

Contributions

from the Museum of Paleontology, University of Michigan

VOL. 34, NO. 3, PP. 17–33

JANUARY 18, 2022

MORPHOLOGIC EXPRESSIONS AND PALEOGEOGRAPHIC IMPLICATIONS OF EARLIEST KNOWN (FLOIAN, EARLY ORDOVICIAN) HYBOCRINIDS

BY

THOMAS E. GUENSBURG¹ AND JAMES SPRINKLE²

Abstract — The early hybocrinid *Syndiasmocrinus apokalypto* n. gen., n. sp. (late Floian, Early Ordovician, Laurentia), furnishes well preserved nearly complete crown morphology. The new taxon's tegmen interambulacral, or perforate extraxial, regions consist of many small platelets and epispines with the hydropore plate separate from the peristome region. This interambulacral plating extends out the arms as lateral plate fields. *Syndiasmocrinus* tegmen morphology concords with *Hoplocrinus* from the Middle to Late Ordovician, of Baltica, but not the similar aged *Hybocrinus*, of Laurentia, where interambulacra are each formed of single circumorals. In contrast, *Syndiasmocrinus*' posterior plating includes an anal X in agreement with *Hybocrinus*, but *Hoplocrinus* lacks this plate. Lateral plate fields of *Syndiasmocrinus* are unlike any other known hybocrinid but resemble those occurring in earliest crinoids such as *Apektocrinus* and *Titanocrinus*. An even earlier hybocrinid, *Parahybocrinus sieversi* n. gen., n. sp. (early Floian, Early Ordovician), posterior cup plating includes two small posterior plates distal to anal X, an expression unknown among hybocrinids until now, but widespread among other early cladids.

urn:lsid:zoobank.org:pub:1C3F1E27-939E-45A8-BA01-7DE58ECE6F75

¹IRC, Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605 (tguensburg@fieldmuseum.org)

²Department of Geological Sciences, Jackson School of Geosciences, University of Texas, 1 University Station, C1100, Austin, Texas 78712-0254 (echino@jsg.utexas.edu)

INTRODUCTION

Hybocrinids have long evoked fascination among crinoid students (e.g. Wachsmuch and Springer, 1883; Ausich et al., 2018). Aspects of their anatomy are unusual (Fig. 1). For instance, the cup base circlet is aligned with stalk meres below, in violation of the “Law of Wachsmuch and Springer” (Ubaghs, 1978). This condition has been referred to as “pseudomonocyclic” plating (Öpik, 1935; Warn, 1975; Sprinkle, 1982). Hybocrinids have non-branching food gathering structures expressed either as short atomous arms or armless ambulacra upon the cup surface, and a non-elevated posterior tegmen (Figs. 2, 3) (Sprinkle and Moore, 1978; Sprinkle, 1982; Wright et al., 2017). Some taxa are known to express a small, short, curved stalk, including *Hoplocrinus* Grewingk, 1867, *Hybocrinus* Billings, 1857, and *Hybocystites* Weatherby, 1880. *Treocrinus* Semenov, Terentyev, Mirantsev, and Rozhnov, 2021, lacks a stalk entirely.

Here, we describe earliest known hybocrinids *Syndiasmocrinus apokalypto* n. gen., n. sp. and *Parahybocrinus siewersi* n. gen., n. sp. and compare these to later taxa to which they are most similar, the Middle to Late Ordovician Laurentian *Hybocrinus* and Baltican *Hoplocrinus* (Figs. 2, 3). Analysis of this new data includes identification of body wall regions from the perspective of the Extraxial/Axial Theory (EAT) (Mooi and David, 1998).

Taphonomic data provides useful information for functional interpretations; methodology applied earlier by Tom Baumiller (e.g. Baumiller and Ausich, 1992; others). Specimens are relatively small, requiring hand preparation with fine needles under high magnification. Images were acquired by immersing specimens in water or coating with sublimate of ammonium chloride. Images are multi-focus montages prepared at the Field Museum using a Leica DMS digital microscope and linked software.

INSTITUTIONAL ABBREVIATIONS

NPL (---TX--)	— Non-vertebrate Paleontology Laboratory, University of Texas, Austin.
PE	— Field Museum, Chicago, Illinois.
PIN	— Paleontological Institute, Russian Academy of Sciences, Moscow
UI X	— Prairie Research Institute, University of Illinois, Champaign.

SYSTEMATIC PALEONTOLOGY

CRINOIDEA Miller, 1821
CLADIDA Moore and Laudon, 1943

Discussion.— Moore and Laudon (1943) originally conceived the Cladida as an ordinal rank taxon diagnosed,

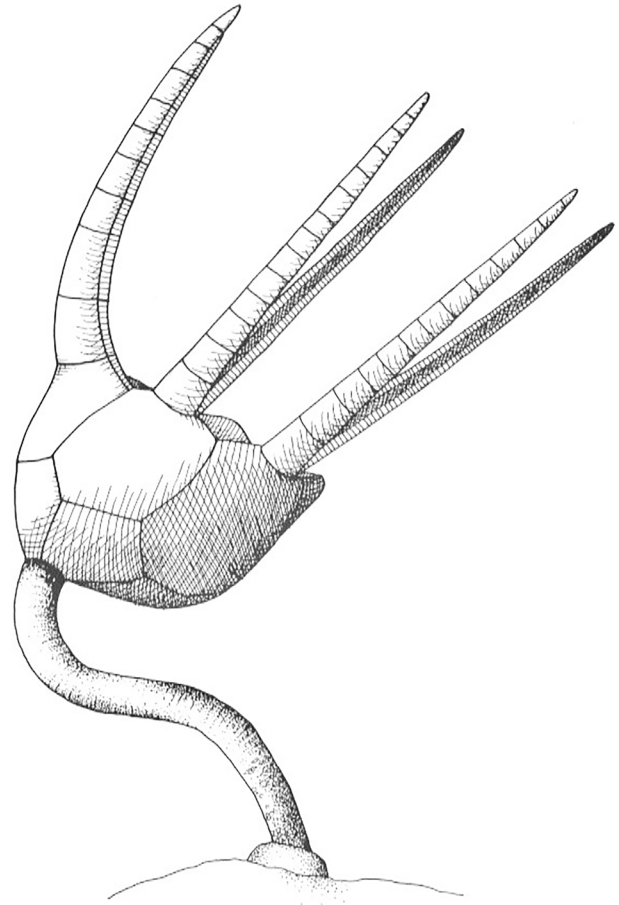


FIGURE 1— Restoration of *Hybocrinus bilateralis* Guensburg, 1984 (copyright, from Guensburg, 1992: fig. 10, reprinted with permission), Late Ordovician (Sandbian).

in part, by a dicyclic cup with infrabasal and basal circlets. Wright, et al. (2017), revised the Cladida to include not only the crinoid crown group, but also hybocrinids, long placed within the monocyclic disparids (see Sprinkle and Moore, 1978). Realignment within the cladids acknowledges the pseudomonocyclic hybocrinid cup in which infrabasals are secondarily lost (Warn, 1975; Sprinkle, 1982, p. 126).

Order Hybocrinida Jaekel, 1918

Discussion.— The diagnosis provided by Sprinkle and Moore (1978: p. T570) is adopted here with the addition that the “monocyclic” cup is pseudomonocyclic, with the assumption that the plesiomorphic condition among cladids is a dicyclic cup with infrabasals forming the cup base.

Family Hybocrinidae Zittel, 1879

Remark.— The familial diagnosis follows Sprinkle and Moore (1978: p. T570)

