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UNIVERSAL ELEMENTAL HOMOLOGY IN GLYPTOCYSTITOIDS, HEMICOSMITOIDS, CORONOIDS AND BLASTOIDS: STEPS TOWARD ECHINODERM PHYLOGENETIC RECONSTRUCTION IN DERIVED BLASTOZOA

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ABSTRACT—Universal elemental homology (UEH) is used to establish homology of thecal plates and elements of the ambulacral system among clades of stemmed echinoderms by placing these structures into a testable hypothesis of homology. Here UEH is used to explore hypotheses of homology in blastoids, coronoids, *Lysocystites*, hemicosmitoids, and glyptocystitoids. This new approach to analyze homology is particularly powerful in understanding the nature of the thecal plates of blastoids and how they relate to other taxa in a common nomenclatural lexicon. In blastoids, deltoids are interpreted as oral plates that are homologues to oral plates of glyptocystitoids and hemicosmitoids whereas side plates are interpreted to be ambulacral floor plates. Thecal plates are homologous among blastoids, coronoids and *Lysocystites* but these morphologies cannot be reconciled with plate circlets of glyptocystitoids and hemicosmitoids. A phylogenetic analysis of these taxa presents the origin of blastoids as sister taxon of coronoids within a testable series of homologies.

INTRODUCTION

One of the most striking patterns in the echinoderm fossil record is the sudden appearance of a diversity of body plans associated with the Cambrian Explosion and again with the Ordovician Radiation (Sprinkle, 1980a). Echinoderms diversified in both of these dramatic evolutionary events becoming notable components of both the Cambrian and Paleozoic Evolutionary Faunas (Sepkoski, 1981; Sprinkle, 1992; Sprinkle and Guensburg, 1995). The extreme morphological disparity exhibited by echinoderms has resulted in a taxonomic division of the clade into some 21 classes, but the polyphyletic nature of several of these classes—particularly Eocrinoidea, Rhombifera, and Diploporita—masks an even higher diversity of major clades (Paul and Smith, 1984; Sumrall, 1997). Indeed, total echinoderm body plan disparity is rivaled only by that of Mollusca and Arthropoda (Foote, 1992).

Although modern echinoderms seem relatively diverse, being placed into five classes by most classification systems, this apparent disparity is somewhat misleading. Four of the classes, Echinoidea (sea urchins and sand dollars), Holothuroidea (sea cucumbers), Asteroidea (sea stars) and Ophiuroidea (brittle stars) form a single clade, Eleutherozoa, that includes one extinct class Ophiocistioidea (Sumrall, 1997; Janies, 2001; Sumrall and Wray, 2007). The other living class, Crinoidea (feather stars and sea lilies), is represented by one small group, Articulata, compared to a tremendous disparity found in Paleozoic rocks worldwide (Foote, 1992, 1994; Ausich, 1998a, 1998b). In contrast to modern echinoderm diversity, fossil taxa are divided into approximately 30 distinct clades, showing a bewildering array of morphological disparity manifested in body plan symmetry, evolution of respiratory structures, feeding appendages, body plating, and many other features (Sprinkle, 1973, 1980a; Sumrall and Wray, 2007).

The study of the systematics of stemmed echinoderms is in its early stages. Although several studies place Echinodermata into a phylogenetic framework (Paul and Smith, 1984; Paul, 1988; Smith, 1984, 1990; Mooi et al., 1994; Sumrall, 1997; Sumrall and Sprinkle, 1998; David et al., 2000; Janies, 2001), little consensus currently exists. Much of the problem in recovering the true phylogeny of echinoderms has centered on different interpretations of homology. Some advances have been made accessing homology of regions of the echinoderm body based on their developmental origin, the Extraxial-Axial Theory (EAT) (Mooi et al., 1994, 2005; Mooi and David, 1997, 1998, 2008; David and Mooi, 1998; David et al., 2000). This theory assigns homology regionally to plate series based on their presumed developmental origin and style of growth. The EAT theory has been useful for understanding homology at the highest taxonomic levels where deep structure is illuminated by these regional homologies. Universal elemental homology (described here for stemmed echinoderms) takes the understanding of homology to the next level by allowing the identification, in many cases, of individual plates across clades. Thus evolutionary changes in shape or plate contact relationships can be used to generate characters that are useful for reconstructing phylogeny at the lowest taxonomic levels.

