligaments that opened and closed the crown, and how were these bottom-dwelling crinoids positioned with respect to currents. Stereom is evaluated to infer the connective tissues that bound movable calceocrinid facets. Accordingly, calceocrinids had only ligaments present to mediate opening and closing the crown. Three potential crown postures are considered, including an erect arm posture with currents striking the aboral side of the arms and an erect arm posture with currents striking the oral side of the arms. The third, proposed herein, is a partially opened, subellipsoidal posture. It is not possible to reject any of these potential feeding orientations or postures, although ligament stretching may have imposed limitations on erect postures. It is possible that two or more of these alternative postures could have been employed to exploit changing ambient environmental conditions.

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INTRODUCTION

Stereotypically, crinoids are sessile, passive suspension feeders with an erect column that positions the crown for feeding up within the benthic boundary layer and into various epifaunal tiers (Ausich and Bottjer, 1982; Bottjer and Ausich, 1987). However, through the Phanerozoic several crinoid clades deviated from this Bauplan to exploit other ecological roles. Examples include crinoids attached to floating logs (*Traumatocrinus* Wöhrmann, 1889, see Hagdorn and Wang 2015; *Seirocrinus* Gislén, 1924, see Hess, 1999), and crinoids that lacked a column as an adult. Examples of the latter include a calyx cemented directly to the substratum (*Holopus* d'Orbigny, 1837), crinoids with a convex proximal calyx and no column (*Agassizocrinus* Owen and Shumard, 1852 and *Paragassizocrinus* Moore and Plummer, 1940; e.g., Ettensohn, 1975, 1980, 1984), post-Paleozoic feather stars with the proximal calyx comprised of a centrodorsal and articulated cirri, and post-Paleozoic uintacrinids that lack both a column and cirri.

Calceocrinids represent one of the more radical departures from the idealized crinoid Bauplan (Fig. 1). Rather than an erect column, the column of calceocrinids is interpreted to have lain prostrate along the substratum. Further, the crown shape and symmetry were modified for life on the sea floor. In the oldest calceocrinids, pentameral symmetry was replaced by a crown with four arms (A, B, D, and E rays) and poor bilateral symmetry (e.g., *Cremacrinus* Ulrich, 1886 and *Paracremacrinus* Brower, 1977; Fig. 1A–B). More crownward calceocrinids (e.g., *Calceocrinus* Hall, 1852 and *Halysiocrinus* Ulrich, 1886; Fig. 1C–F) had a crown with an E-BC plane of bilateral symmetry that was coincident with the axis of the column. The shapes of the basal plates were modified to form a crescent-shaped basal circlet with a straight articular ridge that was articulated in life to a similar ridge on the apposing radial circlet. Similar to the basal plates, radial plate shape was highly modified to form a radial circlet with a flat, subtrapezoidal or flattened subtubular shape (Fig. 1E–F).

As discussed below in detail, many authors have speculated on the paleoecology of these unusual crinoids, but questions remain. For example, how were calceocrinids positioned with respect to current flow? How did calceocrinids open and close the crown using the basal circlet-E inferradial plate synarthrial articulation? In this contribution, various outstanding aspects of calceocrinid paleoecology are considered.

GEOLOGICAL HISTORY OF THE CALCEOCRINIDAE

The Calceocrinidae are a well-defined family that was first recognized by Meek and Worthen (1869) and is still consistently recovered as a clade (Ausich, 2019). At present, only 25 calceocrinid genera have been described; but, the Calceocrinidae has the longest duration of any well-defined crinoid family (Fig. 2). They range from their first appearance during the Middle Ordovician (Sandbian) to the lower Permian (Artinskian). Total familial duration is as much as
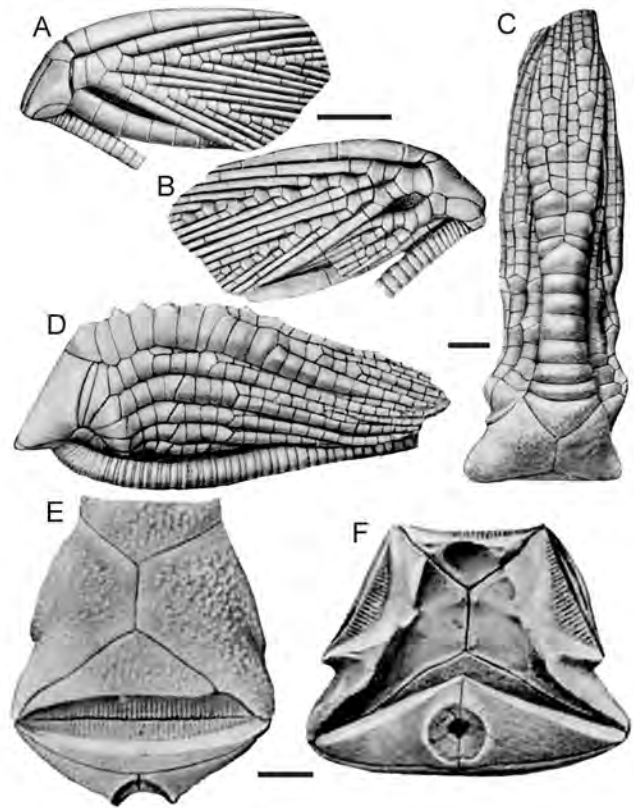

FIGURE 1 — Representative calceocrinids. **A**, **B**, Lateral views of the four-armed *Cremacrinus tubuliferus* Springer, 1926 crown (Sandbian), A, from top to bottom, E arm, A arm, and anal sac, B, from top to bottom, E arm, D arm, and B arm; **C**, **D**, Lateral views of the three-armed *Halysiocrinus tunicatus* crown (Viséan), C, view of E ray arm, D, view of D ray arm. **E**, **F**, Aboral cup of *H. tunicatus*, E, external view of open aboral cup, internal view of closed aboral cup. Images from Springer, 1926; scale bars = 5 mm.

170 million years and comprises a mixture of long- and short-duration genera (Fig. 2).

As a whole, the Calceocrinidae were eurytopic and lived in a wide variety of epeiric sea habitats. For example, the common early Mississippian calceocrinid, *Halysiocrinus tunicatus* (Hall, 1860), studied here, lived in numerous settings (Table 1). Also, Brett (1981) discussed the range of habitats for some Silurian calceocrinids.

The biodiversity of calceocrinid genera was the highest from the Hirnantian to the Givetian (peaking during the Silurian; Fig. 2). Ausich (1986) hypothesized that the significant decline in biodiversity and occurrences of calceocrinids after the Givetian was due, in part, to competition for space on the sea floor during the radiation of fenestrate bryozoans during this time. After the middle Viséan, only two calceocrinid occurrences are known: Bashkirian (Pennsylvanian) and Artinskian (Permian), with both occurrences being *Epihalysiocrinus* Arendt, 1965.
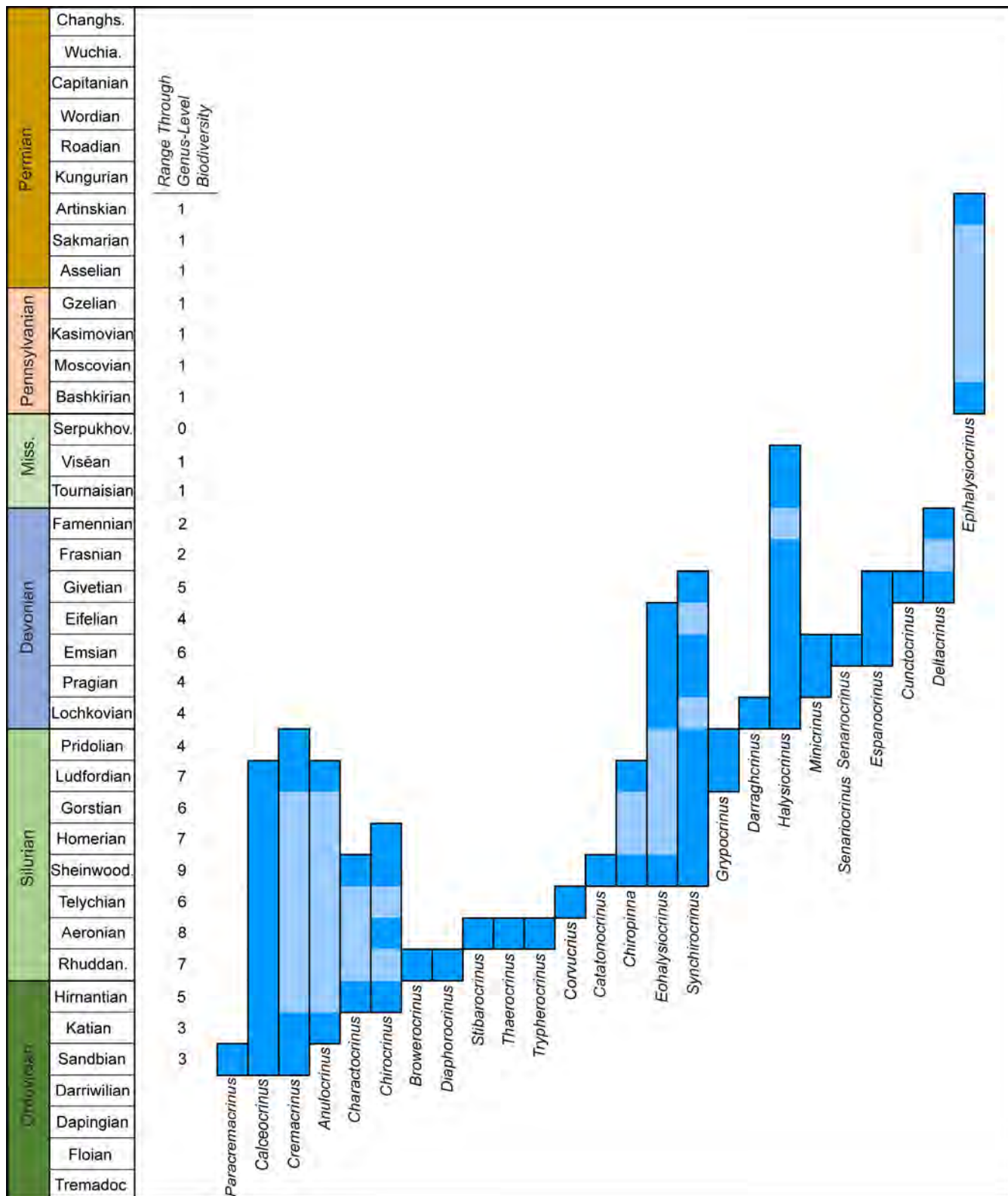
FIGURE 2 — Range chart of calceocrinid genera; dark blue presence of a genus in given time bin, light blue; range through occurrences. Range through genus diversity to the right of the time scale.

