A RE-INTERPRETATION OF THE AMBULACRAL SYSTEM OF *EUMORPHOCYSTIS* (BLASTOZOA, ECHINODERMATA) AND ITS BEARING ON THE EVOLUTION OF EARLY CRINOIDS

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Abstract: Recent debates over the evolutionary relationships of early echinoderms have relied heavily on morphological evidence from the feeding ambulacral system. *Eumorphocystis*, a Late Ordovician diploporitan, has been a focus in these debates because it bears ambulacral features that show strong morphological similarity to early crinoid

outer portion of the arm; a single supporting thecal plate for the extension of the arm (herein referred to as a radial plate); and the presence of a coelomic canal. We show that phylogenetic analyses support *Eumorphocystis* as the sister group of crinoids and character optimization supports the suggestion that these arm features are homologous, and the hypothesis that crinoids are rooted within blastozoans.

UNIVERSAL ELEMENTAL HOMOLOGY

A common problem in echinoderm palaeontology is that skeletal elements are commonly named based on location or function rather than evolutionary lineage. Such naming schemes can result in individual names being used for a variety of unrelated plate types across echinoderm groups; this issue is highlighted within the stemmed echinoderm group (see Sumrall & Waters (2012) for a comprehensive list of problematic names for homologous skeletal elements across Palaeozoic echinoderms). These issues act as a barrier to understanding skeletal element homology in echinoderms. As morphological characters for phylogenetic analysis are constructed as hypotheses of homology (Patterson 1988; Sumrall 1997), understanding the homology of these elements prior to phylogenetic coding the morphology is of critical importance when trying to infer accurate evolutionary relationships.

Universal elemental homology (UEH) identifies ambulacral homology using the Carpenter system (Carpenter 1884), which focuses on the plate types bordering the peristome and the ambulacral system (Sumrall 2010, 2017; Sumrall & Waters 2012; Kammer et al 2013). This homology scheme is useful for identifying deep homologies within Echinodermata. The other leading homology scheme that is used for echinoderm phylogenetics, the extraxial–axial theory (Mooi et al 1994; Mooi & David 1997, 1998, 2008; David et al 2000) is much coarser and differentiates the echinoderm skeleton into two large categories: axial (skeletal parts associated with the mouth and ambulacral system) and extraxial (the body wall); UEH refers only to elements within the axial system (Sumrall 2017).

For the purposes of this study, certain morphological terms are defined here. True arms are defined following Zamora & Smith (2011): those arms with a central lumen, or coelomic canal, which are directly connected to the theca. Guensburg et al (2016) added to this definition, suggesting that arms also have both axial and extraxial skeletal components together with the coelomic canal. An erect ambulacrum is one that is not attached to the surface of the theca distally; it may or may not have an extension of the extraxial skeleton or brachioles.

PREVIOUS ARGUMENTS CONCERNING BLASTOZOAN–CRINOID ANCESTRY

Morphological arguments

Arguments against shared blastozoan and crinoid ancestry have primarily emphasized differences between crinoid and blastozoan morphology (e.g. Guensburg & Sprinkle 2001, 2007, 2009; Guensburg et al 2016) and are rooted in arguments of homology versus homoplasy. These arguments were made by highlighting ÔkeyÕ features that drove the separation between the blastozoan and crinoid groups, rather than using rigorous phylogenetic methodology. Guensburg et al (2016) also asserted that superficial similarities shared by blastozoans and crinoids (e.g. homoplasy) are probably related to plesiomorphic pentaradial patterns of stemmed echinoderms, an argument that is not rooted in phylogenetic understanding, as it confuses the definitions of homology and homoplasy (Sumrall 2017). In contrast, phylogenetic arguments are rooted in the discovery of suites of synapomorphies providing support for nodes within proposed evolutionary trees.

Previous arguments posit that crinoids were probably derived from a Cambrian edrioasteroid ancestor (see Guensburg & Sprinkle 2001, 2007; Guensburg et al 2016). Morphological evidence for this hypothesis focuses on shared biserial floor plates bearing through-going pores and branched ambulacra in both edrioasteroids and crinoids. Branching of ambulacra is well documented in blastozoans including the eocrinoid *Lyracystis*, the hemicosmitid *Caryocrinites*, and several glyptocystitoids including *Stribalocystites* and *Callocystites*. Further, Guensburg & Sprinkle (2001, 2007, 2009) argued that blastozoans have no extraxial components of the arms and lack coelomic

fully consistent with their placement within the blasto-
zoan tree; numerous groups of blastozoans appear at
the same time as the crinoids with no obvious deeper
lineages (e.g. all major groups of diploporitans (Kesling
1967; Lefebvre et al 2013), parablastoids (Sprinkle &
Sumrall 2008) and new glyptocystitoid rhombiferans