Unfortunately, we cannot simply rely on the published literature for providing a series of plate names to illuminate homology (e.g., Moore, 1954). Homologous plates in related echinoderm clades often have different names and nonhomologous plates can have the same name (Table 1). These problems are especially evident in the nomenclature of plates associated with the ambulacra and peristome of derived blastozoans such as blastoids (see Sprinkle and Sumrall [2008] for a brief discussion in parablastoids). The purpose of the present paper is to address this issue with a case study of the homology of thecal plates in four closely related clades, the hemicosmitoids, glyptocystitoids, coronoids, and blastoids using universal elemental homology as derived by Sumrall (2008, 2010). The UEH framework provides a clear understanding of homology to describe characters such that echinoderm phylogeny can potentially be resolved.

HOMOLOGY

Homology is the central concept of systematics and can be defined as "similarity due to inheritance from a common

TABLE 1—Plate homologies in rhombiferan, coronoid and blastoid echinoderms.

Rhombiferan	Coronoids	Blastoids	Preferred name
Theca			
Basals?	Basals	Basals	basals
Lateral	No homologue	No homologue	Laterals[1]
Infralateral	No homologue	No homologue	Infraleterals[1]
Radials	No homologue	No homologue	Radials[1]
No homologues	Radials	Radials	Radials[1]
Orals	Deltoids; coronal plates	Deltoids	Orals
No homologue	Trunk mounting plate	Lancets	Lancets
Ambulacra			
Primary, secondary floor plates	Brachiolar trunk arm complex	Side plates; outer side plates	Primary, secondary ambulacral floor plates
Cover plates	Cover plates	Cover plates	Ambulacral cover plates
Brachioles	Brachioles	Brachioles	Brachioles
Respiratory structures			
Endothecal; pectinorhombs	No homologue	No homologue	Pectinorhombs[1]
No homologue	Exothecal; coelomic canals	No homologue	Coelomic canals[1]
No homologue	No homologue	Endothecal; hydrospires	Hydrospires[1]
Oral Openings and covering plates			
Mouth	Mouth	Mouth	Mouth
Primary peristomal covering plates	Oral cover plates	Summit plates	Primary peristomal covering plates
??	??	Spiracles	??
Periproct	Anus	Anus; anispiracle	Anus
Anal pyramid	Anal cover plates	Anal cover plates	Anal cover plates
Periproctal membrane	No homologue	No homologue	Periproctal membrane [1]
Gonopore	Gonopore	Gonopore	Gonopore
Hydropore	No homologue	No homologue	Hydropore
Attachment			
Stem	Stem	Stem	Stem

[1] These plate names are used to describe homologous thecal elements either within rhombiferans or the three clades bearing blastoid-like thecal plating. They do not imply homology between these two groups.

ancestor" (Hillis, 1994). Patterson (1988) suggested three tests to distinguish homology from homoplasy in taxonomic characters: similarity, congruence and conjunction. Similarity can be used to falsify hypotheses of homology of morphological features, using ontogeny and comparative anatomy (or both) of the particular structure in question. Detailed differences in structure and origin are incompatible with features being homologues. The conjunction test is used in morphology to distinguish between two structures deemed homologous by first passing the similarity test. If both structures are present in the same organism at the same time then they cannot be homologues as one "homologue" would be unable to transform into the other (Williams, 1993). Congruence is the most decisive test in morphology. If a feature is required by phylogeny to be derived independently in different clades, then the structures cannot be of homologous origin. Shared similarities are homologies when they diagnose monophyletic groups and are congruent with further homologies that diagnose the same group (Williams, 1993).

As mentioned above, current schemes of plate nomenclature cause significant confusion in determining homologies in extinct stemmed echinoderm clades (Table 1). Indeed, cases exist in which plates have been interpreted as homologues simply because they have the same name (Breimer and Ubaghs, 1974). For example, the term "oral plates" is used for cover plates over the mouth in edrioasteroids (Bell, 1976a, 1976b) and food groove bearing peristomial bordering plates in glyptocystitoids (Kesling, 1968). Similarly, deltoids are peristomial bordering plates in blastoids (Beaver et al., 1967) whereas they are interradial plates below the orals in parablastoids (Sprinkle, 1973; Sprinkle and Sumrall, 2008). We know from positional and functional arguments that deltoid plates of blastoids and oral plates of glyptocystitoids appear to be homologous (Sumrall and Sprinkle, 1995; Sprinkle and Sumrall, 2008; Sumrall, 2010).