TABLE 1 — Stratigraphic and paleoenvironmental occurrences of *Halysiocrinus tunicatus* (lower Mississippian, lower to middle Viséan) of the United States.

Formation	State	Paleoenvironmental Setting	Reference
Edwardsville Formation	Indiana	Delta platform, siltstone facies	Lane (1973)
Edwardsville Formation	Indiana	Delta platform, siliciclastic mudstones facies	Ausich (1983)
Edwardsville Formation	Indiana	Delta platform, crinoidal packstone buildups	Ausich (1983)
Ramp Creek Formation	Indiana	Delta platform, mixed carbonate and siliciclastics facies	Lane (1973)
New Providence Shale Member, Borden Formation	Kentucky and Indiana	Prodelta, siliciclastic mudstone facies	Kammer (1984)
Keokuk Limestone	Illinois, Iowa, Missouri	Platform, carbonates	Kammer et al. (1997)
Warsaw Formation (lower)	Illinois, Iowa, Missouri	Platform, mixed carbonate and siliciclastics	Kammer et al. (1997)
Warsaw Formation (upper)	Illinois, Iowa, Missouri	Platform, siltstone	Kammer et al. (1997)
Fort Payne Formation	Kentucky	Basinal, siliciclastic mudstone facies	Ausich and Meyer (1980)
Fort Payne Formation	Kentucky	Basinal, crinoid packstone buildups	Ausich and Meyer (1980)
Fort Payne Formation	Kentucky	Basinal, wackestone buildup facies	Ausich and Meyer (1980)
Muldraugh Member, Borden Formation	Kentucky	Platform, mixed carbonate and siliciclastics	Ausich et al. (2000)

PALEOECOLOGY: HISTORICAL REVIEW

As summarized by Ausich (1986), three primary paleoecological models have been proposed for calceocrinids including drooper (Ringueberg, 1889), runner (Jaekel, 1918; Springer, 1926; Ramsbottom, 1952; Moore, 1962; Brower, 1966, 1977, 1990; Kesling and Sigler, 1969; Breimer and Webster, 1975; Brett, 1981; Ausich, 1986, and others; Fig. 3), and free-swimming pelagic (Schmidt, 1934). Variations of the standard runner model are the weathervane (Kesling and Sigler, 1969) and the kite (Breimer and Webster, 1975). Complete columns with holdfasts are rarely preserved on calceocrinids, so morphological adaptations demonstrating an obligate column posture along the substratum are relatively rare. However, calceocrinids are known with cemented or otherwise attached holdfasts that affixed to the substratum, which eliminates a free-swimming habit for at least these forms.

Jaekel's (1918) life reconstruction depicted *Synchirocrinus nitidus* (Bather, 1893) with the runner model and the column draped across corals and/or stromatoporoids and the crown open. The arms are erect with ramules extended and evenly spaced (Fig. 3). The arms are positioned so that the currents strike the ambulacral side of the arms. The runner model (column prostrate along the sediment-water interface) is confirmed in a few calceocrinids. In specimens of *Calceocrinus longifrons* Brower, 1977 (Sandbian, Ordovician), complete columns were shorter than the arms, negating the drooper model. An obligate, prostrate posture for the column was also demonstrated in Silurian crinoids.
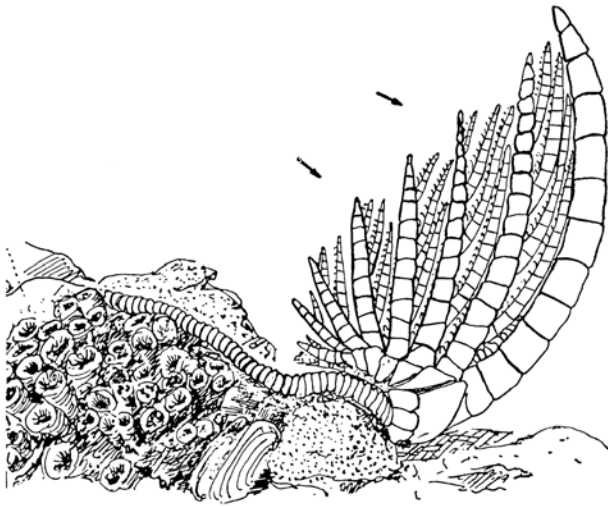
FIGURE 3 — Life reconstruction of *Synchirocrinus nitidus* in a runner mode (Jaekel, 1918: fig. 2). Arrows represent flow.

Wedge-shaped columnals in the distalmost portions of the column were reported in *Calceocrinus chrysalis* (Hall, 1860) (Brett, 1981). In *Trypherocrinus brassfieldensis* Ausich, 1984 (Aeronian, Llandovery), one specimen had a short segment of the distalmost column oriented vertically, and this section was separated from the remainder of the column by a wedge-shaped columnal making the majority of the column obligate prostrate along the substratum (Ausich, 1984). Eckert (1984) and Brett (1984, 1985) reported holdfasts with the holdfast-column articulation oriented vertically. This also produced an obligate runner orientation for the column.

Furthermore, taphonomic evidence may support the runner model. In several diverse crinoid occurrences studied by the author, specimens preserved with the arms intact appear to be more abundant for calceocrinids than for other crinoid taxa. If true, this anecdotal observation would be consistent with the runner model because a crinoid living at the sediment-water interface would have been more likely to be buried and preserved intact. Accepting the runner model as their life posture, calceocrinids fed lying on the sediment-water interface, which would have been the lowest epifaunal suspension-feeding tier.

MATERIALS AND METHODS

This study is based on experience collecting and describing Ordovician, Silurian, and Mississippian calceocrinids (e.g., Ausich, 1984; Ausich et al., 1997, 2015; Boyarko and Ausich, 2009; Ausich and Copper, 2010), as well as studies attempting to understand the evolutionary paleobiology and phylogeny of calceocrinids through the Paleozoic (Ausich, 1986; Harvey and Ausich, 1997). The specimens studied in detail herein are *Halysiocrinus tunicatus* (Hall, 1860) from the lower Viséan (upper Osagean, Mississippian) New Providence Shale Member of the Borden Formation at Button

Mold Knob in north-central Kentucky (Kammer, 1984). This locality was a fossiliferous glade located in Bullitt County; but unfortunately, this classic collecting site has been destroyed by development. Material studied herein includes partial aboral cups, articulated basal plate circlets, articulated radial plate circlets, and individual radial plates. Standard petrographic thin sections were prepared from two basal plate circlets and two isolated radial plates. Two thin sections were made from each of these specimens, with the plane of thin sections perpendicular to articular facet (basal circlet facet and arm facets on radial plates).

INSTITUTIONAL ABBREVIATION

OSU — Orton Geological Museum, The Ohio State University (OSU).

CALCEOCRINID MORPHOLOGY

Crown

The synarthrial articulation between the basal circlet and the radial circlet is unique to calceocrinids. In *Halysiocrinus tunicatus*, this ridge extends across the entire E inferradial plate, and forms the proximal margin of the radial circlet. The basal circlet has three plates. The distal-most basal plate extends across the entire basal circlet margin and has one, long fossa with an articular ridge across the entire plate (Figs. 4, 5A–C). This articulates with a comparable fossa and articular ridge on the E inferradial plate (Fig. 4). Overall, the inside of the basal circlet is gently convex with the possibility of four fossa. These are arranged symmetrically on either side of the opening for the column axial canal. The distal two fossae are subtriangular and the proximal fossae subtriangular but narrower (Fig. 5).