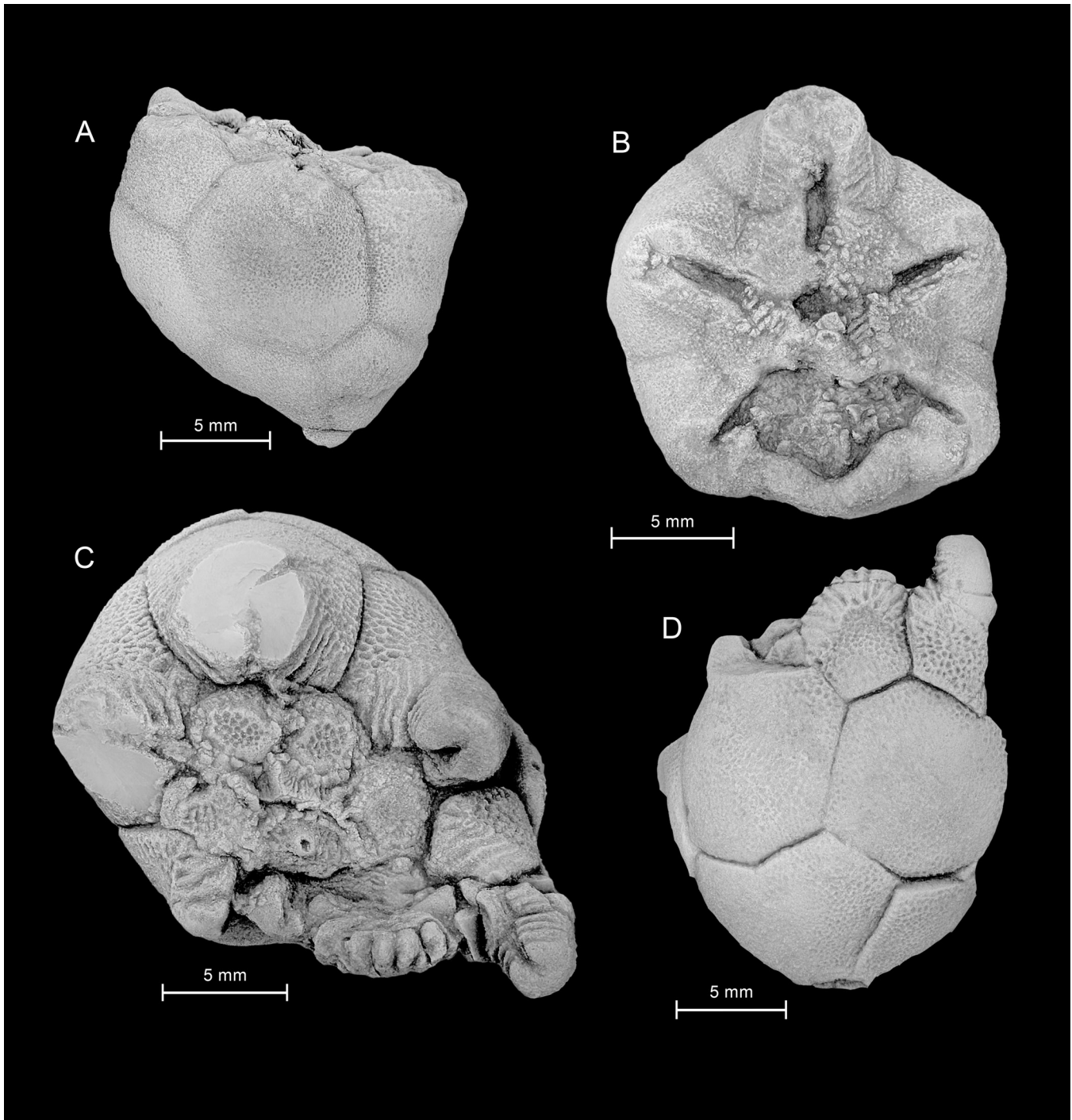


FIGURE 2 — Calyx morphology of the Late Ordovician (Sandbian) *Hybocrinus bilateralis* Guensburg, 1984. Photographs of two specimens from the same shaly interbed, morphology exemplifying the Laurentian genus *Hybocrinus*: UI X 5867 **A, B**, undistorted specimen showing fine reticulate ornament in B view of calyx (**A**); oral view (**B**), A ray at top, large circum-orals rigidly sutured to radials, pitted extraxial ornament in continuity across radials and circum-orals, radials with strong “oralward” (inward) curvature so that the tegmen is restricted to the circum-orals and peristome, hydropore plate in CD interray, incorporated into circum-oral ring; UI X 5868 **C, D**, slightly crushed specimen in oral view (**C**), with intact ambulacra, cover plates form a 2-1-2 ambulacral pattern, coarse reticulate ornament crossing from radials to circum-orals, parallel grooves extending laterally from ambulacral grooves in radials, first C brachial; Cup in CD orientation (**D**), crenulated, thickened, anal X distal margin.

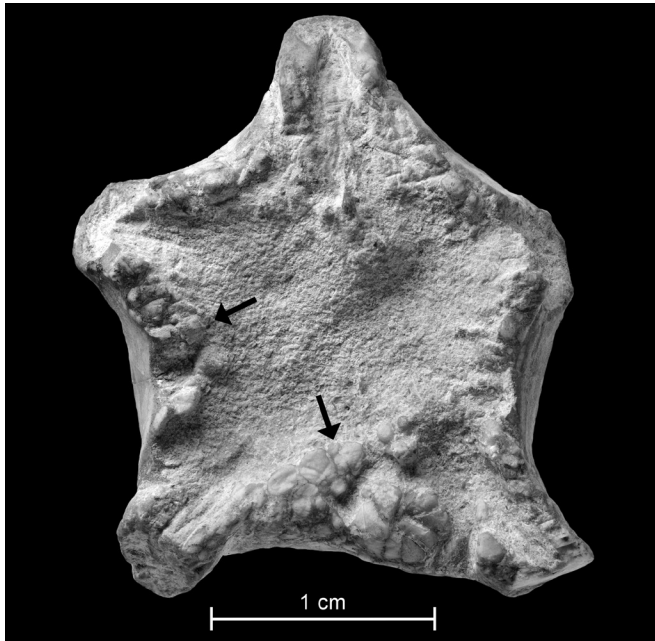


FIGURE 3 — *Hoplocrinus estonus* Öpik, 1935. PIN 4125/9, photograph of oral view of calyx showing areas with small platelets, two marked with arrows, coated. Image courtesy of S.V. Rozhnov, Paleontological Institute, Russian Academy of Sciences.

Genus *Syndiasmocrinus* gen. nov.

Type species.— *Syndiasmocrinus apokalypto* new species

Diagnosis.— As for the type species, by monotypy

Etymology.— Compounding of syndiasmos, Greek, meaning combination, in reference to morphology combining both *Hybocrinus* and *Hoplocrinus* traits, and crinus, latinized from the Greek krinos, lily.

Syndiasmocrinus apokalypto sp. nov.

Figs. 4 – 8, 9B, 9C, 9E, 9F, 10

Type specimens.— Four specimens comprise the hypodigm, the holotype 1780TX13, and paratypes: 1781TX12, 1780TX14, and 1778TX17.

Taphonomic considerations. — *Syndiasmocrinus apokalypto* n. gen. n. sp. (hereafter *Syndiasmocrinus*, as the genus is monotypic) specimens preserve relatively complete tegmen and arm lateral plating. The four known specimens were collected in float, partly weathered free from shaly matrix. Weathering obscures plate boundaries locally, but this is a relative minor issue in terms of data loss, because most plate shapes can be confidently inferred. More significant are effects of calcitic overgrowths on small skeletal elements. In general, diminutive tegmen interray plating is darker calcite in comparison with thicker, lighter colored, cup and hydropore plates. The holotype tegmen is virtually complete and intact

with minor overgrowths but shifted slightly toward the A-B side of the calyx, resulting in most complete exposure of C-E regions (Fig. 7C). Paratype 1778TX14 tegmen is more seriously affected by calcitic overgrowths but these are translucent allowing discernment of original plate outlines under strong light. As preserved, interambulacral regions sag inward in both specimens, indicating a pliable tegmen in life. The conical anal pyramid is preserved in the holotype but folded outward. Lateral plates are well-preserved in the holotype but flattened. One partially preserved arm of paratype 1778TX17 shows laterals covering an inflated region, extending well beyond, above the brachials.

Diagnosis.— A species of hybocrinid with tegmen slightly narrower than maximum cup width, tegmen interradii, interambulacra, with plate fields of tiny plates with apparent epispines, presumably embedded in a flexible integument, hydropore plate separated from the peristome, and tegmen interambulacral fields transitioning to non-pore-bearing lateral plate fields extending out atomous arms in all rays.

Occurrence.— All specimens of this new taxon were collected from the middle Ninemile Shale, *Pseudozybele nasuta* Zone, trilobite zone J (Hintze, 1973; Adrain et al. 2009) in Whiterock Canyon, Eureka County, Nevada. Specimens are from an unknown distance above the slope at WR-2 or 2A (Narrows Section), approximately 1.2 km up Whiterock Canyon from the end of the north side access track. This locality is approximately 56 km southwest of Eureka, Eureka County, Central Nevada. This age falls in the upper Blackhillsian Stage, Ibexian Series, late Floian Global Stage, late Early Ordovician.

Description.— A small hybocrinid with relatively short arms; largest specimen, paratype 1780TX14, maximum cup height as measured along the C ray approximately 12.5 mm, the smallest specimen, the holotype, approximately 8.8 mm. Cup approximately as tall as wide in largest specimen paratype 1780TX14, slightly taller than wide in holotype; cup sides diverging from stalk facet at approximately 60 degrees in holotype, 70 to 80 degrees in paratype 1781TX12; C ray higher than other rays, resulting in canted oral surface and asymmetrical calyx. Cup bulbous, umbonate, slightly incurving at top, cup plates ornamented with fine pustules in holotype and paratype 1778TX17, fine reticulation in paratype 1780TX13. Cup base distinctly curved toward the posterior in holotype, slightly curved toward the anterior in paratype 1781TX12; these result in off-axis stalk attachments. Low broad ray ridges in paratype 1780TX14 (Fig. 9E), vague in other specimens.

Basals five, forming approximately lower 30% of cup; wedge-shaped with small undulating stalk facet; BC basal largest, upper facets for radial insertions slightly curved. Radials largest; anterior (A, B, D, E) radials largest cup plates with distal margins slightly curved inward toward the tegmen on average, curvature variable, A and E radials subpentagonal, B and D radials irregular hexagonal with each contacting the radianal and C radial. C radial relatively small, forming the high point of the cup, upper margin slopes distinctly away

from the C radial facet. Radial facets angustary, projecting slightly to distinctly above main body of radial, oriented nearly straight upward to angling diagonally outward. Radial large, much larger than C radial or anal X (Figs. 4H, 9E), irregular hexagonal, bounding two basals below, B and D radials laterally, the C radial on the upper right, and anal X on the left. Anal X on the upper left, rectangular, the upper surface forming the cup top across CD and separating C and D radials, much smaller than C radial.

Tegmen (oral surface) morphology primarily taken from holotype, augmented by paratype 1778TX12 (*Taphonomic considerations* above); ambulacra (axials) in holotype narrow, converging in 2-1-2 arrangement over the peristome. Cover plate pattern obscure, larger, composed of squared-off lateral cover plates, apparent much smaller medial cover plates visible along the ambulacral mid-line (perradial suture) (Figs. 7A, B). Interambulacra composed of a network of platelets, estimated 50 per interray, these form fields in holotype and paratype 1778TX12; individual platelets approximately 100 μm across, with estimated two to four marginal epispires along their scalloped margins, particularly well exposed in the DE interray of holotype and AB interray of paratype 1778TX12. CD interray wider than other interrays in holotype, with large ovoid hydropore plate in the holotype, distal to the peristome in CD, irregular surface with deep grooves (Figs. 6-8); at least one other large plate beyond the hydropore plate nearing the periproct. Periproct a steep-sided cone in holotype, formed of several elongate wedge-shaped plates.

