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Crinoid ancestry without blastozoans

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At present, a debate in the paleontologic literature focuses on whether or not the immediate ancestry of the Crinoidea lies in an unidentified member of the Blastozoa, which includes eocrinoids and an assemblage known variously as the “cystoids”. Those proposing to derive crinoids from within the blastozoans have recently argued for homologies in the construction of the oral region of certain derived taxa from both groups. An opposing viewpoint, outlined here, finds evidence that aside from plesiomorphies, proposed similarities are superficial and homoplastic. We suggest these superficialities represent convergent adaptive strategies. Earliest crinoids express ambulacral traits unlike any blastozoan but that are expressed in the only other pentaradial echinoderms with a known record early enough to be considered in the context of crinoid origins, edrioasteroids and edrioasteroid-like stem echinoderms.

Key words: Blastozoa, Edrioasteroidea, Crinoidea, origin, homoplasy, Ordovician.

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Introduction

Debate over the origin of crinoids continues with two contrasting, entrenched views (most recently Guensburg 2012; Ausich et al. 2014, 2015a, b). Both sides agree that ultimate ancestry must lie with Cambrian edrioasteroid or edrioasteroid-like, early pentaradial, forms. Disagreement arises over whether or not there is a blastozoan (eocrinoid, “cystoid”) intermediary. Phylogenetic analyses are available in which arguments are presented for rejecting or accepting a blastozoan outgroup (Guensburg 2012; Ausich et al. 2015b, respectively).

The core of this analysis focusses primarily on posited character interpretation since 2012, during which time additional arguments have been advanced for oral region homologies linking blastozoans and crinoids (Kammer et al. 2013; Ausich et al. 2015a, b; Sumrall 2015). Here, for the first time, comprehensive argumentation is presented challenging that conclusion; instead it finds further evidence in support of crinoid ancestry completely independent of blastozoans. This paper is organized into three sections: a background review of the issues and examination of basic assumptions and points of view, a summary of the Ordovician record of

stemmed echinoderms with rationale for relevance, and, interpretations of the lines of evidence and reasoning.

Character interpretation is inevitably subjective to varying degrees, and therefore resultant phylogenetic analyses are inevitably subjective to varying degrees as well. Phylogenetic analyses are only as rigorous as the character analyses that should precede them. The path forward must begin with explicated character evaluation, such as that undertaken here. Only when interpretations are clearly available and documented can we turn to sound scientific phylogenetic analysis.

Institutional abbreviations.—MNHN, Muséum national d’Histoire naturelle de Paris (Courtesole and Griffé Collection), France; MP, Guizhou University, Guiyang, China; OU, Noble Museum, University of Oklahoma, Norman, USA; PE, Field Museum of Natural History, Chicago, USA; TMM-TX, NPL-TX, University of Texas, Austin, USA; UI X, University of Illinois, Urbana, USA.

Other abbreviations.—HP, hybocrinid pattern. Terminology used in this study follows the Treatise on Invertebrate Paleontology (Ubaghs 1978b).

Background

Competing views of crinoid origin.—The origin of the Class Crinoidea has been the subject of speculation for more than a century (e.g., Wachsmuth and Springer 1887; Bather 1899). This debate most recently took on new vigor beginning with argumentation favoring a blastozoan (sensu Sprinkle 1973) ancestry for the Crinoidea (e.g., Ausich 1998a, b; Ausich et al. 2015a, b; Sumrall 2015). Proponents of blastozoan ancestry (Kammer et al. 2013; Ausich et al. 2015a) posit that morphology of the oral region was conserved among all pentaradial echinoderms during early echinoderm diversification, and that putative homologies are sufficient to indicate derivation of crinoids from a blastozoan (Ausich et al. 2014, 2015a; Sumrall 2015). Important for that perspective is that potential oral region homologies have also long been debated (see Wachsmuth and Springer 1887).

In addition, data in support of a blastozoan sister-group for crinoids are insufficient. This conclusion is based in part on implications of the discovery of the oldest known crinoids (Tremadocian, Early Ordovician) that document plesiomorphic morphology of undisputed crinoids (the Cambrian *Echmatocrinus* excluded) (Guensburg and Sprinkle 2003, 2007, 2009; Guensburg 2012). Our analysis, here, finds the view favoring a direct blastozoan ancestor overlooks evidence supplied by the salient features of these earliest crinoids, as well as basic anatomy of the body wall structure and coelomic configurations of living crinoids. Our data, particularly from earliest crinoid oral regions and appendages, together with an overview of stemmed echinoderm evolutionary dynamics, provide rationale for distinguishing homoplasy from homology.

A character analysis approach.—Differences of interpretation raise the issue of taxon recognition. Cladistic, phylogenetic treatments extend clades or taxa back to the earliest-recognized member of any putative monophyletic assemblage; once the hypothesized homologous characters have been designated among clades previously deemed separate, geologic range is concomitantly extended. As blastozoans are known from the Cambrian, the blastozoan hypothesis at least potentially extends the range of true crinoids (Ubaghs 1978a, b) downward beyond their known record (Ausich et al. 2015a; Sumrall 2015). We argue that such an interpretation implicitly assumes its conclusion through character treatment during analysis. Specifically, we present evidence indicating that the characters used in support of the blastozoan hypothesis are variously homoplastic (e.g., orals, any cup or lower thecal plating) or plesiomorphic. These skew phylogenetic analyses toward a blastozoan origin of crinoids. This is not a semantic argument as has been

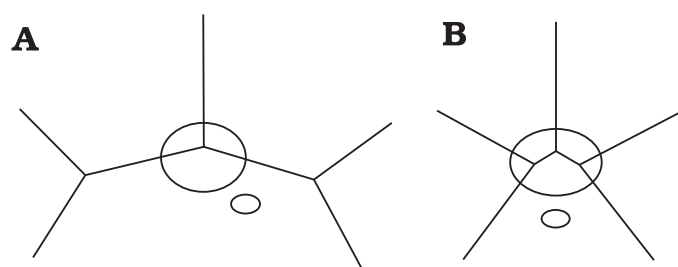


Fig. 1. Orals in early pentaradial echinoderms. **A.** Plesiomorphic template expressing the 2-1-2 pattern. **B.** Near pentameric symmetry, showing potential pentaradiality through shortening initial branches during ontogeny.