Both the A and D radial plate arm facets are symmetrical with an articular ridge extending across most of the facet (Fig. 4A–B, 5G–I). A single, elongate aboral fossa is present along the outer margin of the articular ridge. Two adoral fossae are present on the inner side of the articular ridge (Fig. 5I). These adoral fossae are subtriangular in shape. They begin centrally on the inside of the facet and expand upward and outward toward the outer margins of the facet.

The E-ray arm articulates with the E superradial plate (Figs. 4A–B). This articulation has an articular ridge extending across the entire width of the plate; and only one, long, narrow fossa is present on the aboral side.

Kesling and Sigler (1969) depicted *Cunctocrinus* in a runner life position. They included reconstructions in both a closed, resting posture and an open, vertical fan posture (Messing et al., 2021) with the arms fully extended for feeding. In a resting posture, the radial plate circlet and arms close down over the basal circlet and onto column. When feeding, the classical interpretation is that the hinge is wide open, and the arms are erect. To attain this fully open posture, the synarthrial articulation between the basal and radial circlets would need to open by ~70°.
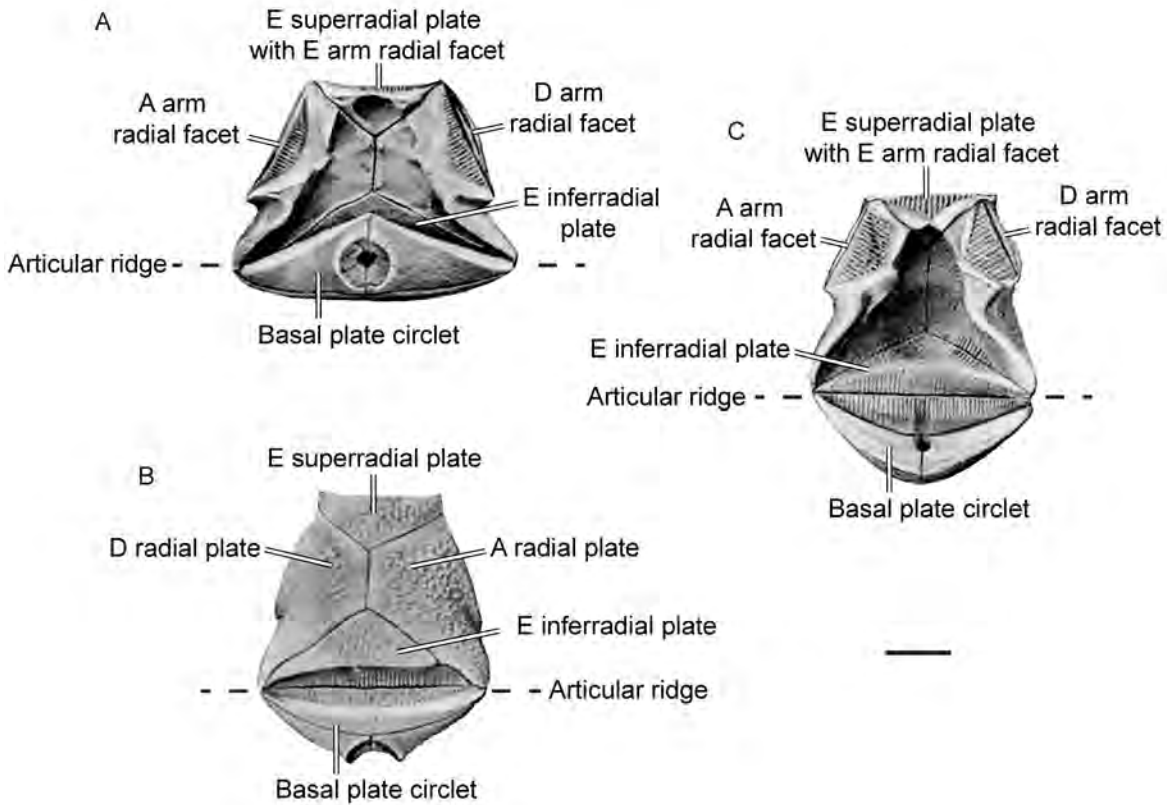
FIGURE 4 — *Halysiocrinus tunicatus* aboral cup in various orientations and with detailed explanation of the morphology. **A**, Internal view of radial plate circlet and distal view of basal plate circlets, aboral cup in a closed position; **B**, Internal view of radial and basal plate circlets, aboral cup in a an open position; **C**, External view of radial plate and basal plate circlets, aboral cup in an open position. Images from Springer, 1926; scale bar = 5 mm.
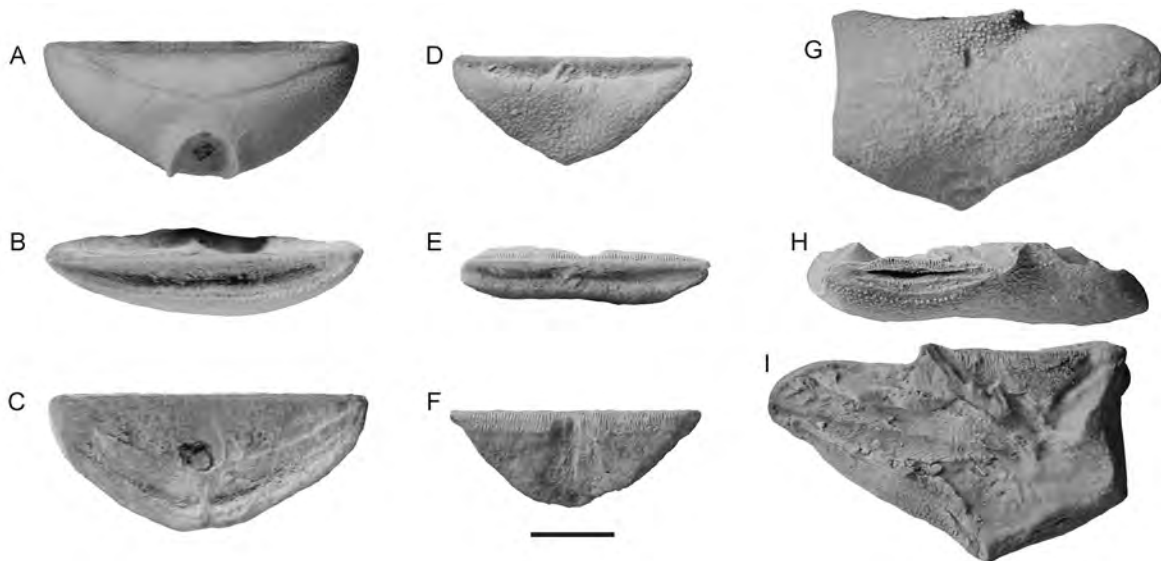

FIGURE 5 — Isolated aboral cup plates of *Halysiocrinus tunicatus*. **A–C**, basal circlet (OSU 54985), **A**, outside surface, **B**, basal circlet articular ridge and outer fossa, **C**, inner surface; **D–F**, E-superradial plate (OSU 54986), **D**, outside surface, **E**, basal circlet articular ridge and outer fossa, **F**, inner surface; **G–I**, E-superradial plate (OSU 54987), **G**, outside surface, **H**, basal circlet articular ridge and outer fossa, **I**, inner surface; all specimens coated with ammonium chloride, scale bar = 5 mm.

The synarthrial articulations were sites of marked movement. The basal circlet-E inferradial articulation opened and closed the crown. Tissue contraction on the outer fossae of the basal circlet-E inferradial articulation would have opened the crown, whereas contraction of tissue on the inner surface of the proximal portion of the radial circlet presumably closed the crown. Similarly, contraction of tissues on the outer fossae of the A and D radial plates and the E superradial plate would have opened the arms. On the A and D radial plates, two subtriangular fossae on the inside and beneath the articular ridge housed tissues that would have closed the arms with contracted.

Stereom Microstructure

Mesodermal calcareous plates in echinoderms have stereom microstructure, which is an echinoderm synapomorphy. Stereom is a cross-connected calcareous meshwork comprised of calcareous trabeculae that surround open pore space, which was filled with mesodermal tissue during life. Various types of stereom commonly reflect different functions (e.g., Macurda and Meyer, 1975; Roux, 1970, 1971, 1974, 1975; Macurda et al., 1978; Smith, 1980; Riddle et al., 1988; Gorzelak et al., 2014; Gorzelak, 2018). Remnants of the original stereom may be preserved in fossil echinoderms, especially in echinoderm plates preserved in siliciclastic mudstones and shales. Examples of stereom preserved in fossils include preserved stereom on the surface of plates (e.g., Strimple, 1972; Lane and Macurda, 1975; Ausich, 1977, 1983; Głuchowski, 1982; Gorzelak et al., 2014; Thomka and Smith, 2019), as well as preserved stereom on plate interiors (e.g., Ausich, 1983; Riddle et al., 1988).