Five short atomous arms; tips incomplete, maximum length estimated at slightly longer than cup height judging by arm taper in large paratype 1778TX17, slightly shorter than cup in holotype. Brachials approximately 1.5 times longer than wide in paratype 1778TX17, up to two times longer than wide in smaller holotype. Lateral plate fields separate brachials from axial plating (ambulacrals and cover plates), tapering outward, consisting of thin imbricate elongate ovoid platelets in holotype D ray; inflated ?A ray lateral field of paratype 1778TX17 nearly as wide as adjacent brachials, expanding toward the tegmen. Cover plate pattern uncertain, only exposed in holotype over the peristome; primary cover plates large, elongate, approximately twice as long as wide, squared off at the distinctly sinuous median suture in holotype sutures (Fig. 7A).

Proximal stalk segment preserving 12 very thin columnals in paratype 1780TX14; narrow, approximately 1.3 mm wide at cup juncture, tapering (Fig. 9E). Columnals with traces of pentameres, short rounded, but rough epifacets. Lumen large, pentalobate, each lobe aligned with mere, CD interray lobe larger than others.

Etymology.—*Apokalypso*, Greek, to uncover, reveal, make known, in reference to the remarkable new data furnished by this taxon's discovery.

Remarks.— Each of the four type specimens provides overlapping data representing nearly all portions of the skeleton, excepting the distal stalk and holdfast. Overlapping data also furnish some evidence for phenotypic variation,

plate shape, and ornamentation, much as has been observed in *Hybocrinus* (Guensburg, 1984) and *Hoplocrinus* (Rozhnov, 1985; 2007). See COMPARATIVE ANALYSIS OF THE *SYNDIASMOCRINUS* TEGMEN below.

Paleoenvironmental context.— The Ninemile Shale is interpreted have been deposited in relatively deep shelf environment, where soft, unconsolidated substrates prevailed (Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1995). This setting was unfavorable for early crinoids in general, judging by their relative rarity. Crinoids required suitable exposed firm or hard sites upon which to attach cementing type holdfasts.

Syndiasmocrinus sp. A
Figs. 9A, 9D

Occurrence.— A single specimen, PE 52754, from the Wah Wah Formation, approximately 2 meters above the contact with the Fillmore Formation, ridge east of Square Top, Square Top East Section, southeast quarter of the southwest quarter of the northwest quarter, Section 32, Township 21 south-Range 13 west, Millard County, Utah. This stratigraphic horizon is in the *Pseudocybele nasuta* trilobite zone J of Hintze, 1973, and Adrain et al., 2009, Blackhillsian Stage, late Floian global stage.

This taxon is represented by a single collapsed cup with parts of arms still embedded in dense matrix. Cup plates are slightly disheveled.

Remarks.— A single specimen is here referred to *Syndiasmocrinus* based on general resemblance of cup shape and plating and but without details of the tegmen and arms, assignment is tentative. Posterior plating resembles *Syndiasmocrinus apokalypso*, except that anal X is a proportionately larger plate, suggesting the possibility of a distinct species.

Paleoenvironmental context.— The single specimen was draped over a small *Calathium*-sponge mound along with other crinoids, including a small iocrinid and another taxon of unknown affinities.

?*Syndiasmocrinus* sp.
Fig. 9G

Occurrence.— Ninemile Shale, 27-29 meters above the base of the Ninemile Shale. Locality is *MJ-1* of Sprinkle, 1973 (p. 195), just out of the west gully below southwest side of Meiklejohn Peak, northeast quarter of Section 24, Township 12 north, Range 47 east, approximately 7 miles east of Beatty, Nye County, Nevada (Bare Mountain 15-minute quadrangle).

Remarks.— A single specimen, 1968TX2, is a deeply weathered crown and stalk. Partial mouldic preservation of the cup; small, thin, tapering stalk, and atomous arms all suggest a hybocrinid with arms at least twice cup height and stalk length at least 1.3 as long as crown height. Columnals grow thicker away from the crown. Preservation is insufficient for definitive assignment.

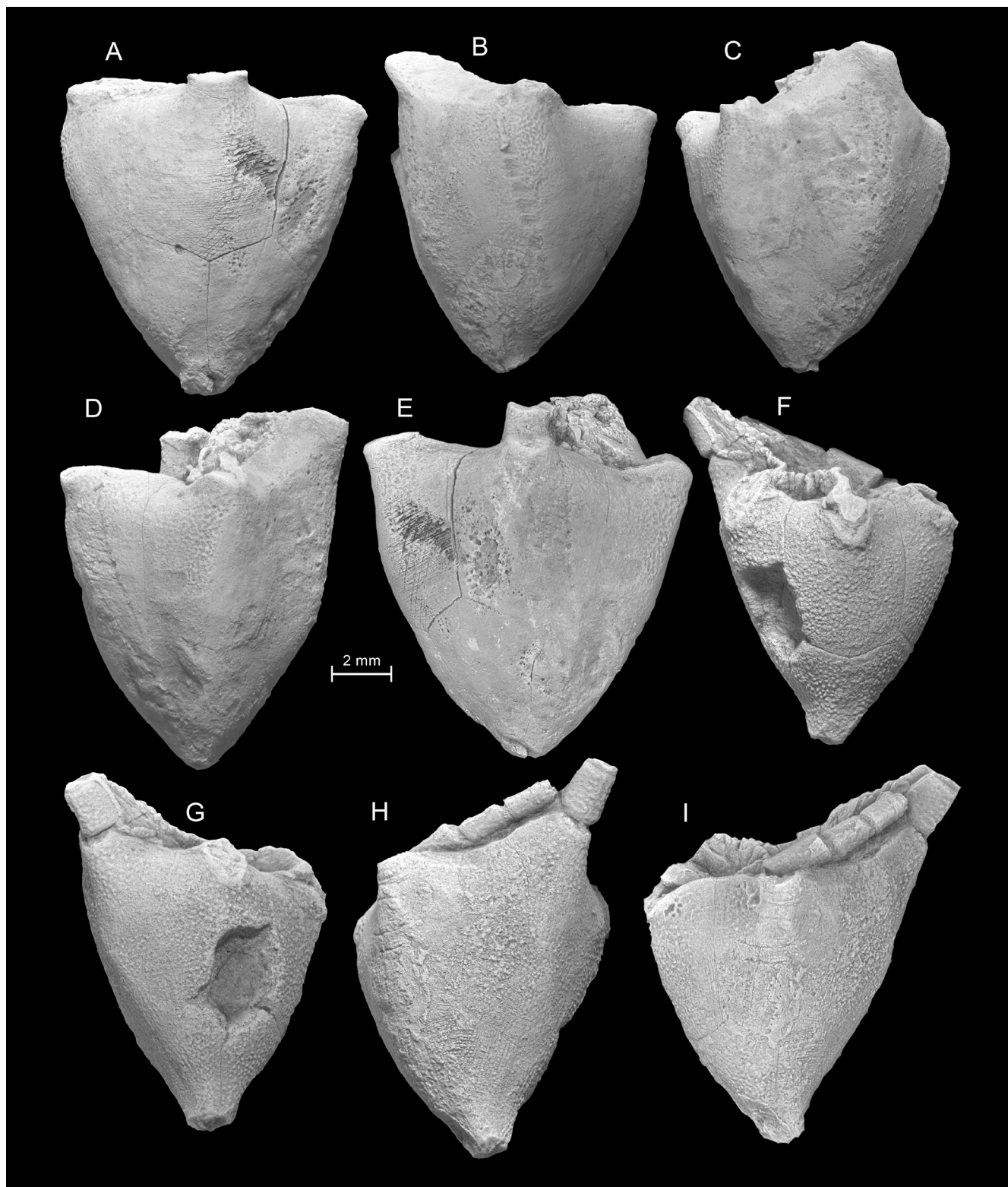


FIGURE 4 — *Syndiasmocrinus apokalypto* n. gen., n. sp. Photographs of cups in lateral views: paratype 1981TX12 A–E, which has fine reticulate ornament; A, A, B, B, C, CD, D, D, and E, E ray views. Holotype 1980TX13 F–I, which has fine pustulose ornament, in F, A, G, B, H, CD, and I, D ray views.