Two major clades were recovered; the Þrst clade contains
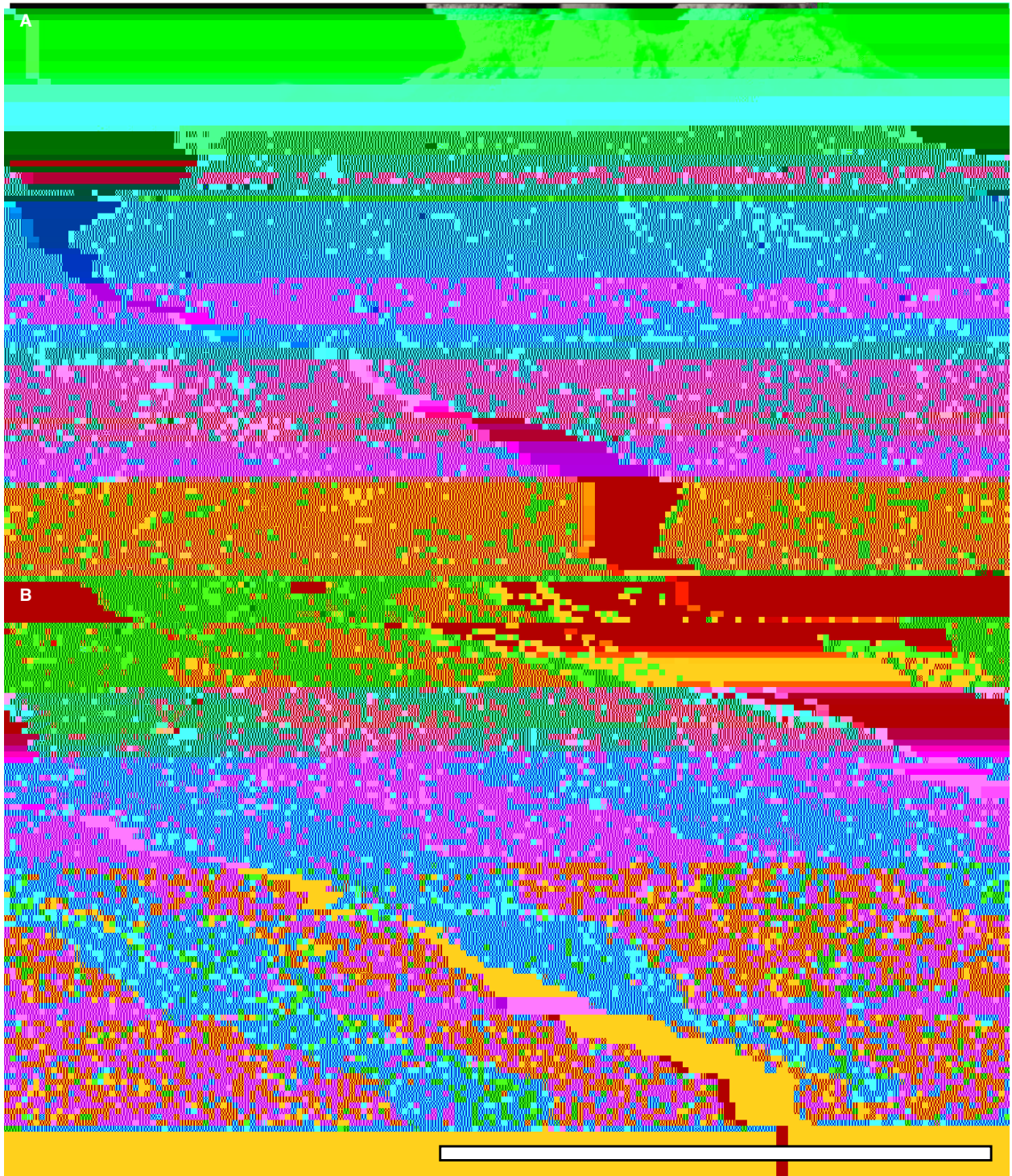all crinoids (Carabocrinus and Hybocrinus

FIG. 3. Arm morphology of *Eumorphocystis multiporata*. A, radial view of erect arms of *E. multiporata*. B, radial view of erect arms of *E. multiporata* with triserial arm arrangement interpretation. Blue = uniserial, extraxial brachial plates derived from thecal plates, with supporting radial plate initiating the series. Green = singly biserial, axial ambulacral floor plates. Yellow = axial ambulacral cover plates. Red = oral plates. Note the coelomic canal that is positioned between the brachial plates and the ambulacral floor plates. Scale bar represents 0.5 cm.