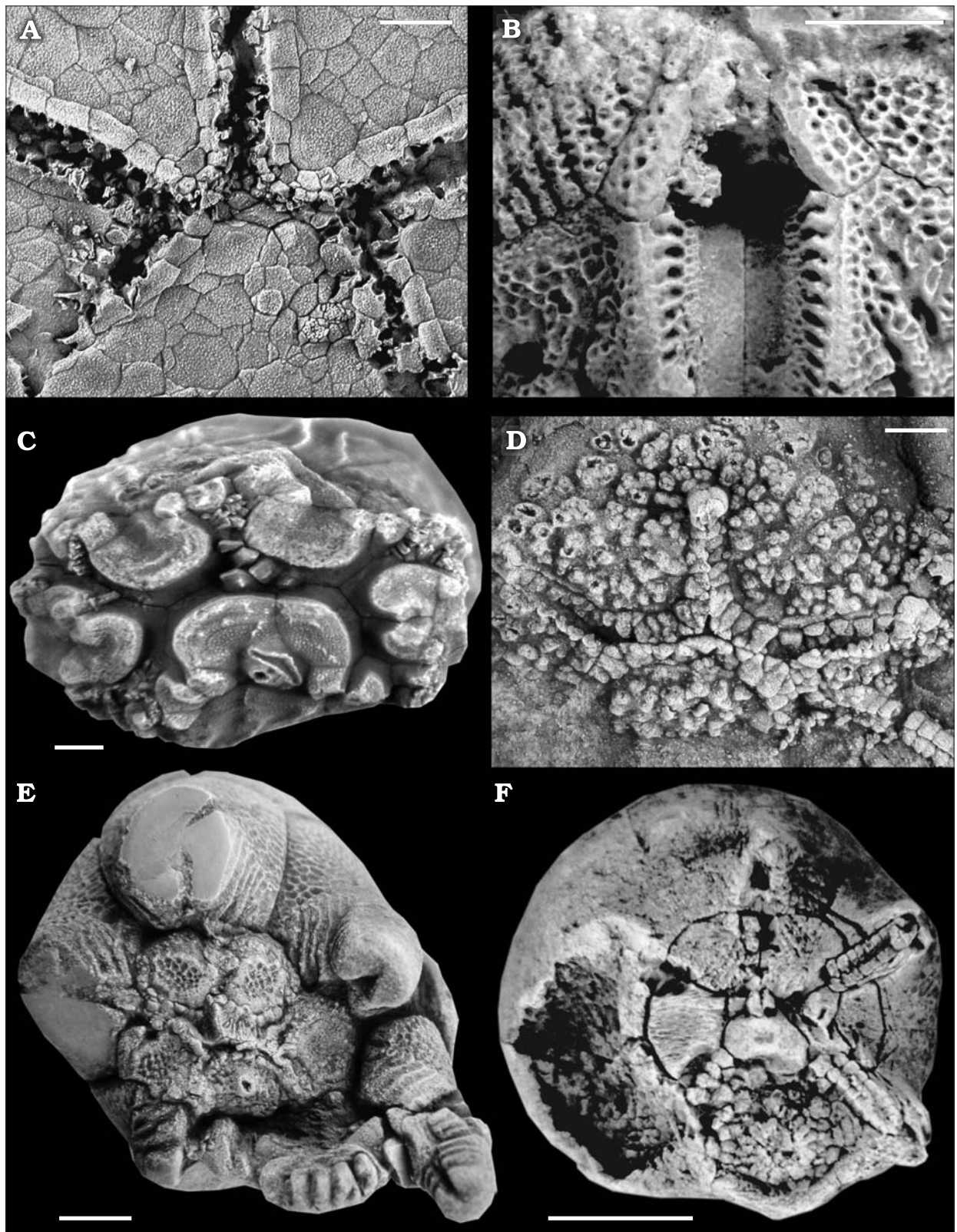
suggested (Sumrall and Brochu 2010), but one of testable character analysis using the available fossil material.

A monophyletic crinoid clade based on a blastozoan ancestry has not been demonstrated to range from or prior to the first true crinoid appearance. Further, no specific stemward taxon or clade with the inclusive blastozoan-group has been designated by blastozoan origin proponents.

Competing viewpoints agree on certain characteristics of the ultimate hypothetical crinoid ancestor. Blastozoans, edrioasteroid-like forms, and crinoids comprise a pentaradial echinoderm clade, present by the early Cambrian and only slightly younger than the oldest-known echinoderms. Second, an oral surface with 2-1-2 ambulacral symmetry, hydropore location off the C-ray in the CD interray, and presence of cover, floor, and interambulacral plates are plesiomorphic among pentaradials (Guensburg et al. 2013; Kammer et al. 2013; Sumrall 2015), these expressions serving as the template for evolution of the pentaradial oral region. It is important to note that little modification is required to transition from the plesiomorphic 2-1-2 pattern (Sprinkle 1973) to near pentaradiality, and therefore this adaptation can only have limited phylogenetic significance (Fig. 1). A third point of agreement is that, except for interradial elements forming the ambulacral junctures, peristomial cover plates (those that roof the oral region) were initially operable hinged elements similar to more distal elements covering the ambulacra.

In recent treatments (Ausich et al. 2014, 2015a, b), those finding for direct blastozoan ancestry combined morphological data from a broad range of six taxa representing eo-crinoids, rhombiferans, and diploporans; no specific sister taxon was identified. Such selection must rely on inferences of “potential” or “plausibility”, which inevitably are subjective and cannot be rigorously tested. Potential or plausibility argumentation is intended to persuade; we argue that scientific advancement comes through challenging, if not disproving, hypotheses. Further, the fact that selected taxa are widely distributed, recognized in taxa younger than the oldest crinoid, and not directly linked to earlier blastozoans,

Fig. 2. Oral regions of early echinoderms. **A.** Cambrian Series 3 edrioasteroid “*Kailidiscus*” *chinensis* Zhou, Sumrall, Parsley, and Peng, 2010 (GM 2103), Guizhou Province, China, here interpreted with extraxial “orals” outside floor plates; interior surface shows these plates integrated into the oral frame. **B.** The derived Late Ordovician edrioblastoid *Astrocystites* sp. (PE 52760), Missouri, USA; showing differentiated peristomial cover plates similar to those of blastozoans, but for which the record supports an independent acquisition in that these are lacking in known earlier taxa (e.g., *Cambroblastus* and →



Lampteroblastus). **C.** The derived Late Ordovician rhombiferan blastozoan *Glyptocystella loeblichii* (Bassler, 1943) (OU 9084), Oklahoma, USA; showing a rhombiferan ambulacral pattern. **D.** Oral surface of plesiomorphic middle Cambrian eocrinoid blastozoan *Gogia* sp. (1804TX1), Utah, USA; showing plesiomorphic ambulacral pattern, similarity to pentaradial template seen in A. **E.** The derived Late Ordovician *Hybocrinus bilateralis* Guensburg, 1984 (UI-X 5868), Tennessee, USA; intact but distorted oral surface, with cover plates and exposed lateral cover plates. **F.** The derived Late Ordovician *Hybocrinus nitidus* Sinclair, 1945 (TMM 1278TX14), Oklahoma, USA; weathered oral surface with cover plates eroded away exposing slat-like ambulacral floor plates in B and C rays. “*Kailidiscus*” image provided by Ronald Parsley (Tulane University, New Orleans, USA). Scale bars 2 mm.

combine to support homoplastic derivation, thereby indirectly arguing against homology and a blastozoan ancestry.

Recent studies advocating blastozoan ancestry for crinoids (Kammer et al. 2013; Sumrall 2015; Ausich et al. 2015a, b) assumed that the plates of the oral region (i.e., differentiated elements surrounding the peristome) are axial sensu Mooi and David (1997), and thereby part of the ray structure. Because the “oral” plates were deemed axial by these authors, it was then concluded that they likely were conserved during major phylogenetic changes and therefore homologous individual plates can be identified between groups, in this case between various blastozoans and crinoids.

First, this interpretation conflates skeletal elements with soft tissues. Even if it is reasonable that soft tissues forming the esophagus were retained during phylogenetic transition, it is not necessarily true that the associated skeletal elements endured the posited major evolutionary transitions. Second, it is debatable that oral plates in early echinoderms are exclusively axial (e.g., *Kailidiscus*; Fig. 2A). Finally, and perhaps most importantly, all characters identified in these papers, as summarized by Ausich et al. (2015b: 2R), are also found among edrioasteroids and edrioasteroid-like taxa. No autapomorphies have been identified by these authors that serve to unite blastozoans and crinoids apart from edrioasteroids; that is, all identified characters are arguably plesiomorphic and hence cannot serve to place any blastozoan between crinoids and edrioasteroid-like taxa.

Certain blastozoan and crinoid oral cover plate patterns are superficially similar (Kammer et al. 2013), but such similarity can be traced back to the plesiomorphic pentaradial pattern. In some cases, larger differentiated plating roofs the oral region (Fig. 2B), but there is no sequence of fossils connecting those of blastozoans with crinoids or other pentaradial forms.