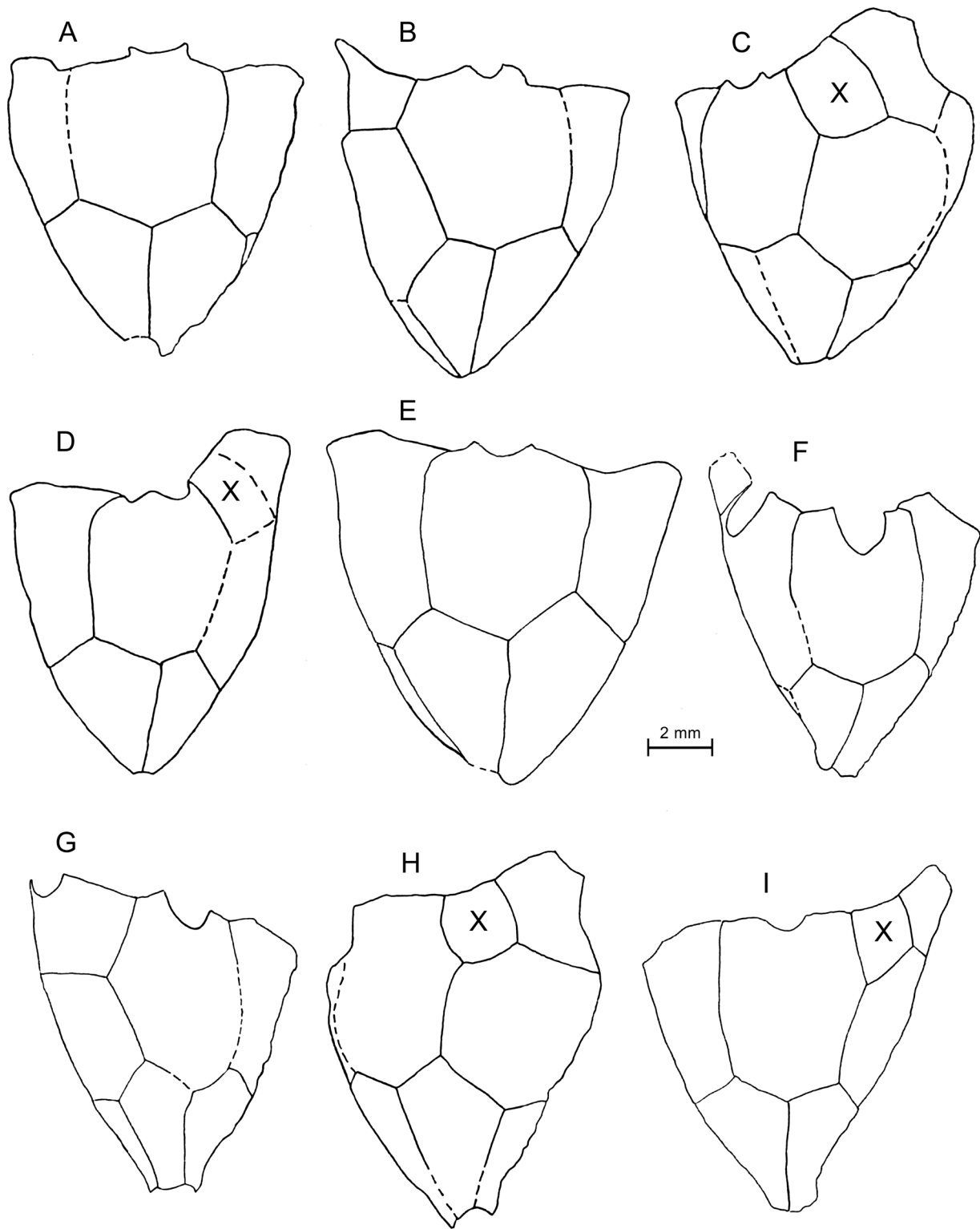


FIGURE 5 — *Syndiasmocrinus apokalypto* n. gen., n. sp. cup morphology: Tracings showing cup plate boundaries from FIGURE 4; anal X plates indicated, and other plates forming cup top are radials; plate subjacent to C radial is the radialian.

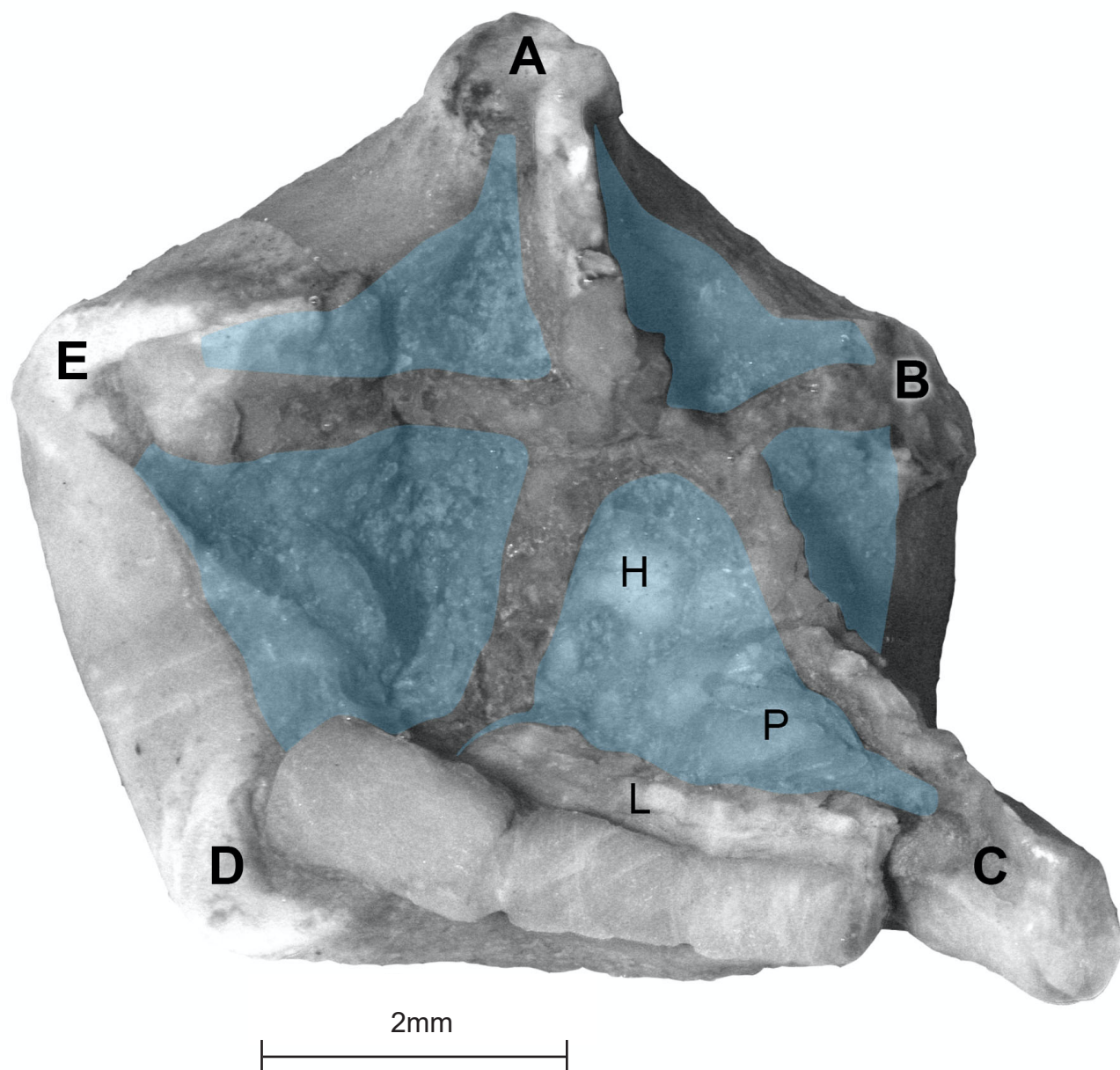


FIGURE 6 — *Syndiasmocrinus apokalypto* n. gen., n. sp., holotype 1980TX13, immersed in water, oral surface with features coded for reference to FIGURE 7. Blue shaded areas indicate interradial, perforate extraxial, portions of tegmen, separated by unshaded ambulacra, axial, area; bold letters indicate rays; H, hydropore plate; L, lateral plates of arm; P, periproct/anal cone.