Of particular interest is that different types of stereom are commonly indicative of different connective tissues, which in turn have different behavioral properties (Macurda and Meyer, 1975; Roux, 1975; Macurda et al., 1978; Smith, 1980; Gorzelak, 2018). Smith (1980: table 2) recognized ten primary types of stereom microstructure in echinoids. Relevant for the present study are imperforate, galleried, rectilinear, and labyrinthic stereom (= massive, galleried, rectilinear galleried, and labyrinthic stereom, respectively, of Macurda and Meyer, 1975). In the present study, galleried stereom is identified if linearity in the stereom is preserved as opposed the orthogonal nature of rectilinear stereom.

Specimens were examined for remnants of original stereom on both the surface of plates and within plate interiors (using thin sections). Several specimens have a fine rectilinear stereom preserved on the outside surface of the basal circlet. The key areas examined are the outer fossa and inner surface of the basal circlet, the stereom on the inner surface of radial plates, and E inferradial plates that would have housed tissue responsible for opening and closing of the crown. Also examined were the radial facets of the A radial plate, D radial plate, and E superradial plate that housed tissues for arm movement. Each is discussed separately below.

Basal circlet crescent-shaped fossa on the outside of the basal circlet.— As noted above, the distal margin of the basal circlet has an articular ridge and fossa, both extending the full width of the basal circlet (Figs. 4 and 5). The top and outer surface of the articular ridge is commonly preserved with a denser, darker colored calcite than the surrounding calcite. The denser stereom is consistent with the stereom of articular ridges and other bearing surfaces among crinoids (e.g., Macurda and Meyer, 1975; Ausich, 1977, 1983) and is comparable to the imperforate stereom of Smith (1980). Both the internal and exterior sides of this articular ridge have ridges and furrows that are perpendicular to the bearing surface of the articular ridge (Figs. 5C, 6E). Within the fossa, little stereom is preserved.

However, galleried stereom is inferred along the inside surface of the basal circlet beneath the articular ridge. This stereom is at a slight angle from perpendicular to the articular ridge. The galleried stereom is tilted toward the left on the left side of the (Fig. 6A) and toward the right on the right side (Fig. 6C).

Relatively little stereom is revealed in thin sections of basal circlet plates. In cross section, the basal circlet is an irregular crescent shape with the distal end tapering to a narrow, blunt proximal end; and the distal end is much wider with two high points separated by an indentation (Fig. 7). The high point on the concave side of the facet is the articular ridge, the indentation is the crescent-shaped aboral fossa, and high point on the convex side of the circlet is the outer edge of the crescent-shaped facet. Very faint linearly aligned stereom is present beneath the bottom of the basal circlet fossa and is interpreted to be very poorly preserved galleried stereom (Fig. 7C). Also as illustrated in Figure 8, approximately half of the interior of one specimen has poorly preserved rectilinear stereom.

In summary, little evidence of tissue-specific stereom is preserved on or in basal circlet fossae. What is preserved is all indicative of ligament tissue, and no evidence for labyrinthic stereom is present. Both the galleried stereom at the base of the basal circlet fossa (Fig. 7) and the galleried stereom along the vertical ridges and grooves in the inner surface below the articular ridge (Fig. 6) are interpreted to represent ligament tissue that connected the basal circlet to the E inferradial plate articulation.

Medial area of radial plate interiors.— Typical reconstructions of calceocrinid crowns (Brower, 1985: fig. 2; Brower, 1990: fig. 2) infer soft tissue connecting the interior of the radial plates with, perhaps the interior of basal circlet. One specimen has preserved stereom in the proximal portion of the interior a radial plate (Fig. 9). On this specimen, galleried stereom is on the plate surface. This stereom is present on the inside of a ridge adjacent to the suture between the A radial plate and the E-inferradial plate. The stereom is inclined proximally (Fig. 9A), back toward the distal portion of the basal circlet (compare to Fig. 4A and Fig. 4B).

As with the basal circlet, radial plate interiors (based on thin sections) only have preserved rectilinear and galleried stereom. In contrast to the basal circlet, the radial plates
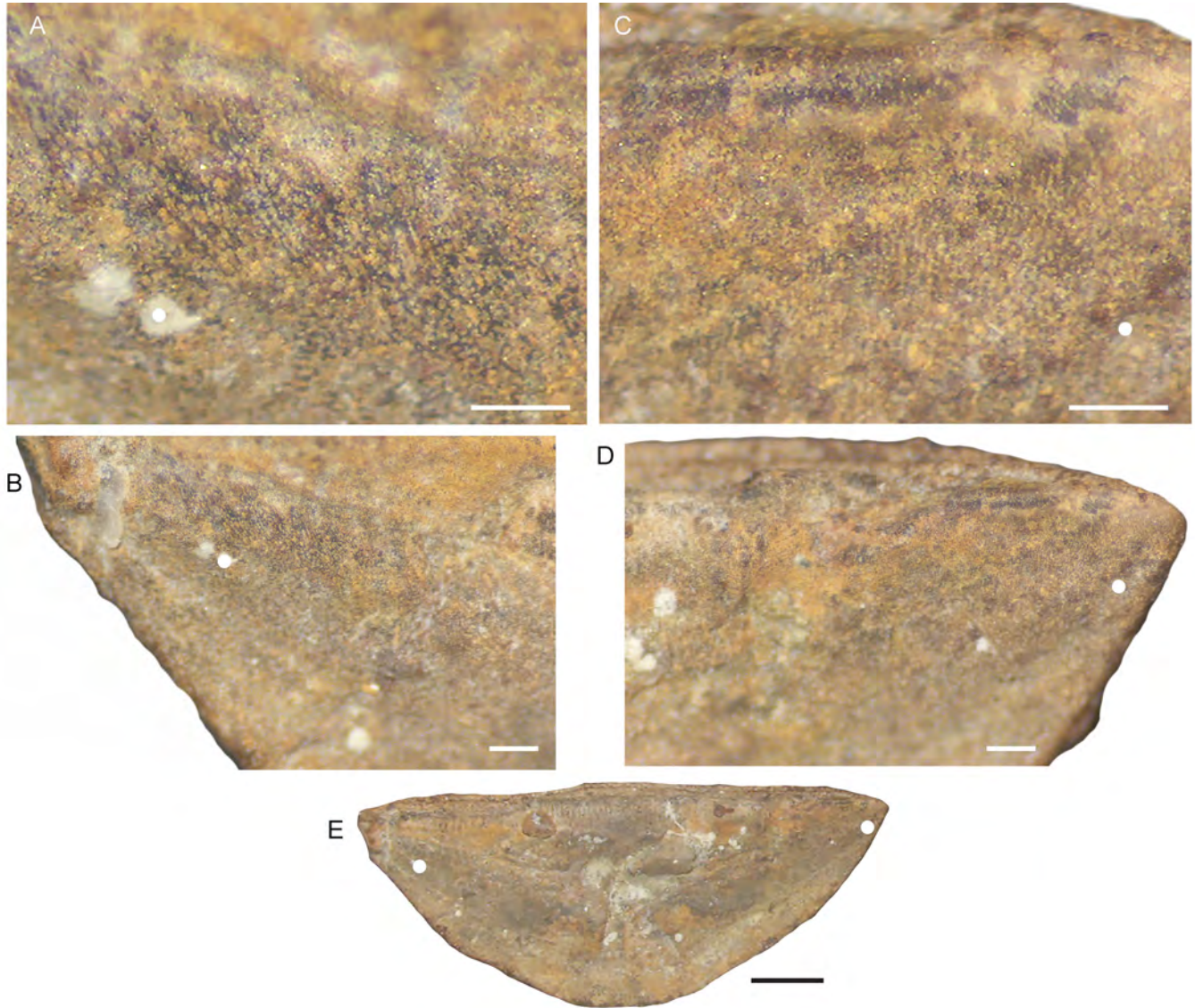
FIGURE 6 — Inner surface of a *Halysiocrinus tunicatus* basal circlet (OSU 54988). **A**, Left side of area beneath the articular ridge, enlargement of B, scale bar = 0.33 mm; **B**, enlargement of right side of area beneath the articular ridge, scale bar = 0.33 mm; **C**, Left side of articular ridge area beneath the articular ridge, enlargement of B, scale bar = 0.5 mm; **D**, Right side of area beneath articular ridge, scale bar = 0.5 mm; **E**, interior D radial plate, scale bar = 2.5; White dots are landmark points for orientation.

examined have much stereom preserved within the plates. As noted above, Figure 10 rectilinear stereom is preserved throughout the entire radial plate. However, stereom changes from rectilinear to galleried along the inner margin of the plate (Figs. 10, 11).