Arm expressions have been integral to the diagnosis of the Crinoidea from the time of the earliest research on the group and long formed the core of the argument for phylogenetic separation of blastozoans and crinoids (Ubaghs 1953; Sprinkle 1973; David et al. 2000; Mooi et al. 2005; Guensburg et al. 2010; see also below). If blastozoans, or a subset thereof, constitute an exclusive sister taxon of crinoids, then either (i) features such as calycinal coelomic slots, slat-like floor plates, and podial basins and pores were first lost and then re-emerged as synapomorphies of the pertinent blastozoan with crinoids; or (ii) they were retained in blastozoans not yet discovered in the fossil record. Posited loss and re-emergence of a part of the system deemed essential by blastozoan origin proponents (Kammer et al. 2013; Ausich et al. 2015a, b) in itself constitutes a fundamental, if indirect, challenge to the significance of the axial system. We argue that at the current level of understanding, the fossil record can be taken at face value, and that phylogenetic linkage between known Early Ordovician crinoids and any pentaradial echinoderm cannot be justified without strong data from feeding appendage expressions of coeval or more ancient exemplars; plausibilities, however appealing, are not data.

Earliest crinoids post-date earliest blastozoans by over 25 my, yet crinoids used to argue for blastozoan derivation are nearly another 25 my younger than the oldest crinoids. If the earliest record of crinoids represented by the protocrinoids and other taxa is unrepresentative and misleading (see Guensburg 2012, for an argument in favor of these earliest crinoids in fact being representative), it should be possible to trace development of crinoid expressions from a blastozoan ancestry in an overlapping stepwise fashion. However, no evidence-based argument to remove protocrinoids and other earliest crinoids from a basal or near basal position has been presented. Earliest crinoids had already diversified into camerate, cladid, and disparid clades, but they are linked by a series of traits not present among later, more derived, taxa (Guensburg 2012). There is no question the fossil record in this matter is not as extensive as we wish, but strong arguments for fundamental phylogenetic transitions must be founded on more fossil-based data than have been presented.

Morphological disparity of Ordovician stemmed echinoderms

Historical context.—Stemmed echinoderms have, in recent decades, been divided into blastozoans and crinoids (Sprinkle 1973). Blastozoans traditionally constitute several class-rank taxa, some with few included taxa. Crinoids, on the other hand, have always encompassed a single class-level taxon subdivided into a few subclasses (Ubaghs 1978a). As early as Leuckart (1848) and then Bather (1899), these two groups have been combined into the *Pelmatozoa*, whose diagnostic character is the presence of a stem/stalk (pelma, peduncle). A number of other early pentaradial taxa approach and, arguably, achieve (e.g., *Pseudodriophus*, *Archaeopyrgus*, *Lampteroblastus*, *Astrocystites*) stemmed status (Guensburg et al. 2010; Kammer et al. 2013). Earliest crinoids express unique characteristics as compared with all other echinoderms (Guensburg and Sprinkle 2007; see below), but retain features that unequivocally place them at the base of the crinoid clade (Guensburg and Sprinkle 2009; Guensburg et al. 2013).

Blastozoans are known from early in the Cambrian, whereas the earliest crinoids are Early Ordovician. However, the fossil record of stemmed echinoderms, particularly that of crinoids, expands exponentially during the Middle to Late Ordovician (see Sprinkle and Guensburg 2004); hundreds of taxa are known from the Late Ordovician. It is difficult to overstate this change in the echinoderm component of the Early–Middle Ordovician portion of Sepkoski’s Paleozoic Evolutionary Fauna. Class-level blastozoans included eo-crinoids, paracrinoids, diploporans, and rhombiferans. Crinoids achieved a morphologic disparity characterized by diversification throughout their habitats beyond any equivalent time slice since. This event has largely gone unnoticed among non-specialists because representatives of dis-

crete enigmatic clades (e.g., *Tribolocrinus*, *Colpodecrinus*, *Cleioocrinus*, *Ramseyocrinus*, *Tetragonocrinus*) have been incorporated into familiar camerate, disparid, flexible, and cladid subclass-rank taxa. This early period among crinoids has been documented in terms of increased morphospace utilization (Foote 1995; Deline and Ausich 2011). The most obvious examples occur where substrate preferences change with blastozoans occasionally crossing from their usual soft to hard substrates and vice versa for crinoids (Lewis 1982; Brett and Brookfield 1984; Brookfield and Brett 1988; Guensburg 1992). A few derived blastozoans express erect arm-like feeding appendages superficially similar to crinoid arms (e.g., *Eumorphocystis*, *Caryocrinites*, *Comarocystites*) and a few derived crinoids evolved largely recumbent arms (e.g., *Hybocystites*, *Tribolocrinus*). Despite the shared general body plans, basic anatomical distinctions have allowed ready specimen assignment to either blastozoans or crinoids by many authors over many years (see Sprinkle 1975). Recognition of homoplasy has been a long acknowledged, if underreported, finding among stemmed echinoderms.

Morphological trends.—An iterative theme among both groups through the early Paleozoic involves thecal/calyx plate standardization and reduction, yielding stronger, more rigid, designs. It is important to note that general similarity between blastozoan and crinoid oral regions are part of this broader trend involving the entire theca/calyx. This pattern involves loss, perhaps integration by fusion of the internal oral frame among many blastozoans, crinoids, and a few elongate edriasteroids (edrioblastoids), all with stiff ovate to bud-shaped thecae. This common theme raises the potential for homoplasy among blastozoans, crinoids, and elongate edriasteroids, many of which express similar morphology associated with these fixed elevated life modes. Blastozoans and early crinoids were all small, stemmed, radial suspension-feeding echinoderms sometimes living side-by-side, in similar settings, over the same time interval; occurrence of convergent evolutionary events must ultimately be assumed, and attempts made to discredit these must use the full range of morphologic data.

Resulting terminological complexities.—For well over a century, researchers have applied the same morphological nomenclature to taxa representing independent evolutionary pathways; these terms in themselves mislead by suggesting commonality of ancestry. Examples include: basals, radials, stalk/stem, columnal, holdfast, and orals. There is a lack of any clear ontogenetic, positional, or evolutionary pattern supporting homology for these structures, and the terminology has itself brought preconceptions to the table because “the same term is often used for two widely divergent structures in two different groups of echinoderms” (Mooi and David 1997: 306). Mooi and David (1997: 306) go on to suggest that “as cladists interested in the quality of data as well as quantity, we are resisting the implication that the more we know about our characters, the less objective the study will (be)”.

Objective application of homology criteria, such as congruence and conjunction, in particular (Remane 1956; Patterson 1988), suggest that common nomenclature has been applied to different, but superficially similar, structures. Oral-like plate development accomplished a functional need for rigidity surrounding the esophagus following decalcification of the oral frame. This construction is not limited to the oral region, but involves all plate systems encasing the viscera. It can be argued that the success of stemmed echinoderms during the Ordovician and later resulted partly from these parallel trends.

Evidence from early crinoids

As noted, in recent contributions, supporters of a blastozoan ancestry for crinoids have focused on morphology of the oral region (Kammer et al. 2011, 2012, 2013). We argue that, because of the complexities of phylogeny, all aspects of morphology must be incorporated into a robust hypothesis, and further, it is the construction supporting the water vascular system that is crucial here as it is in other echinoderms. This interpretation was clearly stated by Ubags (1968: S55; 1978a: 275) who rejected potential linkage between blastozoans and crinoids based on appendage construction, arguing that stratigraphically late blastozoan feeding appendages only superficially resemble crinoid arms. Subsequently, this observation has been tested and elaborated upon (Mooi and David 1997; David et al. 2000; Guensburg and Sprinkle 2001, 2007, 2009; Guensburg et al. 2010, Guensburg 2012). The recent focus of Kammer et al. (2013) compels us to consider this issue first.