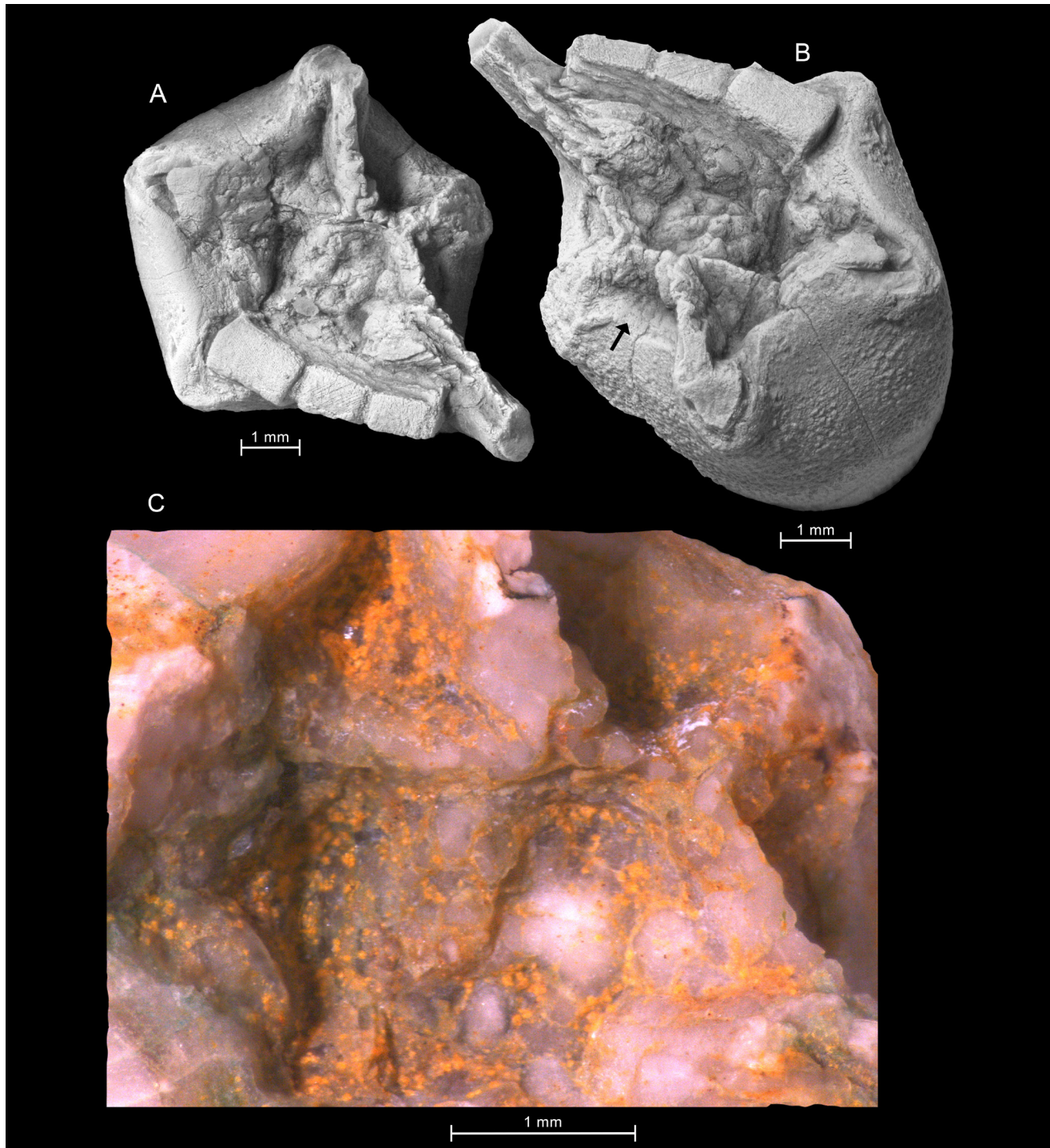


FIGURE 7 — *Syndiasmocrinus apokalypto* n. gen., n. sp. holotype 1980TX13, oral surface; **A**, photograph of entire surface viewed directly downward on coated specimen, standard orientation with A ray at top. The ambulacra are arranged in a 2-1-2 pattern, with cover plates forming sharp ridges elevated above surrounding interambulacral, sinuous perradial suture, rapidly tapering atomous arms, anal cone between C and D arms; **B**, photograph of inclined surface of coated specimen, rotated approximately 180 degrees from the orientation in FIGURE 7A, with the A-ray pointed downward. The arrow indicates BC interray showing small platelets. **C**, enlarged image of oral region, standard orientation. The interambulacra are sunken, sagged, composed of numerous platelets with epispires, large hydropore plate in CD, immersed.

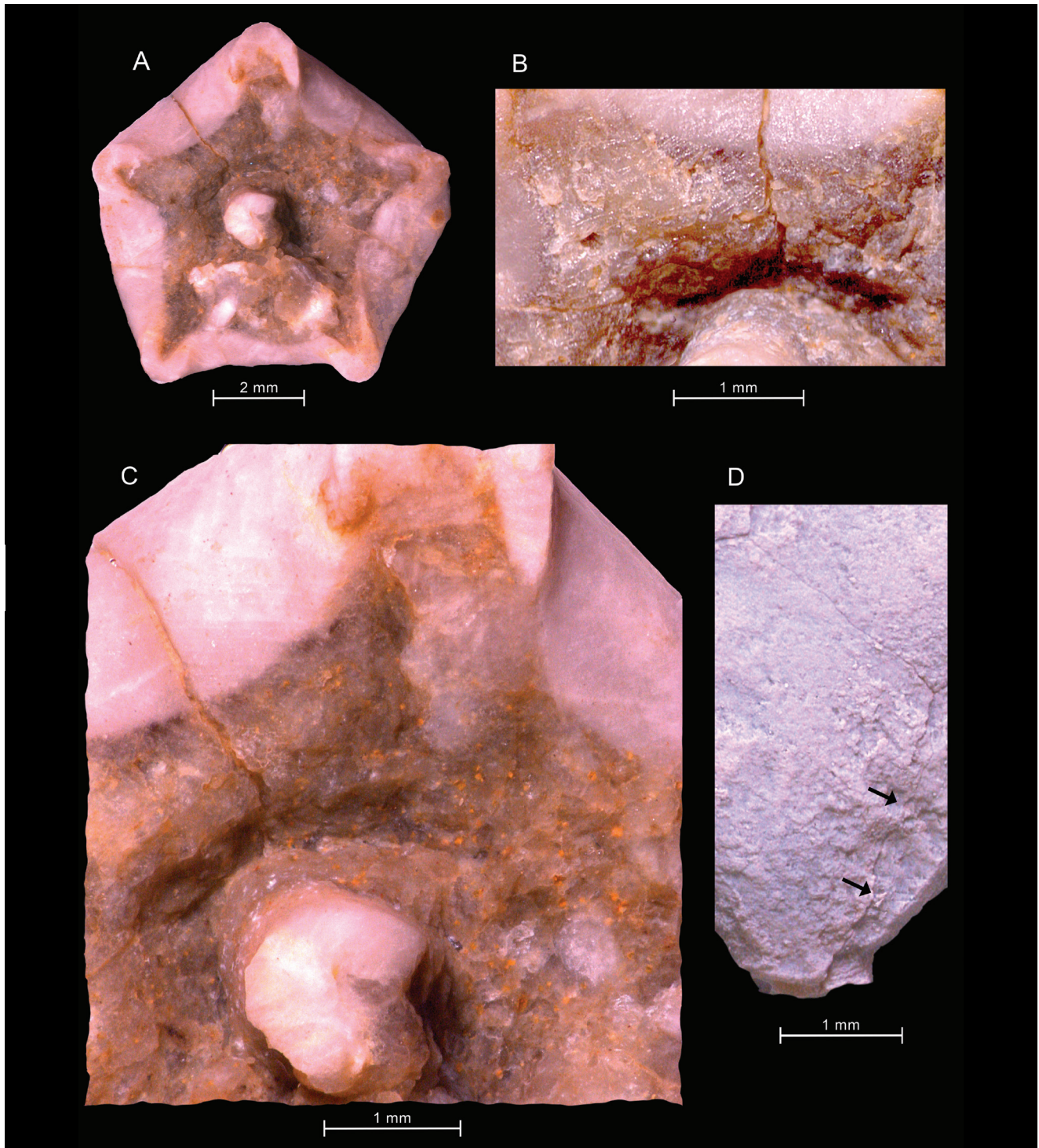


FIGURE 8 — *Syndiasmocrinus apokalypto* n. gen., n. sp.; A–D Photographs of paratype 1781TX12 A–D. Oral region A–C; A, entire surface, isolated brachial over the peristome region, standard orientation with A ray upward, radials with slight inward curvature (compared with *Hybocrinus* species), interambulacrals darker than thicker plates, immersed. B, EA interray, small platelets with syntaxial overgrowths, interambulacral field curved toward peristome which is pushed downward by displaced brachial, uncoated dry image. C, Detail of anterior cup showing lighter radials and blotchy EA and AB interambulacral regions, platelets preserved as darker spots, immersed D, lower cup, same CD orientation as FIGURE 3C, enlargement showing basals and thin proximal columnals, mere orientation uncertain, arrows indicate suture of BC and CD basals, coated.

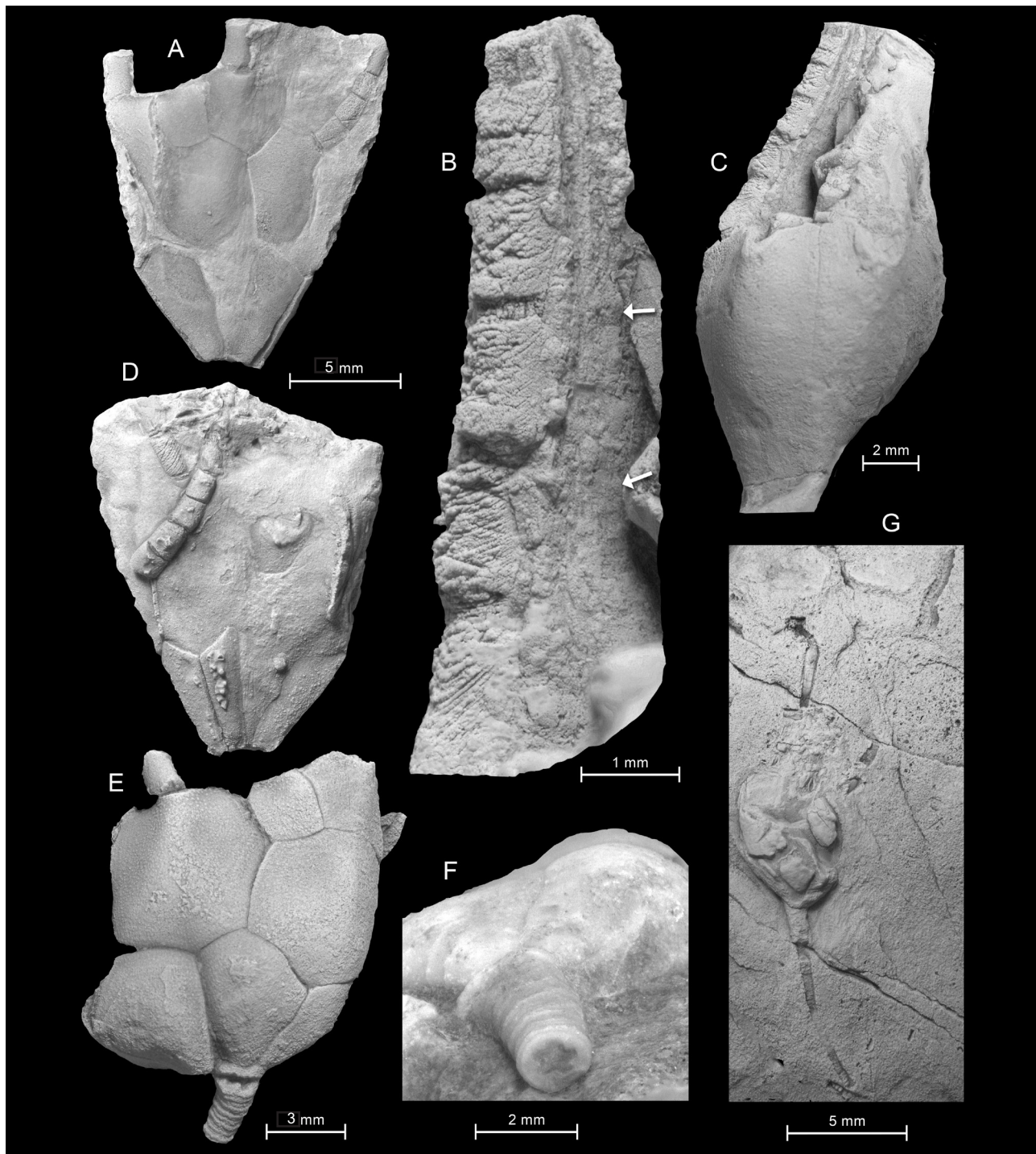


FIGURE 9 — Floian hybocrinids. Photographs of *Syndiasmocrinus* sp. A (PE 52754) A, D, coated. A, C ray orientation of collapsed calyx, relatively tall C radial; anal X above, left of center; D, A ray orientation, specimen largely buried in matrix. Photographs of *Syndiasmocrinus apokalypto* n. gen., n. sp. B, C, E, F. Paratypes 1776TX17 B, C and 1780TX14 E, F; B, C, E, coated, F immersed in water. B, detail of A ray with partial arm at left, brachials deeply weathered, inflated lateral plate field on right indicated by arrows, lateral plate field expanding toward the cup. C, anterior view of entire specimen, lower cup buried in concretion, radials with little inward upper curvature. E, entire specimen, partly flattened, posterior view, low broad ray ridges, pustulose ornament, proximal curved stalk, thin columnals with vague pentamere boundaries. F, basals and stalk showing pentalobate lumen. Photograph of ?*Syndiasmocrinus* sp. 1968TX2 G, Weathered partial crown and stalk.