A and D radial arm facets.— Similar to the articular ridge of the basal circlet, the articular ridge on radial facets is commonly preserved with a denser and darker colored calcite than the remainder of the plate and is interpreted as imperforate stereom (Fig. 12). Also, similar to the basal circlet and E inferradial articular surfaces, the inside surface beneath

the articular ridge has ridges and grooves perpendicular to the articular ridge (Fig. 4). Galleried stereom projects along the inner surface beneath the articular ridge parallel to the ridges and grooves and perpendicular to the articular ridge bearing surface (Fig. 13). In places where stereom is preserved within the margins of the aboral fossa of the radial plates, it is rectilinear and could be either interpreted as rectilinear or galleried stereom.

Subtriangular fossa on the inner side of the facet also has galleried stereom. It more-or-less parallels the surface of the subtriangular facet (Fig. 14). This stereom projects upward
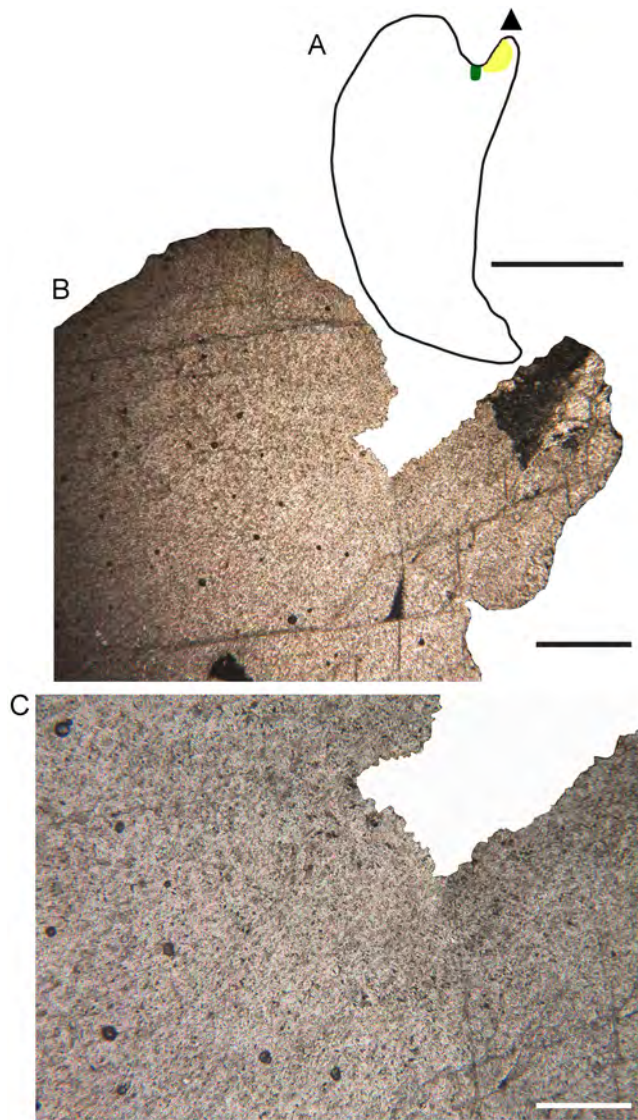
FIGURE 7 — Thin sections of *Halysiocrinus tunicatus* basal circlet (OSU 54981b), photographed in polarized light. **A**, Cross section of basal circlet (triangle, articular ridge; green, galleried stereom; yellow, rectilinear stereom); scale bar = 2.5 mm; **B**, thin section of distal end of basal, scale bar = 500 μm; **C**, enlargement of the bottom of the basal circlet fossa with faintly preserved linear stereom interpreted to be galleried stereom, scale bar = 200 μm.
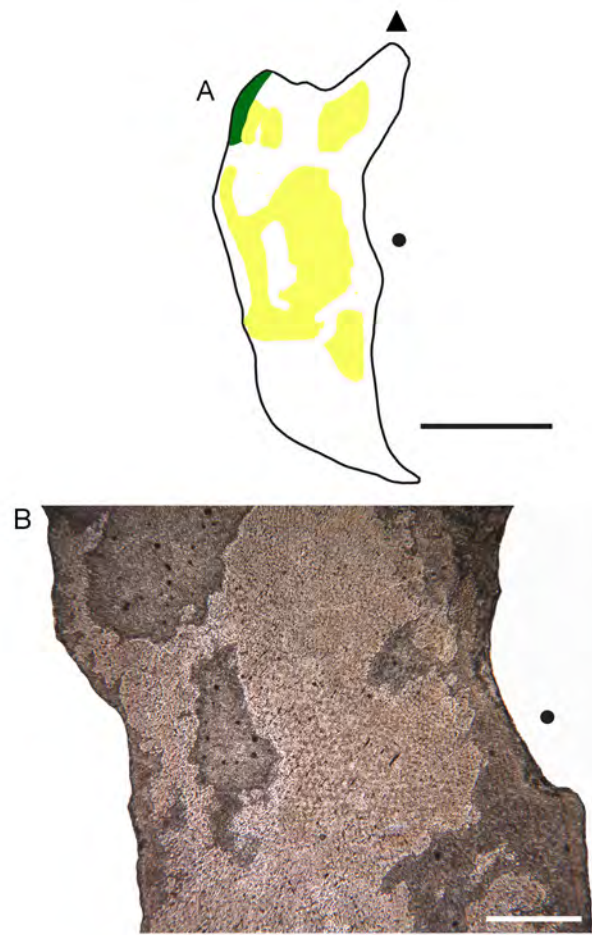

FIGURE 8 — Thin section of *Halysiocrinus tunicatus* basal circlet (OSU 54982a). **A**, Cross section of basal circlet (triangle, articular ridge; green, galleried stereom; yellow, rectilinear stereom); scale bar = 2.5 mm; **B**, thin section of the middle portion of the basal circlet with some, poorly preserved rectilinear stereom, scale bar = 500 μm. Dots are landmark points to identify position of enlargements.

along the surface of the subtriangular fossa (Fig. 14A). In thin section, galleried stereom is preserved beneath the radial facet (Figs. 11A–B).

E superradial plates.— A single, well-preserved E superradial plate is in the present collection (Figs. 5D–F). Similar to the articular ridge on the basal circlet, imperforate stereom is present along the E superradial articular ridge (Figs. 5F, 15). Ridges and grooves extend downward from

the bearing surface of the articular ridge on only the inside of the articular ridge. Again, similar to the basal circlet, galleried stereom is present along the ridges and groves and is perpendicular to the articular ridge bearing surface (Fig. 15). Preserved stereom on the E superradial plate (Figs. 15D–E) would have controlled the opening and closing of the E-ray arm was presumably ligament.

FUNCTIONAL MORPHOLOGY OF THE CALCEOCRINIDAE

Despite all that has been learned since the initial description of a calceocrinid fossil, outstanding questions remain. The two fundamental questions are 1) crown position with respect
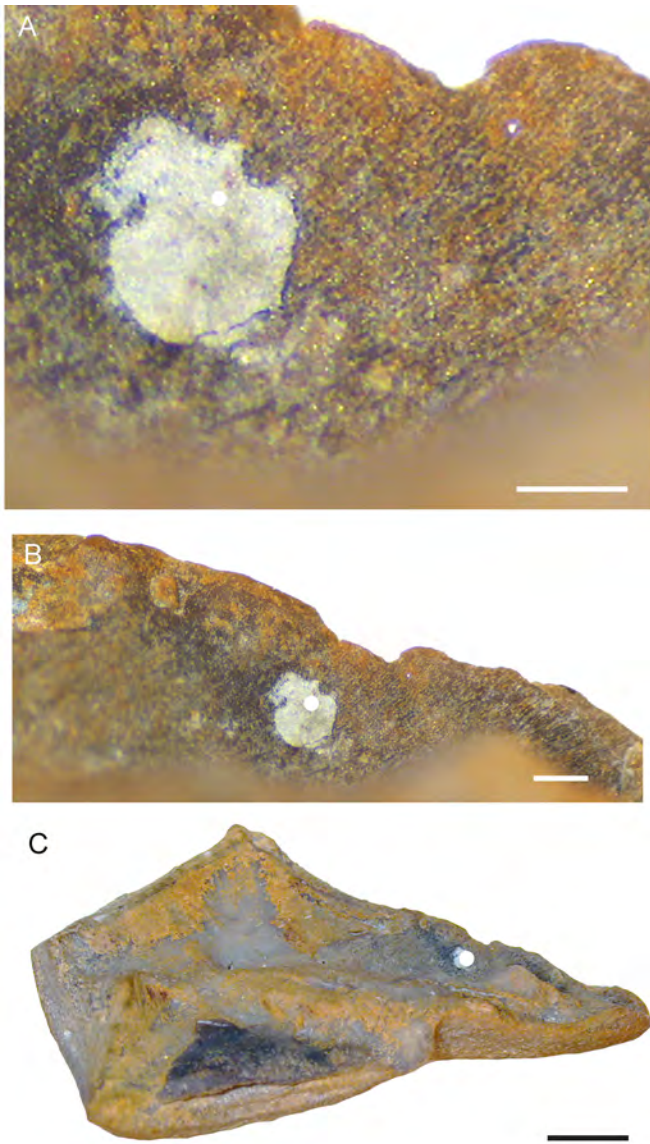
FIGURE 9 — Oblique, upside down view of an A radial facet of *Halysiocrinus tunicatus* illustrating galleried stereom in the inner side if a ridge on the lower portion of the plate (OSU 54987). **A**, scale bar = 0.33 mm; **B**, scale bar = 0.5 mm; **C**, scale bar = 2.5 mm. Dots are landmark points to identify position of enlargements.