Oral region background.—The blastozoan origin model promotes certain Ordovician crinoid taxa as having oral region morphology in common with certain derived blastozoans (Kammer et al. 2013; Fig. 3). These forms are constrained to cyathocrinine cladids and hybocrinids (here considered cladids based on posterior plating), and are referred to here as possessing the hybocrinid pattern (HP). Oral surfaces among these forms are dominated by single, wedge-shaped oral plates that rigidly suture to each other and to adjacent radials. It is this characteristic, imprinted on the

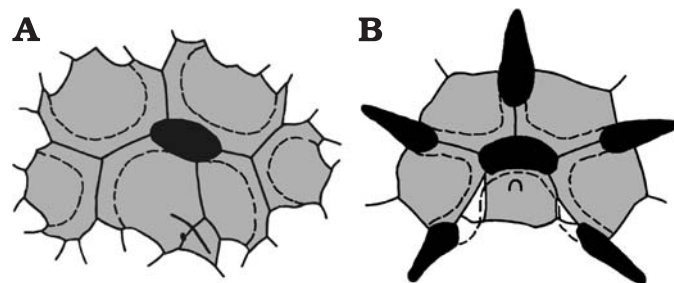


Fig. 3. Line drawings showing oral regions of the derived blastozoan, *Glyptocystella loeblichii* (A) and crinoid, *Hybocrinus nitidus*, five wedge-shaped coelomic slots, and madreporic hydropore (inverted U below peristomial opening) (B). Modified from Sprinkle (1982a, b).

Table 1. Phylogenetic interpretation of Ordovician blastozoan and crinoid morphology.

Region	Interpretation	Traits
Oral	symplesiomorphies—traits presumed to have been present in the last common ancestor of both blastozoans and crinoids	irregular thecal plating with primary and secondary plates
		five ambulacra
		2-1-2 ambulacral disposition
		oral cover plates non-differentiated, hinged (capacity to open and close)
		entrance of water vascular system a hydropore near C ray in posterior interray (unspecified type)
	potential homoplasies—traits interpreted to have been independently acquired as indicated by varied stratigraphic position, and inconsistent distribution within early pentaradial echinoderms	oral region nearly pentaradial (five ambulacral furrows emptying into the peristomial “mouth” opening from exterior)
		large interradial plates surround peristome “orals” (considered by blastozoan proponents to be axial, here the matter considered ambiguous, at least for crinoids and certain edrioasteroid-like forms; considered potentially homoplastic in either case)
		primary oral cover plates (differentiated [wider and/or longer] cover plates at interbranchial arcs)
		interradial plates surrounding peristome mutually articulating beneath “orals”
	crinoid autapomorphies—traits identified only in crinoids among early stemmed echinoderms	rigid construction
		extraoral coelomic slots (openings, slots, at calyx shoulders away and separate from peristome)
	blastozoan autapomorphies—traits only known in blastozoans	madreporic hydropore (intraplate pore, not extending to other plates)
		brachioles
Extraoral	plesiomorphies present among Cambrian edrioasteroids and crinoids but not blastozoans	slat-like ambulacral floor plates
		podial pores/basins
		somatocoelar components present below erect feeding appendage ambulacra
	potential homoplasies	rigid construction
		basals
		radials
		interbranchials
		fixed brachials
		pentameric stem
	early crinoid apomorphies	holomeric (monomeric) stem
		arms gradually merging with theca (interbranchial plates tapering upward from cup into arms between floor plates and brachials)
		triple junctures at cup and stem (stem pentameres originate as wedges that interlock with cup base circlet at triple junctures)
		posterior interray plating extending to stem (posterior cup plating extending to cup-stem juncture, interrupting cup base circlet)
		pentameric proximal stem (all Tremadoc, earliest crinoids)
		arm branch webs (interbranchial platelet webs above arm branch nodes)
		brachials in lateral contact immediately above axillaries (articulate laterally so that there is no separation until higher in the branches)

pentaradial template that produces morphologies in HP oral regions superficially similar to those of derived blastozoans. The posterior oral surface interradius includes a low anal cone arising from a fenestra between posterior orals and the cup wall formed by a large, protruding, often-grooved, anal X plate. Ambulacral cover plates are hinged (operable). Differentiated primary oral cover plates occupy spaces above ambulacral junctures. In the HP, these differ in shape from adjacent cover plates but are similar in size (Table 1).

Oral region construction.—Preservational bias favoring the HP results in many fully-exposed specimens, unlike most other crinoids in which many plates in a pliant, elongate structure are inevitably only partly exposed. Nevertheless,

enough is visible in specimens of these latter forms to at least characterize their basic morphology.

Six Tremadocian taxa comprise the oldest crinoids (Ubaghs 1969; Guensburg and Sprinkle 2003, 2009; Guensburg 2010; Figs. 4, 5). A seventh undescribed form, taxon A, from the earliest Floian, is added to this study. Guensburg (2012) assigned Tremadocian taxa to camerate, cladid, or disparid clades, while also noting commonalities that, collectively, suggest propinquity to the crinoid node. Stated another way, each of these Tremadocian taxa express at least one unique apomorphy of their respective clades while at the same time having traits unlike derived members of their respective clades.