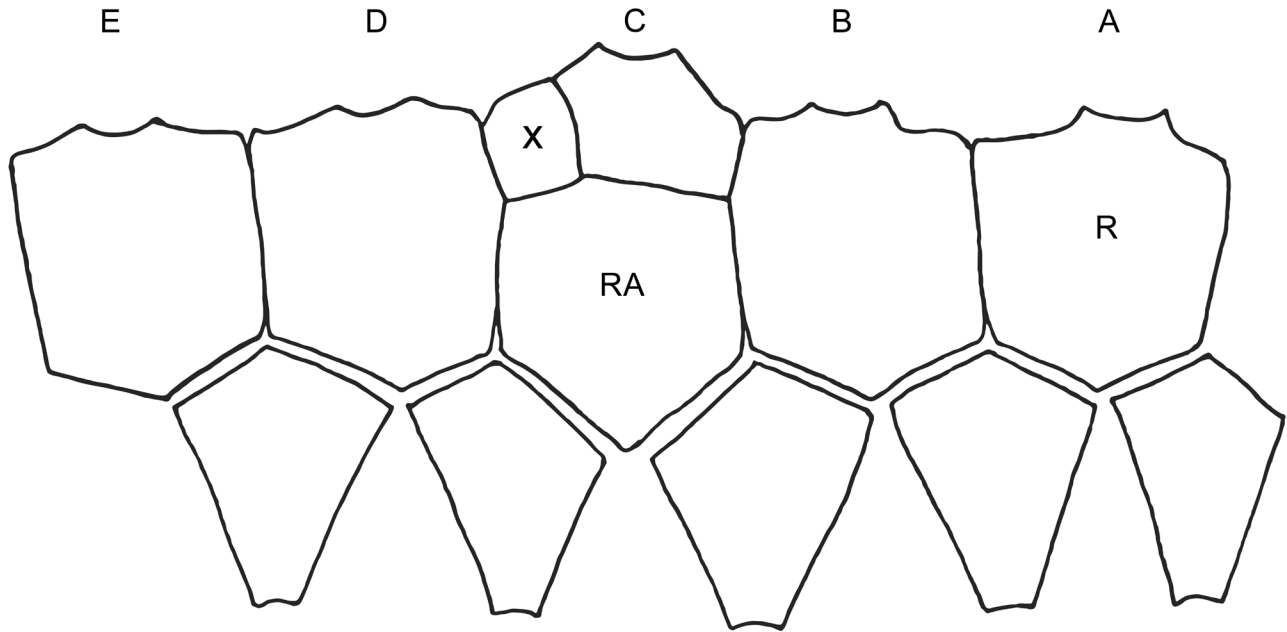


FIGURE 10 — *Syndiasmocrinus apokalypto* n. gen., n. sp., side layout plate diagram, drawn primarily from paratype 1981TX12, posterior supplemented from 1780TX14; Rays indicated above, R= radial (one indicated), RA= radianal, X= anal X.

Parahyocrinus gen. nov.

Remarks.— See *Remarks* following *Parahyocrinus siewersi* description below.

Type species.— *Prohyocrinus siewersi* new species

Diagnosis.— As for the type species, by monotypy

Etymology.— Compounding of para, Greek meaning near, hybos, Greek meaning hump (in reference to a rounded asymmetrical calyx), and crinus, lily, latinized from the Greek krinos.

Parahyocrinus siewersi sp. nov.

Figures 11, 12

Type specimen.— PE 52755

Diagnosis.— A hyocrinid with C radial and radianal approximately equal in size, two small anal series plates above anal X; the larger of the two wedged between upper shoulders of the C radial and anal X, the other smaller plate contacting the C radial.

Occurrence.— The single specimen is from the “Giza Peak megarripple bed”, lower light grey ledge-forming member, approximately 253 meters above the base of the Fillmore Formation; northwest quarter of the northeast quarter of the northwest quarter of Section 25 (unsurveyed), Township 20 south, Range 14 west, House Range, Millard County, Utah. This stratigraphic horizon falls in the *Protopliomerella contracta* zone, or G(2) trilobite biozone, in the Late Tulean North American and Early Floian global stages (near the

Floian-Tremadocian boundary). Associated echinoderms include the “Giza Peak” Megarripple Group of edrioasterid edrioasteroids (Guensburg and Sprinkle, 1994: p. 18), and the type specimens of *Cnemocrinus fillmorensis* Guensburg and Sprinkle, 2003, and as yet undescribed juvenile crinoid.

The single *Parahyocrinus siewersi* specimen consists of a nearly complete but etched small crown. The left margin of the anal X plate is broken away. The specimen is exposed with the posterior side facing up. Matrix was excavated from both sides of the specimen exposing the majority of the cup except for most of the E and A radials; edges of both plates are visible.

Description.— The holotype and single specimen, PE 52754, crown height estimated at 6 mm tall, D arm slightly longer than cup height as measured along the D ray below. Cup strongly asymmetrical, bulbous, cup height 2 mm as measured along D ray, 5.3 mm along C ray, 2.7 mm along B ray, and 2 mm along A ray; base of cup slightly convex, diverging from very narrow stalk at approximately 80 degrees as viewed from the CD orientation. Low thin ray ridges pass from basals to radials, ridges dissipate one third to one half the way up radials.

Basals pentagonal with very small stalk facet, approximately two times taller than wide. Radials, and radianal largest cup plates. A-ray radial short, extending only half the distance upward as adjacent B radial. B radial the tallest cup plate, heptagonal, maximum width at its mid-point, corresponding with the A radial top. C radial highest plate in cup, heptagonal, as large as radianal, slightly wider than tall, contacting radianal