Successful phylogenetic analysis of stemmed echinoderms requires a universal elemental homology scheme. Early attempts to define characters based on elemental homology led to simplistic schemes by many authors for features such as the plating of the theca. Simply counting the number of plate circlets (Paul, 1988; Sumrall, 1997; Ausich, 1996) assumes a priori that these plate circlets are themselves homologous. This seems unlikely given the generalized pattern of echinoderm clades to transition between irregular plating to organized plate circlets (Sumrall, 1997) or to add or remove plates and plate circlets phylogenetically (Simms, 1994; Ausich, 1996; Sprinkle and Wahlman, 1994).

From the perspective of phylogenetic reconstruction, if we incorrectly reject the hypothesis that individual plates within plate circlets are homologous we have made a type 2 error (Baverstock and Moritz, 1990). Our analysis may be less powerful, but such errors are not positively misleading. This may lead to a lack of precision in the resulting phylogenetic hypothesis, but the tree topology will remain congruent with the true phylogeny assuming the presence of other phylogenetic character data. If however, we assume an a priori hypothesis of homology among plate circlets that are not homologous, we will have made a type 1 error (Baverstock and Moritz, 1990). Such errors are positively misleading in the analysis supporting relationships that did not occur phylogenetically. This may lead to greater precision in the phylogenetic hypothesis but at the expense of accuracy. Because our goal is to recover an accurate phylogeny, it is best to err on the side of caution and risk losing precision for the sake of accuracy.

UNIVERSAL ELEMENTAL HOMOLOGY

In this paper, we strive to expand the universal homology scheme (UEH) presented by Sumrall (2008, 2010) for derived stemmed echinoderms. This scheme divides plate types into homologous elements using development, position, function, and symmetry as proxies to generate testable hypotheses of homology. Universal elemental homology is examined in three steps. First is the establishment the homology of individual ambulacra based on the Carpenter (1884) system. Second is the establishment of the homology of individual thecal plates among taxa if any. Third is the establishment of homology of individual elements and series of elements within the peristomial border and ambulacral system using ambulacral symmetry as a template.

Glyptocystitoid rhombiferans form the model organisms upon which UEH was developed (Sumrall, 2008, 2010) because the homology of individual elements is well documented and understood (Kesling, 1968; Paul, 1984). Using this as a template we will establish homologous elements for blastoids, the unusual Silurian taxon *Lysocystites* thought to be closely related to blastoids, coronoids and hemicosmitoids (Donovan and Paul, 1985; Paul, 1988; Sumrall, 1997). *Lysocystites* is less completely understood morphologically than the other taxa discussed here because it lacks known stem holdfast cover plates and feeding appendages (Sprinkle, 1973). Hemicosmitoids were recently reinterpreted using universal elemental homology (Sumrall, 2008) but are included to show variation and establish character polarity in the phylogenetic analysis.

The taxa under discussion here are all closely related. As a group they share similarities of the ambulacra including primary and secondary floor plates, brachioles mounted between floor plate pairs, and well-defined pits lining the food groove (Sumrall, 1997). Blastoidea, Coronoidea and *Lysocystites* form a well-defined clade united by the nearly identical plating of the theca, the loss of the shared ambulacra (joined BC and DE ambulacra proximal to the peristome), and similarity in the structures of the posterior oral plates (Brett et al., 1983; Donovan and Paul, 1985; Gil-Cid et al., 1996; Sumrall, 1997). Here we are reinterpreting blastoids and coronoids in the context of the UEH scheme. We follow conventional terminology restricting the name Blastoidea to the clade including bud-shaped forms with recumbent ambulacra with Coronoidea as its sister taxon either inclusive or exclusive of *Lysocystites* (but see Donovan and Paul, 1985).