junction between the oral plates and the thecal wall (Fig. 5B). While this may seem different, it is effectively

arms (Fig. 4A, B), where: (1) the extraxial brachial plates derive from the theca, and are supported by a radial plate; (2) biserial, axial ambulacral ßoor plates are present; and (3) axial ambulacral cover plates cover the food groove. As is the case with *Eumorphocystis*, the coelomic canal of a protocrinoid is contained between the brachial plates and the ambulacral ßoor plates (the phylogenetic placement of protocrinoids within Crinoidea has been debated; see Guensburg (2012), Ausich *et al* (2015), Cole (2017), Wright *et al* (2017) for discussions concerning their relationships). While Guensburg *et al* (2016) interpreted blastozoans as lacking extraxial brachial plates, it is clear that *Eumorphocystis* does indeed have a triserial arrangement with thecally derived (extraxial) brachial plates (Fig. 3A, B). The uniserial nature of these plates is consistent with the arrangement in early crinoids.

There are some notable differences between the ambulacral systems of early crinoids and *Eumorphocystis*; this analysis does not take the position that every element of the axial skeleton is entirely similar. The proximal food grooves of *Eumorphocystis* are developed on sutures between the oral plates and extend onto the sutures of alternating biserial ßoor plates (Fig. 5A). *Carabocrinus*, the proximal food grooves are conÞned to the oral plate sutures and presumed soft anatomical structures that extend over the coelomic canal as ßoor plates are absent (Fig. 5B). The coelomic canal of *Eumorphocystis* perforates the thecal wall at the junction between the proximal ambulacral ßoor plates and plating of the thecal wall (Fig. 3A, B), whereas in crinoids, such as *Carabocrinus*, the coelomic canal perforates the thecal wall at the
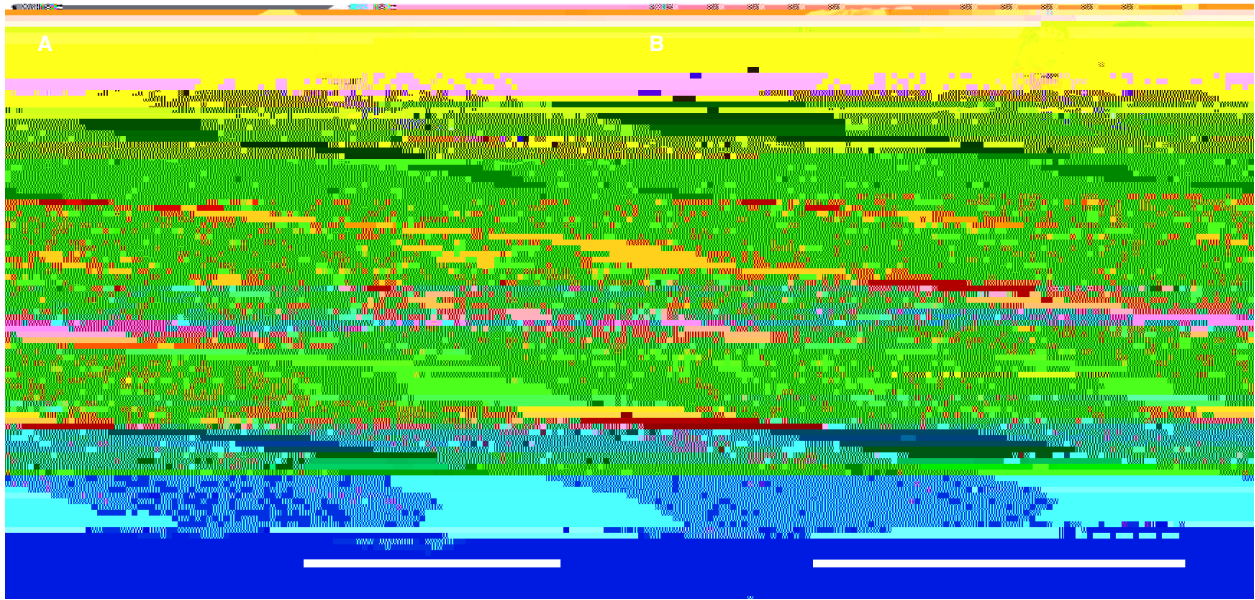
FIG. 5. Constructional differences between *Eumorphocystis* and crinoids. A, the proximal food grooves of *Eumorphocystis* are developed on oral plate sutures and alternating biserial plates (SUI 97598). B, the proximal food grooves of *Cerabocrinus* are confined to the oral plate sutures (OU 9127). Note that the coelomic canal perforates the body at the periphery of the summit at the edge of the oral plate series. Red = oral plates. Blue = primary peristomial cover plates. Yellow = ambulacral cover plates. Green = ambulacral floor plates. Scale bars represent 5 mm. (Modified from Kammer *et al.* 2013.)

model resulted in a tree that was considerably less parsimonious, as it added seven steps to the tree length. A Templeton test, which statistically compared two trees, one without topological constraints and one with topological constraints, indicated that the two trees are significantly different from one another. Our interpretation of these data is that crinoids being rooted within edrioasteroids is not well supported by current data. Based on these results, we reject the hypothesis that crinoids originated from edrioasteroids.