FIGURE 10 — Thin sections of *Halysiocrinus tunicatus* middle section of a radial plate (OSU 54984b). **A**, Cross section of radial plate (triangle, articular ridge; yellow, rectilinear stereom); scale bar = 2.5 mm; **B**, thin section of middle section of plate with rectilinear stereom, scale bar = 500 μm. Dots are landmark points to identify position of enlargements.

to currents during feeding and 2) what connective tissues controlled the opening and closing of the crown from a resting posture along the column to a feeding posture and back again to a resting posture?

Significant to these questions are attributes of the benthic habitat milieu. As noted by Walker and Bambach (1974), the density of organic particles in the water column is greatest at
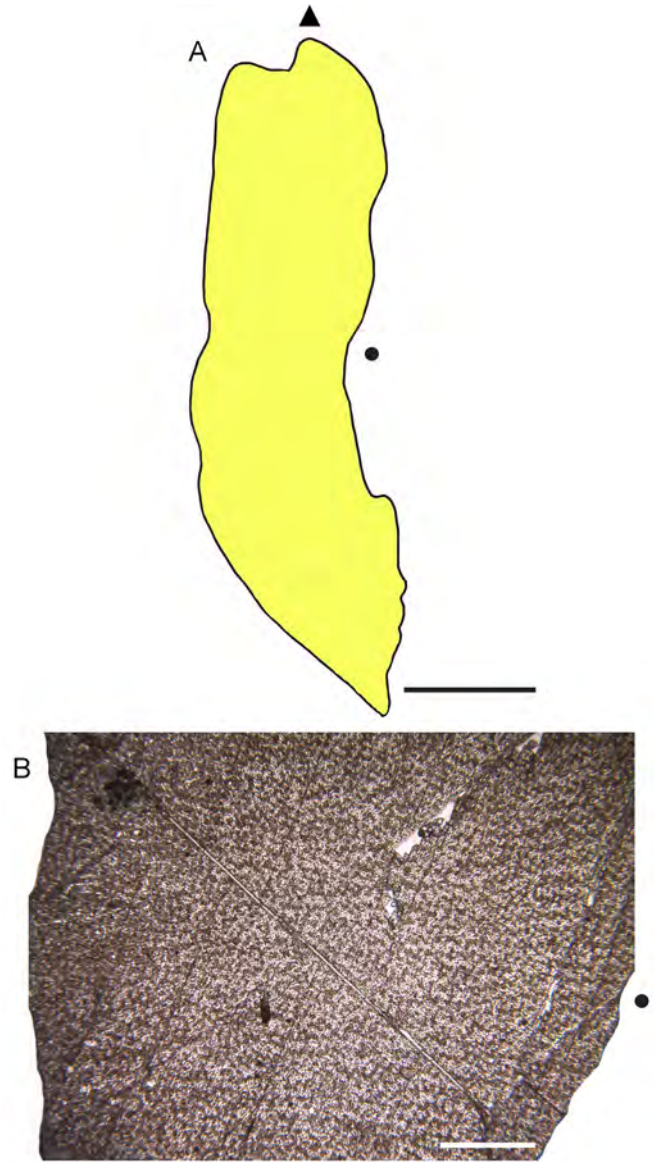
the sediment-water interface, where a flocculent layer high in organics may form. Above the sediment-water interface, the density of organic particulates decreases dramatically (Walker and Bambach, 1974). In contrast, due to frictional effects of the sea floor, current velocities asymptotically decrease toward the sediment-water interface. This height above the sediment-water interface with diminished current velocity is called the
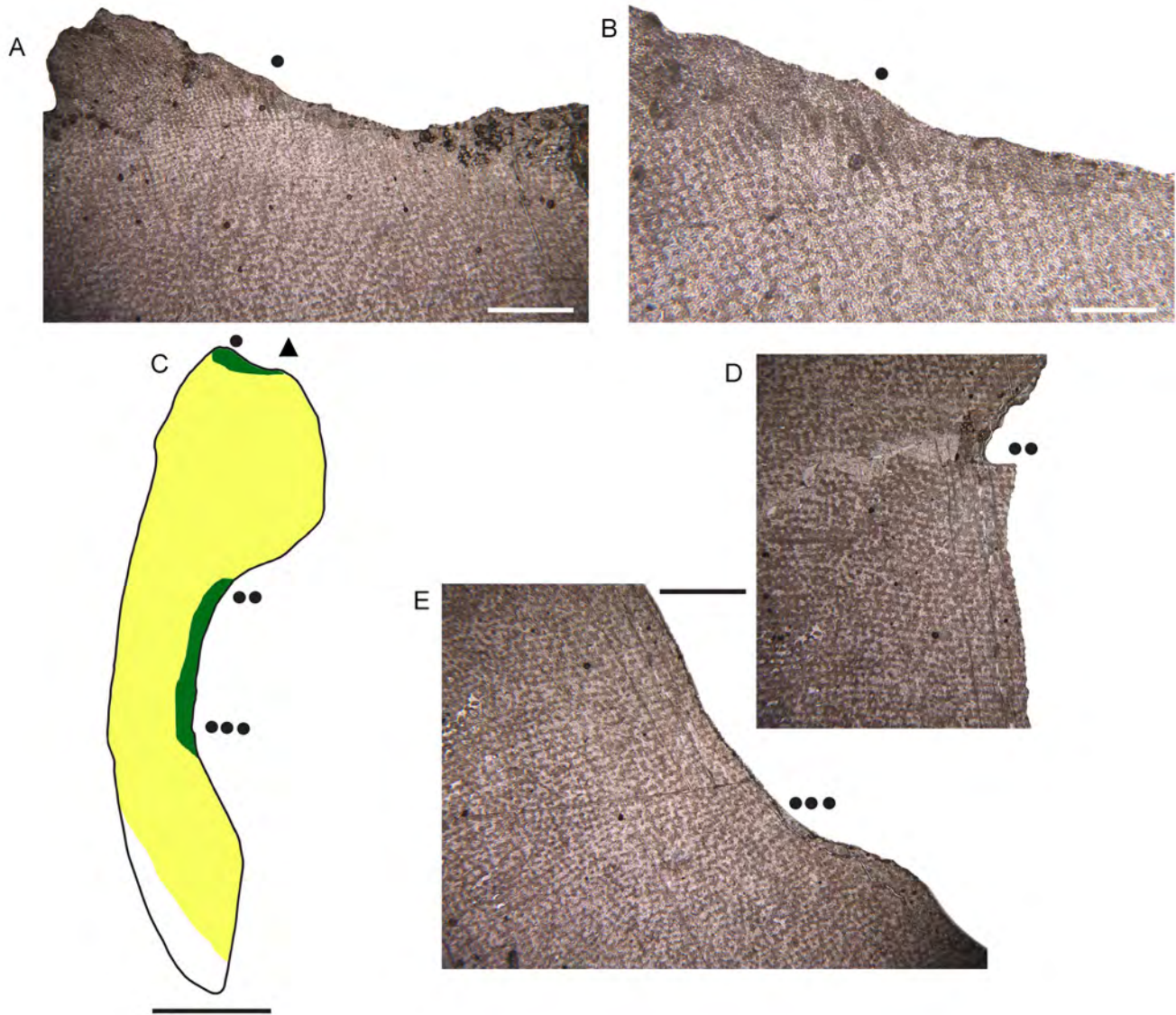
FIGURE 11 — Thin sections of a *Halysiocrinus tunicatus* radial plate; all photographs in plain light (OSU 54984a). **A**, thin section of stereom beneath the radial facet, scale bar 500 μm; **B**, enlargement of A, scale bar 200 μm; **C,** Cross section of radial plate (triangle, articular ridge; green, galleried stereom; yellow, rectilinear stereom); scale bar = 2.5 mm; **D**, thin section of inner margin of plate with rectilinear stereom transitioning outward to galleried stereom, scale bar 500 μm. **E**, thin section of inner margin of plate with galleried stereom, scale bar = 500 μm. D and E scale bar = 500 μm; dot patterns are landmark points to identify position of enlargements.

benthic boundary layer (Rhodes and Boyer, 1982). For passive suspension-feeding organisms, such as crinoids, this produces a nutrient paradox, in which the highest concentrations of potential food exist in the zone of minimal current velocity. Indeed, the entire ecological experiment of pelmatozoan echinoderms was one in which the column elevated the feeding apparatus above the sediment-water interface into a position that maximized the flux of suspended food particles through arms or brachioles. This means that during everyday conditions, calceocrinids must have fed in a setting with much reduced current velocity but a high concentration of organic particles.