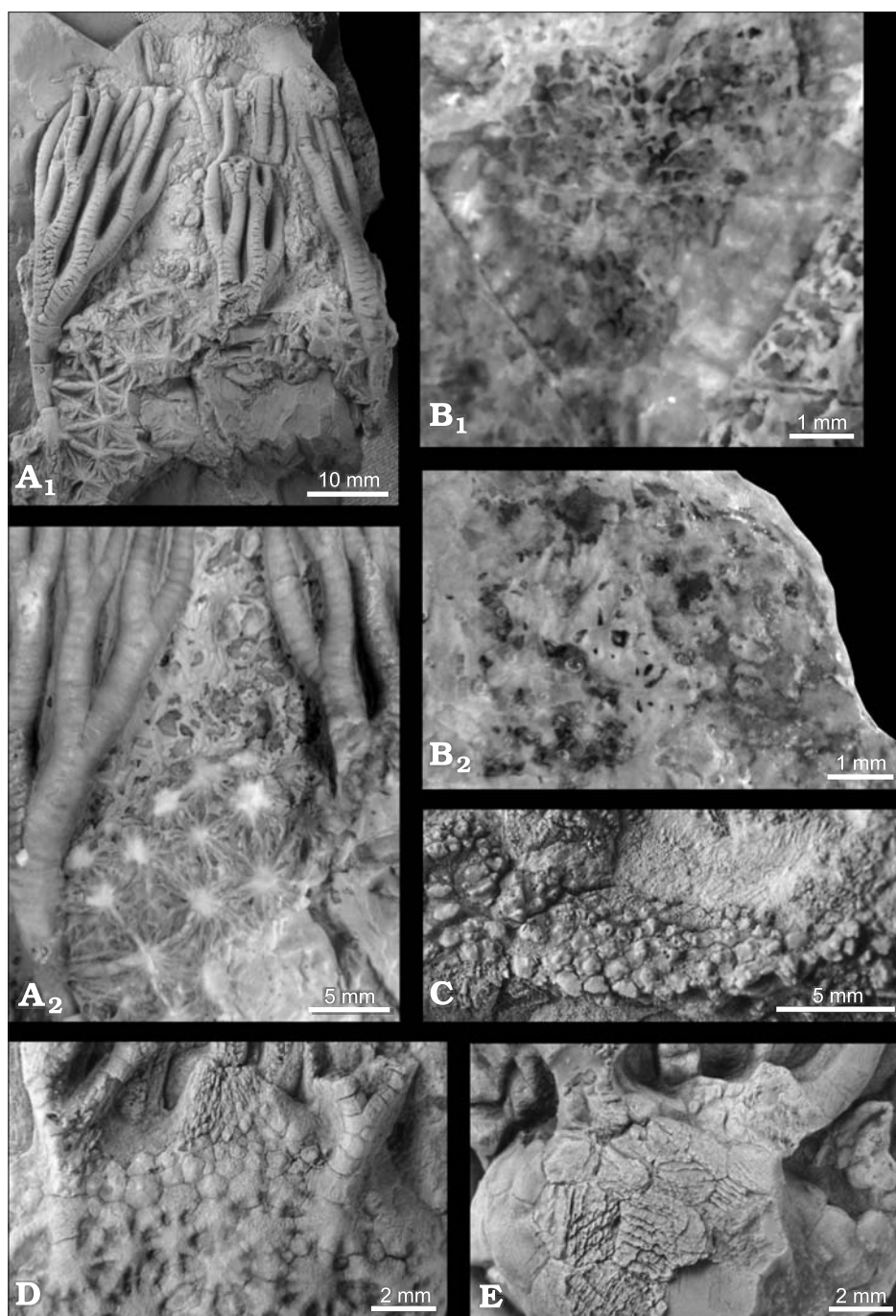
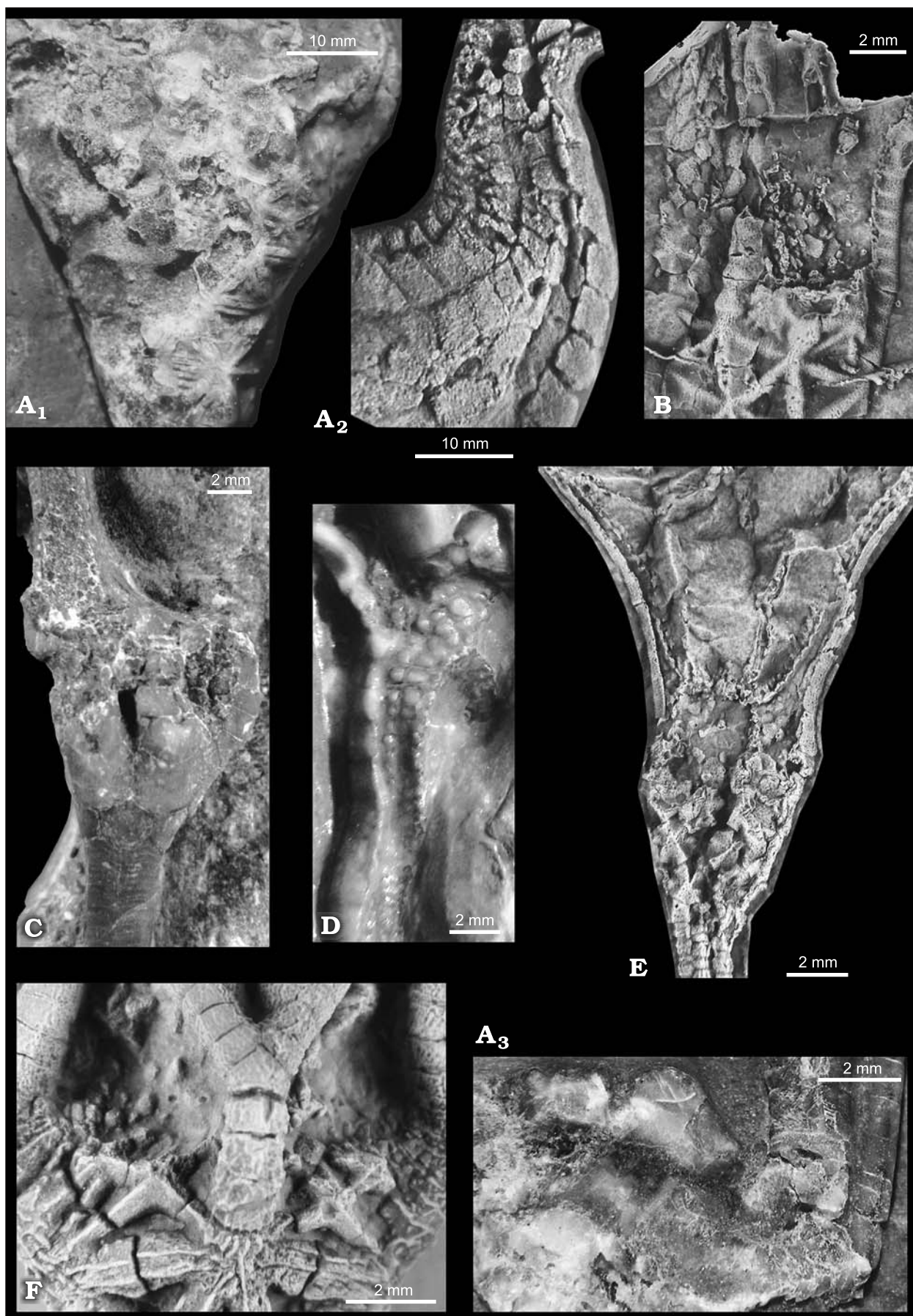


Fig. 4. Oral/tegmenal regions of Tremadoc, Early Ordovician, crinoids from Utah, USA. **A.** Protocrinoid *Titanocrinus* sp. (PE 52723), anterior view, well preserved partial crown with tall conical tegmen, terminating in anal cone (**A₁**); portion of tegmen with interbrachial-like platelets extending to tertibrachial (**A₂**). **B.** **C.** Protocrinoid *Titanocrinus sumralli* Guensburg and Sprinkle, 2003. **B.** PE 52721, **C.** D ray platelets in web above axial, immersed (**B₁**); weathered tegmen section, tegmen platelets close above fixed C ray plates, no cover plates or axial morphology (**B₂**). **C.** PE 52724, weathered tegmen section showing platelets. **D.** Protocrinoid *Glenocrinus globularis* Guensburg and Sprinkle, 2003 (PE 52733), posterior view, tegmen with anal cone similar to *Titanocrinus*. **E.** *Eknomocrinus wahnensis* Guensburg and Sprinkle, 2003 (PE 52734), largely unexposed oral surface, anal cone in posterior interray at right.

Two Tremadoc crinoids *Titanocrinus* and *Glenocrinus*, referred to collectively as protocrinoids, express tegmens comprising many platelets in a domal structure with submerged ambulacra, and an anal cone projecting from the summit (Guensburg 2012). These traits resemble camerate crinoids. *Aethocrinus* (Ubaghs 1969) and *Apektocrinus* (Guensburg and Sprinkle 2009), express oral-like plates within flat or slightly domed interambulacral platelet fields, hinged biserial ambulacra, and a low to high anal cone confined to the CD interradius. In this case, the closest comparison is seen in cladids. *Alphacrinus* and taxon A have a tall anal sac similar to typical disparids. In addition, there is a longitudinal brachial-like anal series branching from the

left side of the C ray resembling typical disparids and early camerates (for the latter see Gahn 2015). Taxon A expresses biserial (paired) ambulacral cover plates transitioning from arms to camerate-like irregular fixed “pebbly” platelets, and then larger differentiated plates over the peristome. *Eknomocrinus* expresses exposed ambulacra on a slightly convex surface, and small posterior anal cone. Plating over the peristome is not exposed. No salient traits allow subclass assignment of this taxon at this time.

Morphological evolution of the oral region.—The early crinoid record, as we now understand it, indicates that the HP was developed over an extended time span both before



and after crinoids originated. Hinged cover plates and the low anal cone resemble more basal pentaradial echinoderms, particularly earlier edrioasteroid-like forms (e.g., *Totiglobus*, *Cambroblastus*), as well as blastozoans. Small differentiated orals could occur early in crinoids (e.g., *Apektocrinus*), but flat single orals filling interradii (as in the HP) resembling the derived blastozoan pattern occur with certainty only later, in the early Middle Ordovician (e.g., *Hybocrinus*, *Hoplocrinus*). Coelomic slots and the madreporic hydropore represent advanced features in crinoids not seen in blastozoans. All these indications support a derived status for the HP, the rigid, flat oral surface having originated from a more complex, many-plated, more pliant construct. Plesiomorphies, such as 2-1-2 symmetry, hinged cover plates, and the low anal cone persist as conserved expressions, but do not influence the phylogenetic conclusions concerning the derived nature of the HP.