SYSTEMATIC PALAEONTOLOGY

Class DIPLOPORITA Müller, 1854
Order GLYPTOSPHAERITIDA Bernard, 1895
Family EUMORPHOCYSTIDAE Branson & Peck, 1940

Genus *Eumorphocystis* Branson & Peck, 1940
Eumorphocystis multiporata Branson & Peck, 1940
Figures 3, 5A, 6

1940 Eumorphocystis multiporata Branson & Peck, pp. 88–92, pl. 13.
1950 Regnellicystis typicalis Bassler, pp 276–277, p. 275, figs 6–8.
1950 Strimplecystis oklahomensis Bassler, p. 277, p. 265, fig. 19.

Type specimens. Eumorphocystis multiporata Branson & Peck, 1940; 6757 University of Missouri.

Description. Theca, approximately 16 mm in height and 13 mm at the widest point, slightly globular to elongate oval shape with large number of irregularly arranged, polygonal plates (Fig. 6A, B); ambulacra arranged in 2-1-2 symmetry and oral plates each bear a high spine and border the peristomial opening; CD interray contains O1, with no evidence of O6 or O7; oral plates are non-diplopore bearing (Fig. 6C). Primary peristomial cover plates are undifferentiated from the cover plate series; presence of either hydropore or gonopore is not discernable. Periproct located in CD interray, 0.25 mm in diameter, in contact with oral plate in the CD interray; appears to be composed of numerous small plates but disarticulation prevents further detailed descriptions. Ambulacra divided into proximal recumbent portion and distal erect portion. Proximally, ambulacral floor plates are highly differentiated from cover plate series, wedge shaped, singly biserial and alternate with primary food groove along periradial suture; periradial suture follows a zigzag pattern across the theca. Floor plates non-diplopore bearing; brachioles are mounted in the centre of each ambulacral food plate. Proximal food groove is covered by doubly biserial ambulacral cover plates; distal food groove is formed into erect, triserially-arranged arms (Fig. 6C).

Portion of arms are exothecally derived from a uniserial extension of the extraxial skeleton; entire arm is supported by a single non-diplopore bearing thecal plate at the base of the arm connecting with the uniserial extraxial plates (Fig. 6A). Uniserial plates are overlain by singly biserial ambulacral floor plates. The

primary generation of plates, are typically between 1.0 and 1.5 mm in diameter, whereas presumably secondary generation plates are typically between 0.25 and 0.5 mm in diameter; smaller plates typically roughly quadrangular. The surfaces of the plates are not marked with pits or granulose textures and without evident growth lines; new plates are irregularly added anywhere within the thecal plating. Ridges running horizontally, vertically and diagonally radiate from each arm (three from each arm) across the theca (Fig. 6A). Ridges run from plate centre to plate edge and are much higher towards centre of the plate than at the edge. The thecal plates are noticeably convex and are arched towards the centre of the plate; the sutures between the plates are clearly deþned and deeply depressed in all places not altered by taphonomic overprint. Diplopores are simple paired perpendicular canals within very shallow elliptical peripores; average distance between the perpendicular canals is 0.5 mm; average diameter of the pores is 0.2 mm. Each pair of perpendicular canals enters the coelom separately. The diplopores are irregularly clustered, generally within the plate centre; some diplopores cross plate sutures, most commonly in conjunction with smaller plates. Thecal plates with raised ridges typically have fewer or no diplopores present.

Basals 4, large, equal-sized, non-diplopore bearing; average basal height is 1.5 mm, average width is 3 mm. Basals have thickened ridge around base of attachment structure (Fig. 6B). Only proximal portion of stem is known, preserved length 4.2 mm, circular in cross section with proportionally small circular lumen piercing the centre (approximately 0.2 mm in diameter). No crenulae present. Holomeric stem comprises two distinct alternating columnal sizes, one that is approximately twice as tall as the other (Fig. 6A).

———— 2017. Generic revision of the Holocystitidae of North America (Diploporita: Echinodermata) based on universal elemental homology. *Journal of Paleontology*, **91**, 755–766.

———— 2018. Data from: A re-interpretation of the ambulacral system of *Eumorphocystis* (Blastozoa, Echinodermata) and its bearing on the evolution of early crinoids. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.q666v01

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