Three possible feeding postures are discussed below. Key factors inferred to be significant to our understanding of calceocrinid paleoecology are the properties of echinoderm ligament tissue; the orientation of the ambulacra relative to prevailing currents, as it affects feeding; whether lift played a role in opening the arms; the ability of the column to
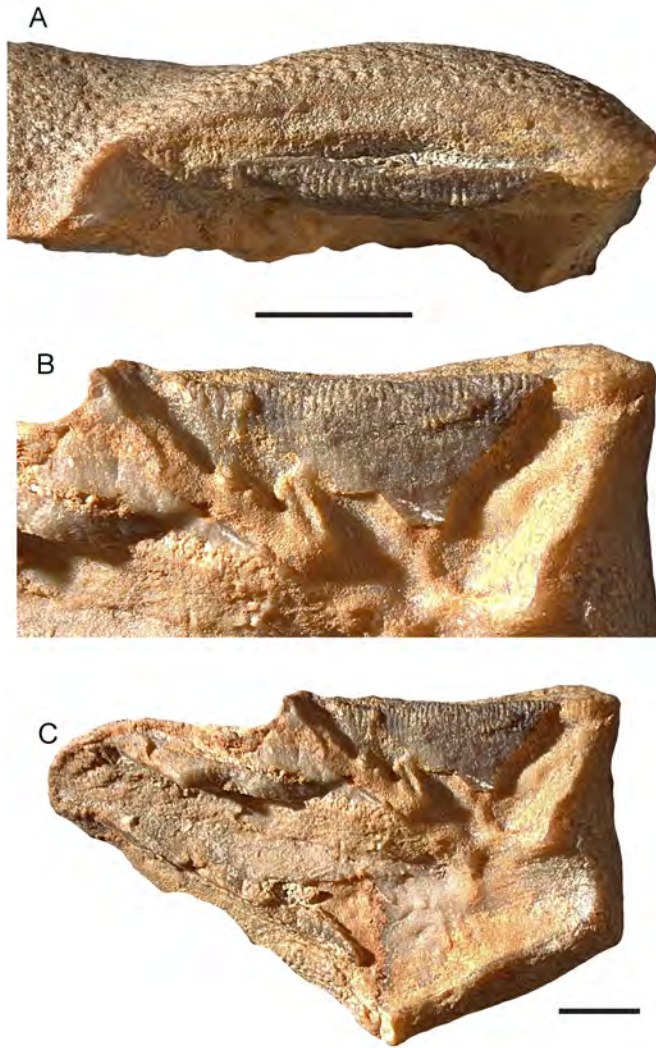
FIGURE 12 — A radial facet of *Halysiocrinus tunicatus* note darker colored and more denser stereom of the articular ridge (OSU 54987). **A, B,** scale bar = 2.5 mm;**C,** scale bar = 2.5 mm.

resist torque resulting from drag on opened arms; fouling of ambulacra with waste; closing the crown; and potential for preservation.

Echinoderm Ligaments

Mutable collagenous tissue (MCT; also catch-connective tissue) is a synapomorphy for the Echinodermata. The unique properties of this tissue have been studied extensively (e.g., Wilkie 1983, 1984, 2005; Motokawa, 1984, 1985; Wilke and Emson, 1988; Wilkie et al., 1992, 1993, 1994; Birenheide and Motokawa, 1994a, 1994b; Motokawa et al., 2004; and Wilkie et al., 2021). MCT is under nervous control. These ligaments are comprised of collagen fibrils (typically in bundles), microfibrils, and neuron-like cell processes, and they can rapidly change from being stiff to flaccid (e.g., Wilkie, 1983,

1984, 2005; Motokawa, 1984, 1985; Wilke and Emson, 1988; Birenheide and Motokawa, 1994a, 1994b; Motokawa et al., 2004; Ribeiro and others, 2011; and Wilkie et al., 2021). MCT makes autotomy of echinoderm body parts and evisceration of holothurians possible. In the stiff mode MCT allows suspension-feeding echinoderms to maintain a feeding posture with minimal expenditure of energy.

In addition to the catch-connective properties, echinoderm ligaments have also recently been demonstrated to have contractile properties (Gimmer and Holland, 1987; Birenheide and Motokawa, 1994; Motokawa et al., 2004). Ligaments have been observed to elongate by as much as 100% (Birenheide and Motokawa, 1994) as well as to contract by as much as 50% (Birenheide and Motokawa, 1996). Thus, although much slower than muscle contractions, ligament contraction can also contribute to organism movement. Unless evidence of labyrinthic stereom is identified on calceocrinid plates, it must be assumed that the degree and speed of movement in calceocrinids fell within the limits allowed by ligament tissue, as inferred by analogy with living echinoderms. As noted above, calceocrinids have a tendency to be preserved with arms intact more commonly than other coeval crinoids. Specimens with no arms but the aboral cup are exceedingly rare. These two observations also suggest that the arms and aboral cup articulations were both held together by the same connective tissues, which is inferred here to be ligaments.

Potential Feeding Postures

Three potential feeding postures are discussed here, which include a vertical fan with the current striking the oral side of the arms, a vertical fan with the currents striking the aboral side of the arms, and a partially open posture. The first is the original model proposed by Jaekel (1918: fig. 83) with the ambulacra facing the current. This posture was assumed for both the kite and weathervane hypothesis (Kesling and Sigler, 1969 and Breimer and Webster, 1975, respectively).

The second posture has a vertical filtration fan oriented with the currents striking the aboral side of the arms, which is the position assumed by most living crinoids in a unidirectional current regime. This posture was supported Brower (1985), Ausich (1986), and Messing et al. (2021).

A third alternative is proposed here, which is a partially open posture. The shape of the arms in this posture would be subellipsoidal. Messing (1994) and Messing et al. (2021) identified a relatively unusual crinoid arm posture in some extant, multiarmed Comatulidae (~40 – 80 arms). The arms are partially open and arched above the disc. This feeding posture was recognized in extant crinoids in a reef setting, where current velocities were sufficiently high to induce an erect posture in other crinoids (Stevens, 1989). A calceocrinid in this feeding posture would have fed primarily from the high concentration of organic particles immediately above the sediment-water interface.

Each of these potential feeding postures would have been affected by numerous factors, as discussed below and summarized in Table 2.

FIGURE 13 — D radial facet of *Halysiocrinus tunicatus* illustrating darker colored and more dense stereom of the articular ridge, and galleried stereom aligned vertically along the inner surface beneath the articular ridge (OSU 54989). **A**, Left side of articular ridge, enlargement of B, scale bar = 0.33 mm; **B**, enlargement of left side of articular ridge, scale bar = 0.33 mm; **C**, Right side of articular ridge, enlargement of B, scale bar = 0.5 mm; **D**, enlargement of right side of articular ridge, scale bar = 0.5 mm; **E**, interior D radial plate, scale bar = 2.5 mm.

Feeding.— In a unidirectional current regime, extant crinoids feed with the aboral side of the arms facing the current. However, food particle capture in extant crinoids is now regarded to be primarily from inertial impaction of food particles striking tube feet rather than from current eddying around the arms (Baumiller et al., 1993). Therefore, in a unidirectional current setting, whether the currents struck the oral or aboral side of the arms was probably immaterial in terms of food capture by tube feet. By the same reasoning, if tube feet were exposed, a partially opened, subellipsoidal posture would presumably have allowed particle capture,

if the crown was open enough and positioning of tube feet was sufficient for currents to penetrate into this fan. Based on analogy to extant crinoids, this posture would be well-suited for a multidirectional current regime, whereas the two erect postures would not. Further, using computational fluid dynamic analyses, Dynowski et al. (2016) concluded that the partially open crown of *Encrinus liliiformis* Lamarck, 1801 would have effectively feed in an environment with variable current conditions.