Apektocrinus and *Aethocrinus* arguably express oral regions/tegmen that compare with basal pentaradial echinoderms, such as early edrioasteroid-like taxa, with orals proximal to a many-plated interambulacrum (e.g., *Cambroblastus*, *Totiglobus*; Guensburg and Sprinkle 2009; Guensburg et al. 2010). Relatively flat oral surfaces and articulating cover plates are similar in both groups, but the many interambulacral (tegmenal) plates of the earlier forms differs from the single elements of the HP. This sequence argues that the HP evolved by reduction later in ontogeny, by paedomorphosis. Examples of such paedomorphic taxa include cladids *Porocrinus*, *Palaeocrinus*, and *Carabocrinus* (Sprinkle 1982c), hybocrinids (close to cladids here) (Sprinkle 1982b; Guensburg 2012), and perhaps the disparid *Cincinnatiocrinus* (Warn and Strimple 1977).

Feeding appendage constructions.—Distinctive feeding appendage morphology separates earliest blastozoans

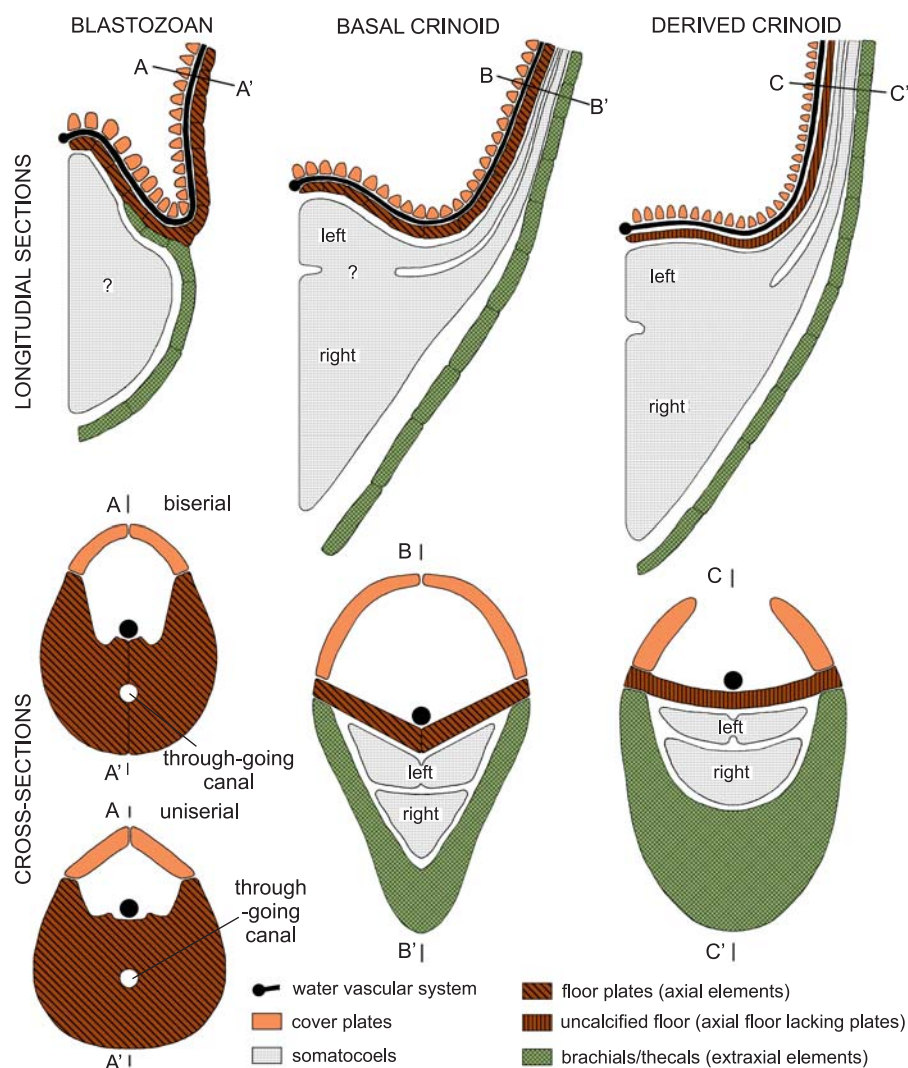


Fig. 6. Colorized schematic cross sections illustrating fundamental differences separating crinoids and blastozoans, tube feet not illustrated (modified from Guensburg et al. 2010).

and crinoids (Guensburg and Sprinkle 2003, 2007, 2009; Guensburg 2012). Earliest crinoids display largely internal, biserial ambulacral floor plates. Beneath the floor plates are large coelomic spaces; these extend downward from arms into the calyx through open slots (Ubaghs 1978a; Guensburg et al. 2010; Figs. 6, 7B, D).

In describing *Apektocrinus*, Guensburg and Sprinkle (2009) illustrated what they interpreted as podial basins, possibly with pores to the coelom below. Another early taxon expressing these is disparid taxon A. These two early crinoids retain morphology resembling Cambrian edrioasteroid-like

- ← Fig. 5. Oral regions of Tremadocian crinoids. **A.** TMM1983TX1, cladid *Apektocrinus ubaghsi* Guensburg and Sprinkle, 2009, Idaho, USA; cup and tegmen, variously weathered (A₁); arm trunk with gradual transition from calyx to arms showing, from left to right, cover plates (both sets exposed), lateral floor plate extensions, interbrachials, and brachials (A₂); flattened, tegmen folded showing presumed “orals” at center of oral area, immersed (A₃). **B.** E. Cladid *Aethocrinus moorei* Ubaghs, 1969, France. **B.** MNHN R 09417, partial crown, with tall anal cone/short anal sac in posterior interray. **E.** MNHN A 49684, crown with disheveled cup, gradual transition from cup to arms, ambulacra extending onto low tegmen, and calcified floor plates much like those of *Apektocrinus*. **C.** D. Disparid taxon A, Utah, USA. **C.** PE 52750, calyx and proximal stem, BC view, anal sac, at left, projecting from second primibrachial of C ray unseen, arched tegmen with many small plates, monocyclic cup, pentameric stem. **D.** PE 52751, specimen with largely disarticulated cup, oral view of arm with biserial cover plates transitioning to irregular camerate-like “pebbly” mosaic tegmen. **F.** Disparid *Alphacrinus mansfieldi* Guensburg, 2010 (PE 52743), Utah, USA; hinged cover plates extending onto tegmen at right, interray plates merge with tegmen platelets at left.