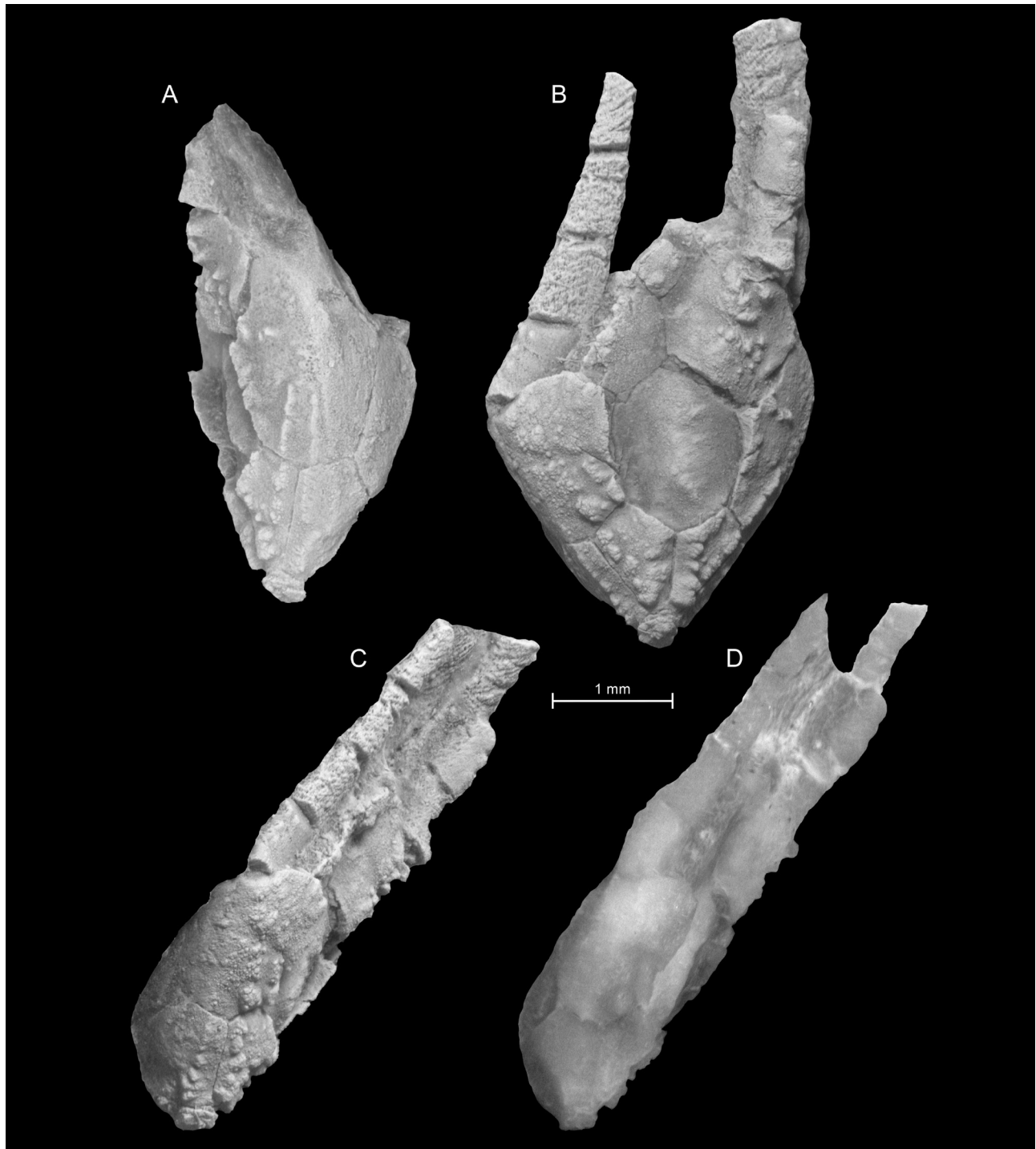


FIGURE 11 — *Parahybocrinus siewersi* n. gen., n. sp. Photographs of holotype PE 52755 A–D; **A**, B ray orientation of cup, tall B radial, one side of the A radial visible on right, and C radial at upper left, ray ridges extending from basals to the lower radials, short, thin stalk stub, with three columnals, coated; **B**, CD orientation, partly collapsed, radianal at center, large C radial at above right, B radial at right, anal X at upper left, contacting upper right shoulder of D radial, with damaged left margin, small diamond-shaped anal plate filling wedge between anal X and C radial, smaller anal plate above contacting the C radial, D arm nearly complete, C ray much taller than D ray; **C**, **D**, D ray orientation, D radial short, wide, D ray arm with four brachials, corner of E radial visible at left, coated and immersed images, respectively.

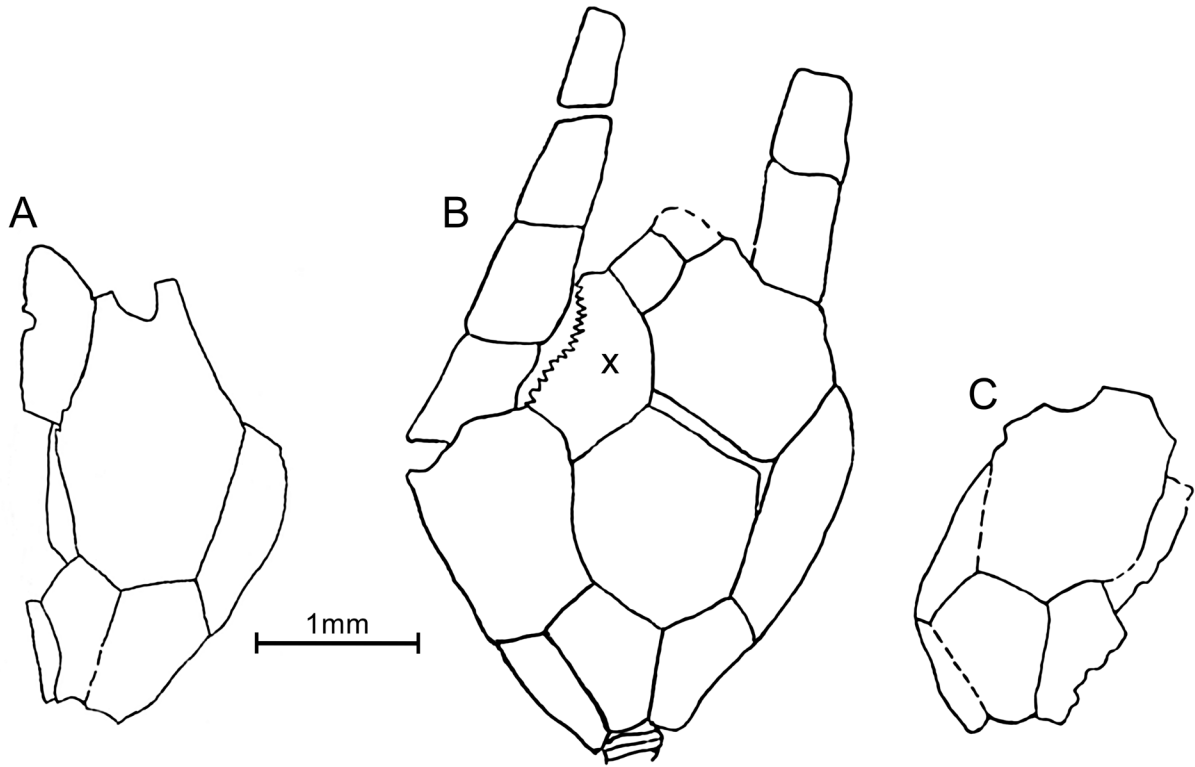


FIGURE 12 — *Parahyobocrinus siewersi* n. gen., n. sp.; Holotype PE 52755 (A–C). Tracings of holotype PE 52755 based on images from Figure 11 showing plate boundaries. Abbreviations: R, radial; RA, radianal; X, anal.

on lower left, left upper shoulder of B radial on lower right, anal X on left, two small anal plates on upper left, and brachial one above. D radial hexagonal, strongly convex, contacting two basals below, the radianal on right, anal X on upper right, E basal on left. Only right margin of E radial exposed, similar in height to D radial. Radianal positioned toward in CD interray; large, hexagonal, contacting a basal on lower left and right, D radial on left, C radial on upper right shoulder. Anal X large, contacting D radial on lower right, C radial on the right, a small anal plate on upper right, broken on the left; small quadrangular anal plate contacting C radial on lower right, anal X on lower left, and another small anal plate of uncertain shape on upper right.

Partial atomous arms preserved on C, D, and ?A rays. A ray arm appears larger than C and D rays. C ray arm with two primibrachials, C ray arm nearly complete, with regular rapid taper, four brachials, ?A arm incomplete with unknown number of brachials, brachials average approximately twice as tall as wide. Stalk stub much weathered, with two, possibly three columnals having low rounded epifacets, lumen apparently pentalobate.

Etymology.— Specific appellation honors Fred Siewers, Geology Department, Western Kentucky University, who assisted the authors with western Utah fieldwork in 1989 and 1990, and made important echinoderm discoveries.

Remarks.— Small size and certain details such as relatively elongate few brachials suggest the type specimen represents a juvenile. However, the relatively wide cup implies an advanced growth stage (for example, contrast Fig. 11B with juvenile of *Hybocrinus bilateralis* Guensburg, 1984, pl. 9, fig. 16).

Information for this new taxon is limited, based primarily upon cup and partial arm morphology. The tegmen, distal posterior cup, arm details, and stalk are lacking. Hybocrinid apomorphies include an asymmetrical tumid cup, short tapering atomous arms, thin stalk, pseudomonocyclic cup, and cup posterior dominated by radianal and, sometimes, anal X plates. Aside from its smaller size, the general configuration of the *Parahyobocrinus* crown is comparable with that of *Syndiasmocrinus* and *Hybocrinus*. The posterior region of *Parahyobocrinus* is unique among hybocrinids in expressing a proportionately larger C radial and two small plates distal to anal X. This plating pattern is intermediate between the basal condition seen in earliest (Tremadocian) cladids such as *Aethocrinus* (Ubaghs, 1969) and later hybocrinids such as *Hybocrinus* (e.g. Sprinkle, 1982, Guensburg, 1984) and *Hoplocrinus* (e.g. Öpik, 1935; Regnéll, 1948). Origin of the relatively flat hybocrinid posterior from an elevated multi-plated condition was proposed by Wachsmuth and Springer (1883: p. 377): “we further hold that the special anal plate

(anal X) in *Hybocrinus* is the first step toward a plated tube which in that genus is reduced to its minimum size, consisting of only a single plate (radial, in *Hoplocrinus*)” (wording in parentheses added to conform with modern terminology and for clarity).

Paleoenvironmental context.—This specimen was draped over the surface of a large storm-generated megaripple bed (see Datillo, 1993) in association with a few other crinoids and edrioasteroid specimens. Modes of life of these echinoderms suggests original association and on a lithified carbonate substrate or hardground in shallow water (Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1995).

COMPARATIVE ANALYSIS OF THE *SYNDIASMOCRINUS* TEGMEN

Tegmen body wall regions using the EAT (Mooi and David, 1998) can be divided into axial—articulated (operable) cover plate, and perforate extraxial—epispire-bearing interambulacral, hydropore, and periproct regions. The latter extend in continuity out arms as laterals (although it is uncertain whether laterals incorporated epispires. Interambulacrals and epispires end abruptly at the cup juncture; suggesting cup plates are part of the imperforate extraxial region.

There is little basis for comparing *Syndiasmocrinus* tegmen regions with other early (Early Ordovician) crinoids for lack of data. *Titanocrinus* Guensburg and Sprinkle, 2003 (Guensburg et al., 2021), among the earliest known crinoids expresses similar tegmen interradials and lateral arm plating. Earliest known cladids *Apektocrinus* Guensburg and Sprinkle, 2009, and *Aethocrinus* Ubaghs, 1969, both express arms bearing lateral plate fields extending from the tegmen. Beyond crinoids, epispires and hydropore apart from the peristome occur in Cambrian pre-crinoid early pentardiate echinoderms such as *Stromatocystites* Pompeckj, 1896 (for instance, see Zamora et al., 2015). This limited information suggests the *Syndiasmocrinus* tegmen represents plesiomorphic, deep seated, conserved morphology.