Torque on the column.— Drag on the crown would produce torque on the column in any posture and in any current
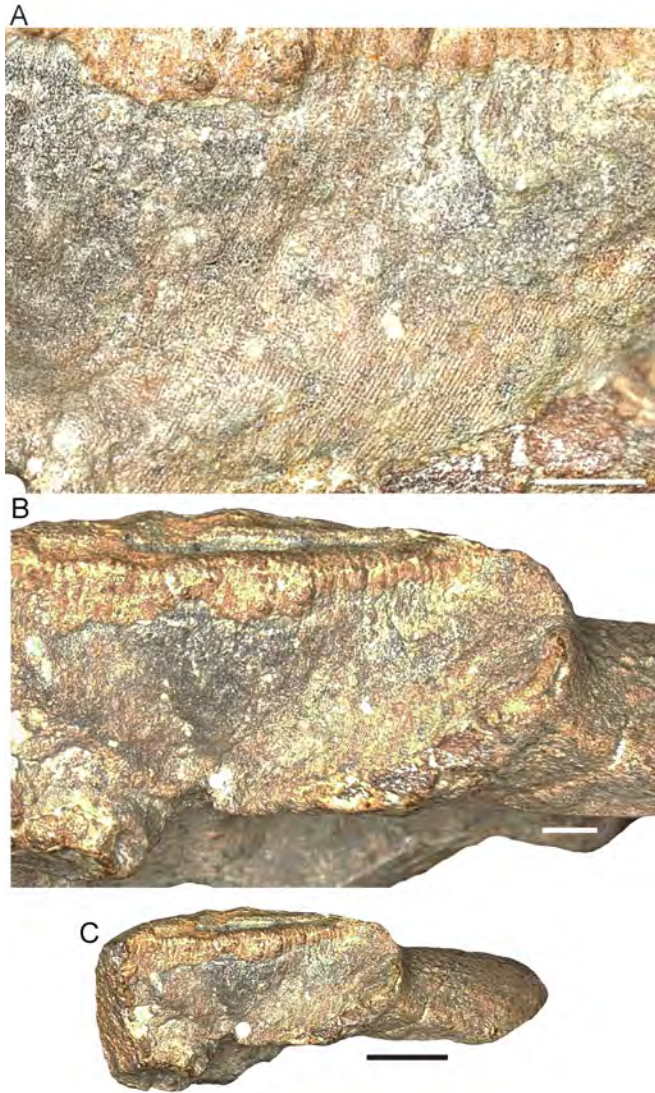
FIGURE 14 — D radial facet of *Halysiocrinus tunicatus* illustrating galleried stereom in the subtriangular inner fossa of a radial facet (OSU 54990). **A**, Enlargement of basal portion of right subtriangular inner fossa, enlargement of B, scale bar = 0.33 mm; **B**, enlargement right subtriangular inner fossa, articular ridge along top, scale bar = 0.5 mm; **C**, radial plate from a lateral perspective, scale bar = 2.5 mm.

direction except if the crown was oriented with currents striking the ambulacra and the current direction parallel to the column. The low profile of a partially open subellipsoidal posture would have experienced the least amount of column torque among the three proposed postures. One might assume that the ligaments in the column would have locked into place to prevent much movement and minimal, if any, damage to the column, but extreme turbulence events would have undoubtedly caused damage to the column, arms, or both, regardless of the arm posture.

The Kesling and Sigler (1965) weathervane mode suggested that with the currents striking the oral side of the arms the crown and column would have pivoted back and forth as dictated by currents and drag on the crown. As presently understood, there is not a single pivot point along the column that would have allowed this motion. Theoretically, it would have been possible for cumulative, coordinated contraction and relaxation of ligaments between columnals to have resulted in movement as predicted by the weathervane mode, but the motion allowed may have been slower and less extensive than imagined by Kesling and Sigler (1965).

Opening the crown.— The primary question about opening the crown is the extent to which it could open. By analogy to living echinoderm ligaments, a calceocrinid could have easily assumed a partially open, subellipsoidal posture. It is also probable that opening and closing of the outer fossae of the basal circlet-E inferradial articulation were well within the limitations imposed by ligaments. The primary question is whether ligaments on the inner surface of the radial circlet could have had contraction and stretching enough to open the crown into a fully erect posture and close it again. It is probable that the ligaments in the proximal portion of the inner radial circlet would have supported fully opening the crown into an erect posture. However, it is doubtful if this was the case for any ligaments higher up along the inner surface of the radial circlet.

Calceocrinid arms would experience lift if the crown was positioned with the currents striking the ambulacral side of the arms. This would aid opening of the crown. Indeed, this lift was the premise for the Breimer and Webster (1975) kite model of calceocrinids in which the crown gained sufficient lift to be elevated into tiering levels above the sediment-water interface. Whereas sufficient lift to slightly raise the crown was probable, the calculations of lift by Baumiller (1992) suggested that insufficient lift would have typically been generated to elevate the crown and column to the extent envisioned by Breimer and Webster (1975). Further, it is improbable that sustained current velocities would have been present low in the benthic boundary layer to maintain an elevated kite position.

In a posture with currents striking the aboral side of the arms, calceocrinids would have had to overcome drag resistance to open their arms against the currents, which is the case for living crinoids, as well as most Paleozoic crinoids that had only ligaments in the crown (Ausich and Baumiller, 1993).

The subellipsoidal posture would have experienced the least amount of resistance opening the crown simply because it opened the least. A multidirectional or unidirectional current regime would have little effect on opening the arms into a partially open subellipsoidal posture.

Closing the crown.— In a unidirectional current regime with currents striking the ambulacral side of the arms, a sudden, catastrophic current burst would severely challenge closure of the arms. Alternatively, calceocrinids feeding in either the partially open subellipsoidal posture or a posture

FIGURE 15 — E superradial plate of *Halysiocrinus tunicatus* illustrating ridges beneath the articular ridge and galleried stereom paralleling these ridges (OSU 54086). **A**, **B**, Exterior of E superradial plate, A an enlargement of the right side of the fossa with poorly preserved ridges beneath and perpendicular to the articular ridge. A, scale bar 0.5 mm, B, scale bar 2.5 mm. **C**, **D**, **E**, Interior of E superradial plate, C, scale bar = 2.5 mm, D, enlargement of E scale bar = 0.33 mm; **E**, enlargement of right side of C, scale bar = 0.5 mm. Dots are landmark points to identify position of enlargements.

with the currents striking the aboral side of the arms would quickly close into a resting posture with the aid of currents. As noted above, these two posture scenarios would also support the anecdotal observation of more common preservation of calceocrinid crowns in many occurrences.

Fouling from waste.— *Senariocrinus maucheri* Schmidt, 1934 is known to have had a very high anal sac that would have helped to disperse waste above and away from open arms. However, this may have presented a problem for most calceocrinids with shorter anal sacs. In calceocrinids with erect arms and currents striking the aboral side of the arms, waste products would have presumably been swept away from the ambulacra and prevented fouling. Alternatively, if arms were erect and the currents struck the oral side of the arms, waste products would have had to have been washed through the arms that were engaged in feeding, and fouling would have been inevitable. Similarly, in a partially open subellipsoidal posture with the anal sac completely enclosed

within the arms, fouling would also be inevitable; however, this is presumably not a limiting factor among living crinoids.

DISCUSSION AND CONCLUSIONS

Calceocrinid crown morphology radically deviated from that of any other stalked crinoid to exploit a suspension-feeding niche immediately above the sediment-water interface. Based on the success of this lifestyle (inferred from the extreme duration of this family), it is surprising that more crinoid clades did not evolve a similar feeding position within tiered, suspension-feeding paleocommunities. Of course, feather stars also lack a column as adults. However, this morphology was inferred to primarily be a consequence of increased predation pressure before and during the Mesozoic Marine Revolution (Meyer and Macurda, 1977; Baumiller et al., 2010), and living feather stars commonly climb to the highest perch possible, presumably to maximize current flow

TABLE 2 — Various positive and negative factors that may have influenced feeding posture in the Calceocrinidae. The "+" symbol indicates a positive factor; the "0" indicates a neutral factor; the "−" symbol indicates a negative factor.

Factors	Arms Erect, Currents Strike Ambulacra	Arms Erect, Currents Strike Aboral Side of Arms	Ellipsoidal Posture
Feeding ability	+	+	+
Feeding in unidirectional currents	+	+	+
Feeding in multidirectional currents	−	−	+
Torque on column due to drag on crown	−	−	−
Lift to help to open crown	+	−	0
Currents help close crown	−	+	0
Higher probability of crown preservation	−	+	+
Fouling from waste	−	+	−

through the arms (e.g., Meyer, 1973, 1979; Messing, 1985, 1994, 1997, 2006; Stevens and Connolly, 2003; Messing et al., 2006, 2021).

Three possible suspension-feeding postures for calceocrinids are described above, including an erect arm posture with currents striking the oral side of the arms, an erect arm posture with currents striking the aboral side of the arms, and a partially open, subellipsoidal posture. Based on skeletal morphology and analogy to living crinoid feeding behavior, preserved stereom microstructure implies that opening and closing of the crown and arm movement was controlled by ligaments. It is probable that contraction and stretching limitations of echinoderm ligaments would have allowed the basal circlet-E inferradial articulation to fully open and close, but it is not clear if this is the case for the ligaments on the inner side of the radial circlet. Assuming that a vertical posture was within the limits imposed by ligaments, all three potential feeding habits are possible. Inferred pluses and minuses can be scored for each posture (Table 2), and none of the alternatives can be eliminated with certainty.

In conclusion, two primary puzzles have persisted surrounding the paleoecology of members of the Calceocrinidae. The first is solved. Based on remnants of preserved stereom, only ligament tissue is inferred to have controlled opening and closing of the crown and arms in calceocrinids. Based on the behavior of ligaments in living echinoderms, ligament tissue was sufficient to open and close the aboral cup and arms of calceocrinids. The second puzzle is calceocrinid posture during feeding. Whereas an erect fan with the current striking the aboral side of the arms has been favored by recent authors (Brower, 1985; Ausich, 1986; and Messing et al., 2021), there is no compelling criterion by which to reject this or other potential feeding orientations and posture positions, with the only caveat being the ligament stretching limits. Therefore, it is possible that two or all of three of these alternative postures could have been employed to exploit changing ambient environmental conditions. The calceocrinids remain a puzzle.

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