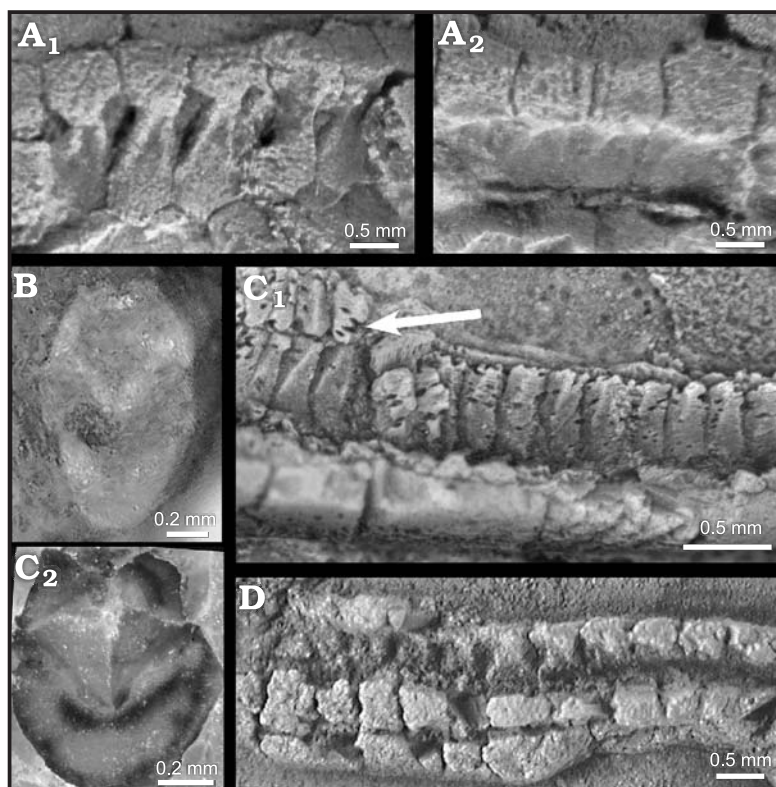


Fig. 7. Slat-like ambulacral floor plates of Early Ordovician echi-noderms expressing podial basins, pores. **A.** Ambulacral details of edriasterid *Paredriophus elongatus* Guensburg and Sprinkle, 1994 (PE 52740), Utah, USA. Wedge-shaped pore slits bordered by raised rims (**A₁**); pore slits filled with syntaxial overgrowths (**A₂**). **B.** Undescribed *Porocrinus*-like cyathocrinine cladid (NPL 1977TX12), Nevada, USA; natural break across distal ?A ray arm showing cross section, floor plates, hints of podial pores, pattern similar to disparid taxon A. **C.** Disparid taxon A (PE 52752), Fillmore Formation, Utah, USA; specimen with intact arm and stem segments strewn over and within a limestone slab, attributed to taxon A using overlapping morphology of five other stratigraphically associated specimens. Slat-like floor plates showing wedge-shaped pores with attenuated rims, well-preserved on left, with open cover plates above (arrow) (**C₁**); polished cross-section of arm, plates slightly ajar with dark syntaxial overgrowths, cover plates, floor plates, large coelomic space (**C₂**). **D.** Cladid *Apektocrinus ubaghsi* Guensburg and Sprinkle, 2009 (TMM 1983TX1), Idaho, USA; B ray mid-arm segment with weathered slat-like floor plates and podial basins.

taxa such as *Totiglobus*, *Cambraster*, or *Paredriophus*, though pores in the crinoids appear smaller and are difficult to document because of calcitic overgrowths (Bell and Sprinkle 1978; Guensburg and Sprinkle 1994; Zamora et al. 2013; Fig. 7B–D). Other early crinoids could also have pores and basins based on partial evidence (Fig. 7B, for instance). No known blastozoan expresses such morphology.

Crinoid feeding appendages (i.e., arms) carry coelomic extensions from extraoral thecal/calycinal slots (Ubaghs 1953, 1978b; Mooi and David 1997). The arms incorporate both axial and extraxial skeletal regions along with their associated coelomic components. Earliest crinoid arms include flooring plates that partition the ambulacral groove from the coelomic cavity (Guensburg and Sprinkle 2001, 2007, 2009; Guensburg et al. 2010; Guensburg 2012; also stated in conclusions in Kammer et al. 2013). However, these partitions are decalcified among derived taxa (Mooi et al. 2005), although they persist as soft tissue shelves that close over the coelom within the brachials. Crinoid brachials are apomorphic modifications of extraxial components extending from the calyx.

Blastozoan feeding appendages (brachioles, erect ambulacra) are axial only, consisting of free flooring plates without somatocoelar cavities below, although there can be a small ovate to circular through-going canal (Sprinkle 1973) that has been interpreted as such (Clausen et al. 2009; Sumrall and Brochu 2010; Kammer et al. 2013). Crinoid brachials also express a through-going channel that is known to contain a branch of the aboral nervous system, but this is in addition to the coeloms that form spaces above

the brachials—a condition unlike that seen in blastozoans. The Ordovician disparid *Columbicrinus* expresses a through-going canal of similar dimensions piercing brachials (Guensburg 1992). Another interpretation considers the through-going canal in blastozoans and crinoids to have accommodated innervation (Guensburg et al. 2010). *Eumorphocystis*, a derived Late Ordovician blastozoan outlier (Parsley 1982), expresses triserial feeding appendages (Fig. 8B), equated by blastozoan origin advocates to the arm structure of early crinoids (Kammer et al. 2013). Thick biserial (paired) free floor plates extending from typical blastozoan fixed floor plates provide most of the support for the entire arm structure, but there is a uniserial plate series, arguably extraxial, forming the aboral region of the appendages that might be equated to “brachials”. However, the through-going canal extends between brachiolars, and not as a coelomic cavity like that seen in crinoids (see Sprinkle 1973; Clausen et al. 2009; Guensburg et al. 2010). Other *Eumorphocystis* feeding appendage morphology contrasting with early crinoids includes: (i) lack of podial pores/basins, (ii) a pinnuliform appendage branching from each free floor plate instead of from the aboral (extraxial) brachial, and (iii) abrupt transition from theca to feeding appendage. In addition there are no calycinal slots. All other parts of the skeleton, including the distinctive diplopore respiratory structures, and monomeric stem with ovate lumen are characteristic of blastozoans, but unknown in early crinoids.

Certain paracrinoids (e.g., *Platycystites*, *?Letenocrinus*), now widely recognized as derived Ordovician blastozoans, have been interpreted to express coelomic passageways