The Laurentian *Hybocrinus* cup plating is very similar to *Syndiasmocrinus*, but the tegmen construction is remarkably different (compare Figs. 2B, C, with Fig. 7C, and Figs. 8A–C). *Hybocrinus* tegmen interradial are occupied by single large circumoral plates. These circumorals articulate firmly to radials, forming a rigid construct (e.g. Kammer et al., 2013). In contrast, no known Baltic hybocrinid expresses rigid circumoral plating (Fig. 3; Rozhnov, 1985, 2007; Semenov et al., 2021, p. 68, Sergey Rozhnov, personal contact, 2021). The many-plated integument of hybocrinids occurs throughout hybocrinid history in Baltica but, excepting *Syndiasmocrinus*, not in Laurentia. No formal phylogenetic analysis is provided here, pending inclusion of all available taxa, particularly those from Baltic material. As such, the data suggest separate histories for Laurentian and Baltican hybocrinids following their divergence from a common ancestor during the Early Ordovician.

ACKNOWLEDGMENTS

Jen Bauer, University of Michigan Museum of Paleontology, skillfully shepherded the manuscript through the various stages of preparation. D. Quednau, Field Museum, applied his considerable skill to figure preparation. The authors gratefully acknowledge two anonymous reviews. Special thanks are due to Sergey Rozhnov, Russian Academy of Sciences, Moscow, for providing the image in FIGURE 2, and important discussions on Baltic hoplocrinids. We also thank Paul Mayer, Scott Lidgard, and others at the Field Museum for helpful discussions.

LITERATURE CITED

- ADRAIN, J.M., N.E.B. McADAMS, and S.R. WESTROP. 2009. Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Paleontologists*, 37: 541–610.
- AUSICH, W.I., D.F. WRIGHT, S.R. COLE, and J.M. KONEICKI. 2018. Disparid and hybocrinid crinoids from the upper Ordovician (Katian) Brechin Lagerstätte of Ontario. *Journal of Paleontology*, 92: 850–871.
- BAUMILLER, T.K. and W.I. AUSICH, 1992. The broken stick model as a null hypothesis for crinoid stalk taphonomy and as a guide to the distribution of connective tissue in fossils: *Paleobiology*, 7: 155–176.
- BILLINGS, E. 1857. New species of fossils from the Silurian rocks of Canada: Canada Geological Survey, Report of Progress for the year 1856, p. 247–345.
- DATILO, B.F. 1993. The Lower Ordovician Fillmore Formation of Western Utah; storm-dominated sedimentation on a passive margin: Brigham Young University Geology Studies, 39, p. 71–100.
- GREYWINGK, C.C.A. 1867. Über *Hoplocrinus dipentus* and *Baerocrinus ungeri*: *Archive für die Naturkunde Liv-, Ehst und Kurlands*, series 1, 4: 100–114.
- GUENSBURG, T.E., 1984, Echinodermata of the Middle Ordovician Lebanon Limestone, Central Tennessee: *Bulletins of American Paleontology*, 86, 100 p.
- _____. 1992. Paleoecology of hardground encrusting and commensal crinoids, Middle Ordovician, Tennessee: *Journal of Paleontology*, 66: 129–147.
- _____, and J. SPRINKLE. 1992. Rise of echinoderms in the Paleozoic evolutionary fauna: Significance of paleoenvironmental controls: *Geology*, 20: 407–420.
- _____, and J. SPRINKLE. 1994. Revised phylogeny and functional interpretation of the Edrioasteroidea based on new taxa from the early and middle Ordovician of western Utah. *Fieldiana, Geology, New Series*, No. 29, 43 p.
- _____, and J. SPRINKLE. 2003. The oldest known crinoids (Early Ordovician, Utah), and a new crinoid plate

- homology system: *Bulletins of American Paleontology*, 364: p. 1–43.
- _____, and J. SPRINKLE. 2009. Solving the mystery of crinoid ancestry: New fossil evidence of arm origin and development: *Journal of Paleontology*, 83: 350–364.
- _____, and J. SPRINKLE, R. MOOI, B. LEFEBVRE, B. DAVID, M. ROUX, and K. DERSTLER. 2021. *Athenacrinus* n. gen. and other early echinoderm taxa inform crinoid origin and arm evolution: *Journal of Paleontology*, 94: 311–333.
- L.F. HINTZE. 1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah: *Brigham Young University Geology Studies*, 20: 3–36.
- JAEKEL, O. 1918. Phylogenie und system der Pelmatozoen: *Paläontologische Zeitschrift*, 3: 1–128.
- KAMMER, T.W., C.D. SUMRALL, S. ZAMORA, W.I. AUSICH, and B. DELINE, 2013. Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms: *PLoS ONE*, vol. 8, p. 1–16. (doi: 10.1371/journal.pone.0077989)
- MILLER, J.S. 1821. A natural history of the Crinoidea or lily-shaped animals, with observations on the genera *Asteria*, *Euryale*, *Comatula*, and *Marsupites*: Bryan and Company, Bristol, 150 p.
- MOOI, R., and B. DAVID, 1998. Evolution within a bizarre phylum: homologies of the first echinoderms: *American Zoologist*, v. 38: p. 965–974.
- MOORE, R.C., and L.R. LAUDON. 1943. Evolution and classification of Paleozoic crinoids: *Geological Society of America, Special Paper 46*, 153 p.
- ÖPIK, A. 1935. *Hoplocrinus*: eine stiellose Seelilie aus dem ordovizium Estlands: *Tartu Ülikooli Geoloogia Instituudi Toimetused* 43: 1–15.
- POMPECKJ, J.A., 1896. Die Fauna des Cambrium von Tejrovic und Skrej in Böhmen: *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, v. 45, p. 495–614.
- REGNÉLL, G. 1948. Swedish hybocrinida (Crinoidea Inadunata Disparata : Ordovician—Lower Silurian: *Arkiv för Zoologie, K. Svenska Vetenskapsakademien*, v. 40 A, 30 p.
- ROZHNOV, S.V. 1985. Morphology, symmetry, and systematic position of hybocrinid crinoids: *Paleontological Journal*, 280: 4–16.
- _____, 2007. New data on perittocrinids and hybocrinids (Crinoidea, Echinodermata) from the Middle Ordovician of the Baltic Region. *Annales de Paléontologie*, 93: 261–276.
- SEMENOV, N.K., S.S. TEREITYEV, G.V. MIRANSTSEV, and S.V. ROZHNOV. 2021. A new hybocrinid genus (Echinodermata, Crinoidea) from the Middle Ordovician of Ladoga Glint on the Volkhov River: *Paleontological Journal*, 55: 54–63.
- SPRINKLE, J., 1973. Morphology and evolution of blastozoan echinoderms: Special Publication, Museum of Comparative Zoology, Harvard University, Cambridge, p. 1–283.
- _____, 1982. *Hybocrinus*: in Sprinkle, J. (ed.) *Echinoderm Faunas from the Bromide Formation (Middle Ordovician) of Oklahoma*: University of Kansas Paleontological Contributions, Monograph 1: 119–128.
- _____, and T.E. GUENSBURG. 1995. Origin of echinoderms in the Paleozoic Evolutionary Fauna; the role of substrates: *Palaios*, 10: 437–453.
- _____, and R.C. MOORE. 1978. Hybocrinida: in Moore, R.C. and Teichert, C. (eds.) *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2(1)*. Geological Society of America, Boulder, and University of Kansas, Lawrence, pp. T564–T574.
- UBAGHS, G. 1969. *Aethocrinus moorei* Ubaghs, n. gen. n. sp, le plus ancien crinoïde dicyclique connu: *University of Kansas Paleontological Contributions, Paper 38*, p. 1–25.
- _____. 1978. Skeletal morphology of fossils crinoids: in Moore, R.C. and Teichert, C. (eds.) *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2(1)*. Geological Society of America, Boulder, and University of Kansas, Lawrence, p. T58–T216.
- WACHSMUTH, C., and F. SPRINGER, F. 1883. On *Hybocrinus*, *Hoplocrinus*, and *Baerocrinus*: *American Journal of Science*, November 1 issue, p. 365–376.
- WARN, J.M. 1975. Monocyclism vs. dicyclism, a primary schism in crinoid phylogeny?: in Pojeta, J. Jr., and Pope, J.K. (eds.), *Studies in Paleontology and Stratigraphy*: *Bulletins of American Paleontology*, 67: 57–69.
- WETHERBY, A.G. 1880. Descriptions of new crinoids from the from the Cincinnati Group of the Lower Silurian and Subcarboniferous of Kentucky: *Cincinnati Society of Natural History Journal*, 2: 245–258.
- WRIGHT, D.F., W.I. AUSICH, S.R. COLE, M.E. PETER, and E.C. RHENBERG. 2017. Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata): *Journal of Paleontology*, 91: 829–846.
- ZAMORA, S., B. LEFEBVRE, I. HÜSGOR, C. FRANZEN, E. NARDIN, O. FATKA, and J. ÁLVARO. 2015. The Cambrian edrioasteroid *Stromatocystites* (Echinodermata): systematics, paleogeography, and paleoecology: *Geobios* 48: 417–426.
- ZITTEL, K.A. von. 1879. *Handbuch der Paläontologie, Volume 1, Paläozoologie, No. 1, Munich, Germany, R. Oldenbourg*, 765 pp.

Museum of Paleontology, The University of Michigan
1105 North University Avenue, Ann Arbor, Michigan 48109-1085
Matt Friedman, Director

Contributions from the Museum of Paleontology, University of Michigan is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. Jennifer Bauer and William Ausich, Guest Editors; Jeffrey Wilson Mantilla, Editor.

Publications of the Museum of Paleontology are accessible online at: <http://deepblue.lib.umich.edu/handle/2027.42/41251>
This is an open access article distributed under the terms of the Creative Commons CC-BY-NC-ND 4.0 license, which permits non-commercial distribution and reproduction in any medium, provided the original work is properly cited.

You are not required to obtain permission to reuse this article. To request permission for a type of use not listed, please contact the Museum of Paleontology at Paleo-Museum@umich.edu.

Print (ISSN 0097-3556), Online (ISSN 2771-2192)