HOMOLOGY OF THE AMBULACRA

General features.—For the purposes of this paper we are expressing all of the ambulacral homologies in the Carpenter (1884) system which designates the ambulacra A–E. There are several different features of the pentaradiate echinoderm body plan that can be used to establish this homology scheme (Sumrall and Wray, 2007). In nearly all plesiomorphic pentaradiate taxa the ambulacral system is arranged into a 2-1-2 symmetry as described by Sprinkle (1973) (Fig. 1). In this arrangement, three ambulacra extend from the centrally located peristome but the two lateral ambulacra distally bifurcate. The A ambulacrum extends along the plane of bilateral symmetry, through the peristome separating the shared BC and DE ambulacra on the right and left sides respectively (Fig. 1). Bifurcation of the shared ambulacra forms the distal B–E ambulacra. In Blastoidea, Coronoidea, and *Lysocystites*, the expression of the 2-1-2 symmetry has been severely reduced to form pseudo five-fold symmetry (sensu Sumrall and Wray, 2007) (Fig. 2.5, 2.6). Here, vestiges of the 2-1-2 symmetry can be seen in the fundamental bilateral symmetry of the peristome and in some cases in the positioning of the primary peristomial cover plates that meet with a 2-1-2 sutural pattern. In glyptocystitoids, the 2-1-2 symmetry is well developed bearing long, shared ambulacra (Fig. 1). In *Hemicosmites*, only the proximal shared ambulacra and the A ambulacrum are present because of paedomorphic truncation of ambulacral development (Sumrall, 2008, 2010) (Fig. 2.3).

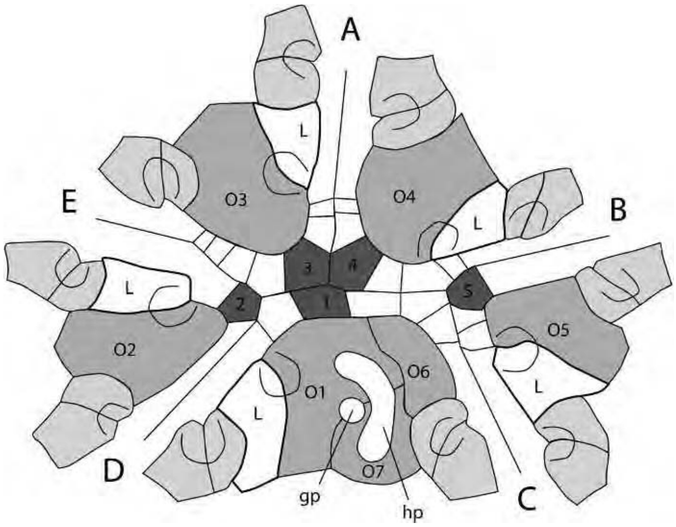


FIGURE *1*—Camera lucida drawing of the oral surface of the glyptocystitoid rhombiferan *Lepadocystis moorei* UC 57349. Light shading=ambulacral floor plates; medium shading=oral plates; dark shading=primary peristomial cover plates; A–E=ambulacral identifications using the Carpenter system; 1–5=the identities of the primary peristomial cover plates; gp=gonopore; hp=hydropore; L=the first left ambulacral floor plates on each of the ambulacra; O1–O7=the identities of the oral plates. (Modified from Sumrall, 2008).

This hypothesis of ambulacral homology can be tested by the position of the major body openings, position of compound oral plates, and details of plating often referred to as Lovén's Law (Sumrall and Wray, 2007). The vast majority of pentaradiate taxa have the hydropore, gonopore, and periproct located proximally in the CD interray (Sumrall and Wray, 2007) (Fig. 2). The CD interray typically has multiple plates (three in many taxa) that form the posterior side of the peristome and are associated with the hydropore and gonopore (Fig. 2.1, 2.3, 2.4). In many cases this number is reduced to two (Fig. 2.2, 2.5). The anal opening is typically in the CD interray either associated with the orals (Fig. 2.2, 2.5) or positioned more distally. In a few taxa, notably glyptocystitoids, the periproct is positioned in a different interray where it is synapomorphic for the clade (Kesling, 1968; Paul, 1984). In some taxa, ambulacra B and D have a similarity manifest in the position of brachiole facets on floor plates that differs from ambulacra A, C, and E (David et al., 1995; Hotchkiss, 1998; Sumrall and Wray, 2007) (Fig. 2.1).

Glyptocystitoids.—In glyptocystitoids (Fig. 2.1) ambulacral homology is straightforward with an obvious 2-1-2 ambulacral symmetry. The CD interray contains three plates pierced along sutures by a hydropore and gonopore. In most members of this clade, the A, C, and E ambulacra have the first brachiole on the left side whereas B and D have the first two brachioles on the left side (Paul, 1984; Sumrall, 2008). The only inconsistency is the placement of the anus on the BC side of the theca. This is a clade-wide synapomorphy and should not serve to falsify the hypothesis of ambulacral homology (Kesling, 1968; Paul, 1984).