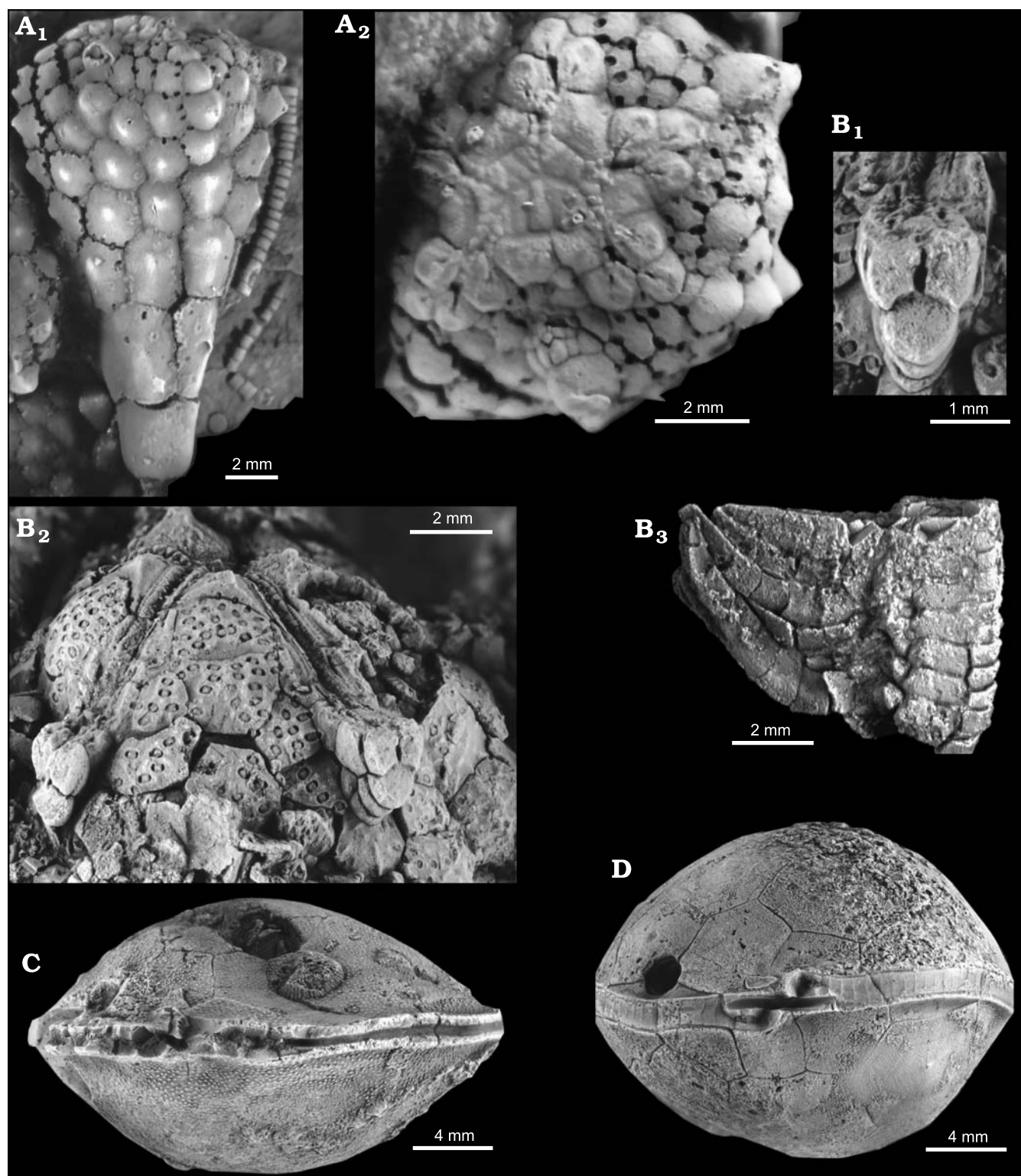


Fig. 8. Examples of derived blastozoans with superficial crinoid-like expressions. **A.** Eocrinoid *Rhopalocystis destombesi* Ubaghs, 1963 (PE 52747), Early Ordovician of Morocco; lateral view (**A₁**), showing derived superficially camerate-like thecal plating, lacking continuity between “fixed brachial”-like plates and feeding appendages, “rays” tapering, not aligned with ambulacra tips above; oral surface (**A₂**), showing typical biserial blastozoan brachiole facets. **B.** Diploporite-like blastozoan *Eumorphocystis multiporata* Branson and Peck, 1940 (TMM 1107TX2), Late Ordovician of Oklahoma, USA; with arm-like appendages superficially similar to crinoids. A ray feeding appendage stub near theca (**B₁**), showing triserial facets, cross-sectional plate shapes and sub-central ovate canal; thecal summit in A-B interray view (**B₂**), showing abrupt boundary between theca and feeding appendages, feeding appendages with thick-plated triserial pattern, diplopore-bearing thecal plates; feeding appendage segment with pinnule-like structures (**B₃**). **C, D.** Paracrinooid, *Platycystites* sp., Late Ordovician of Oklahoma, USA; oral surfaces of lenticular thecae, sub-ambulacral lumens revealed by natural spalling of brachiole-bearing ambulacrals, in continuity with the peristome. **C.** NPL 1113TX17, lumens short. **D.** NPL 1106TX13, lumens long. All Tremadoc crinoids are non-pinnulate.

(Sumrall and Brochu 2010). These originate at or near the peristome, lie along the theca beneath recumbent ambulacra but do not communicate with feeding appendages, and they lack slit-like floor plates typical of early edrioasteroids (Fig. 8C, D) and earliest crinoids.

Earliest camerate and cladid taxa express interbrachial plate fields that extend onto lower arms. This pattern sometimes extends out along arms as platelet webs between arm branches (see Guensburg and Sprinkle 2009; Fig. 4B₁). These basal crinoid traits (Guensburg 2012) are unknown among blastozoans.

Judged from the Cambrian echinoderm record, early differences in ambulacral construction signal basal pentaradial echinoderm arm branching. Crinoid-like appendage construction, particularly coelomic extensions, have been claimed for Cambrian eocrinoids (unspecified “pelmatozoan”, *Dibrachicystis*; Clausen et al. 2009; Zamora and Smith 2012; respectively). None of these expresses the internal floor plates, podial pores/basins, or calycinal slots of earliest crinoids (Guensburg et al. 2010), but the former two expressions do occur in early edrioasteroid-like pentaradial taxa (e.g., *Totiglobus*, *Cambroblastus*).

Calyx and stem construction.—The same issues that contradict homologous orals in blastozoans and crinoids have been discussed in detail for other skeletal elements (Guensburg and Sprinkle 2007, 2009; Guensburg 2012). We provide only a summary of these findings (Table 1). Earliest crinoids lack the well-organized, standardized, often sparse plating that characterizes derived crinoids, indicating this characteristic evolved as an apomorphy within the crinoids. Only a cup base circlet and radial plates occur within the protocrinoid cup, along with scores of disorganized mid-cup and interray plates. Standardized thecal/calyx plating has been proposed to be homologous (Ausich 1998a; Ausich et al. 2015b), but this interpretation conflicts with the earliest crinoid stratigraphic sequence and numerous other structural details (see Guensburg and Sprinkle 2007). The thecal plating of the Early Ordovician eocrinoid *Rhopalocystis* superficially resembles that of derived camerate crinoids in that there seems to be division into a “fixed brachial-interbrachial” pattern in the thecal wall (Ubaghs 1963; Ausich et al. 2015b; Fig. 8A). But these “fixed brachials” taper upward, terminating near ambulacral tips. There is no continuation extending onto arms as is found in crinoids. The oral region of *Rhopalocystis* is typical of blastozoans with biserial brachioles branching from floor plates in recumbent ambulacra. The unipartite thecal base and holomeric stem with small irregular lumen also differ from early crinoids.

Contrasting stem morphology has also been discussed previously (Guensburg and Sprinkle 2007; Guensburg et al. 2010). The earliest crinoids express pentameric stems, meres commonly forming as triangular wedges at triple junctures with the cup base circlet. Distally, these disjunct elements then mutually articulate laterally. More distally, pentameres transition to a plate mosaic above the holdfast (Ubaghs 1969;

Guensburg and Sprinkle 2003). Polymeric, irregularly pentameric, stems are rare among blastozoans, apparently occurring only among certain derived Middle to Late Ordovician caryocystitid stems (Bockelie 1982) and echinosphaeritid diploporans, forms otherwise remarkably unlike crinoids. These blastozoan meric stems achieve full form with lateral articulation directly below the theca, and there is no evidence of the variations along the stem outlined above for early crinoids. Edrioblastoids, on the other hand, display tetrameric stems (Guensburg et al. 2010) as do certain early crinoids (e.g., *Ramseyocrinus*, *Colpodecrinus*).

Conclusions

This analysis finds that proposed synapomorphies of certain blastozoans and crinoids can be attributed to homoplasy. No sister-group relationship linking earliest crinoids to any specific blastozoan or any specific ordinal or smaller subset of blastozoans can be demonstrated. Selection of scattered characters across a wide array of derived blastozoan diversity for phylogenetic analysis is based on the notion of “sufficiency” or “plausibility”; such inference, in and of itself, does not provide argumentation for distinguishing homology from homoplasy. Tremadocian crinoids collectively form a morphologic pattern that is not in accord with blastozoan linkage to later Ordovician hybocrinid or cyathocrinine crinoids, those early crinoids with few-plated rigid constructions considered by blastozoan proponents. Evidence rather indicates that these are derived paedomorphic forms with superficial blastozoan-like morphology. Earliest crinoids express ambulacral traits unknown in blastozoans, but similar to edrioasteroids. This includes thin, slit-like floor plates, wedge-shaped or round podial pores/basins, raised podial pore/basin rims, and large open, presumably coelomic space, beneath the expansive internal floor plate surface. Wedge-shaped basins specifically resemble those of derived edrioasterids (e.g., *Paredriophus*), suggesting phylogenetic linkage. The current controversy over crinoid ancestry is not likely to be resolved by phylogenetic analysis at this time given: (i), polarized views of character interpretation, and (ii), the lack of any outgroup supportable on available evidence. Such an outgroup will need to exhibit sufficient synapomorphies with basal crinoids, at the very least, and lack exclusive synapomorphies with crownward members of any other clade of echinoderms.

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