Hemicosmitoids.—In Hemicosmitoids (Fig. 2.3) the ambulacral system is greatly reduced, but has erect distal floor plates bearing brachioles (Sprinkle, 1975). On the thecal summit, the 2-1-2 symmetry is paedomorphically reduced to the proximal A, shared BC and shared DE ambulacra (Sumrall and Wray, 2007; Sumrall, 2008). The bifurcation of the shared ambulacra by the development of the lateral O2 and O5 orals has been lost, and the arm facets have been placed upon flooring plates incorporated into the thecal summit (Sumrall, 2008). These ambulacral homologies are consistent with the three oral plates present in

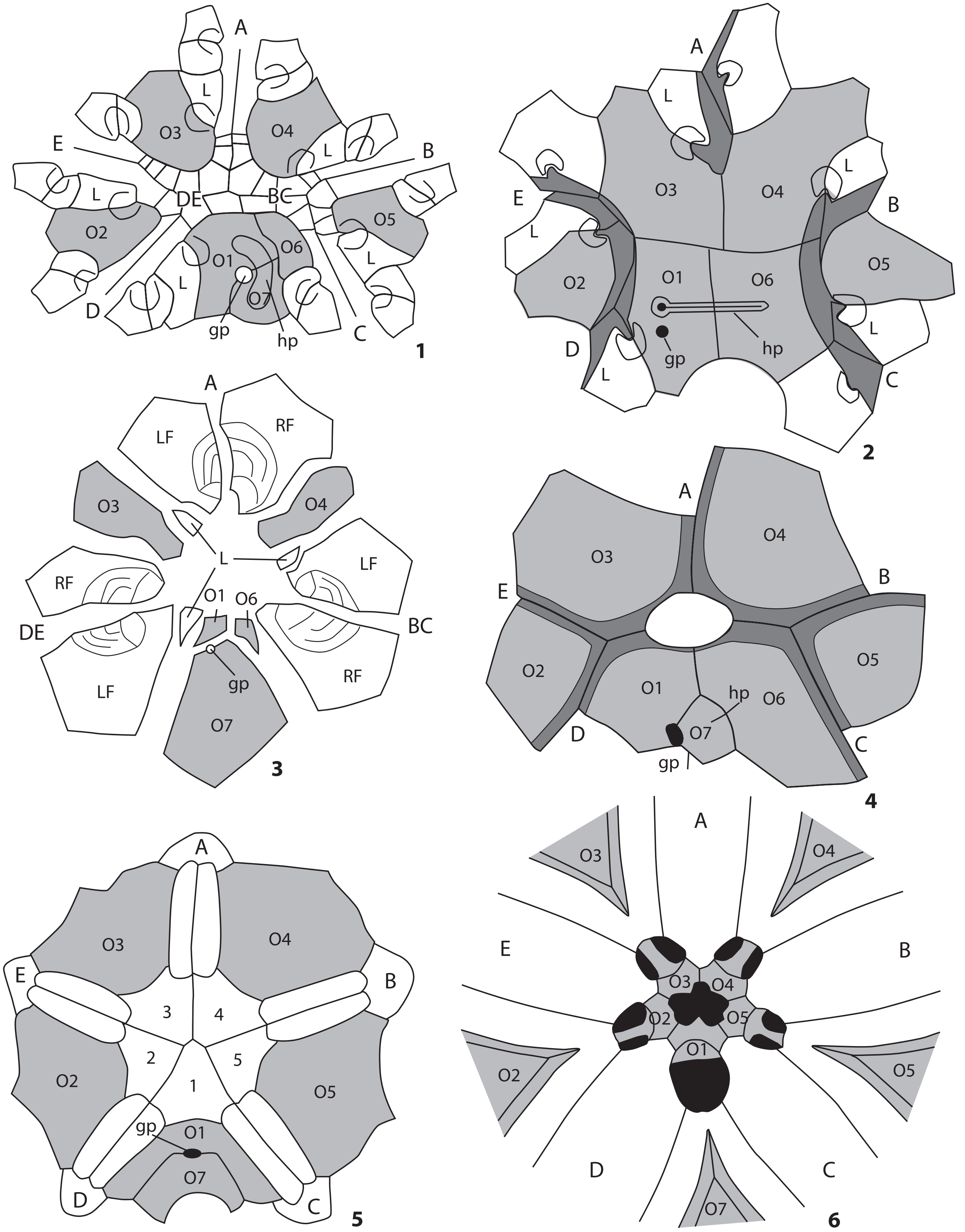
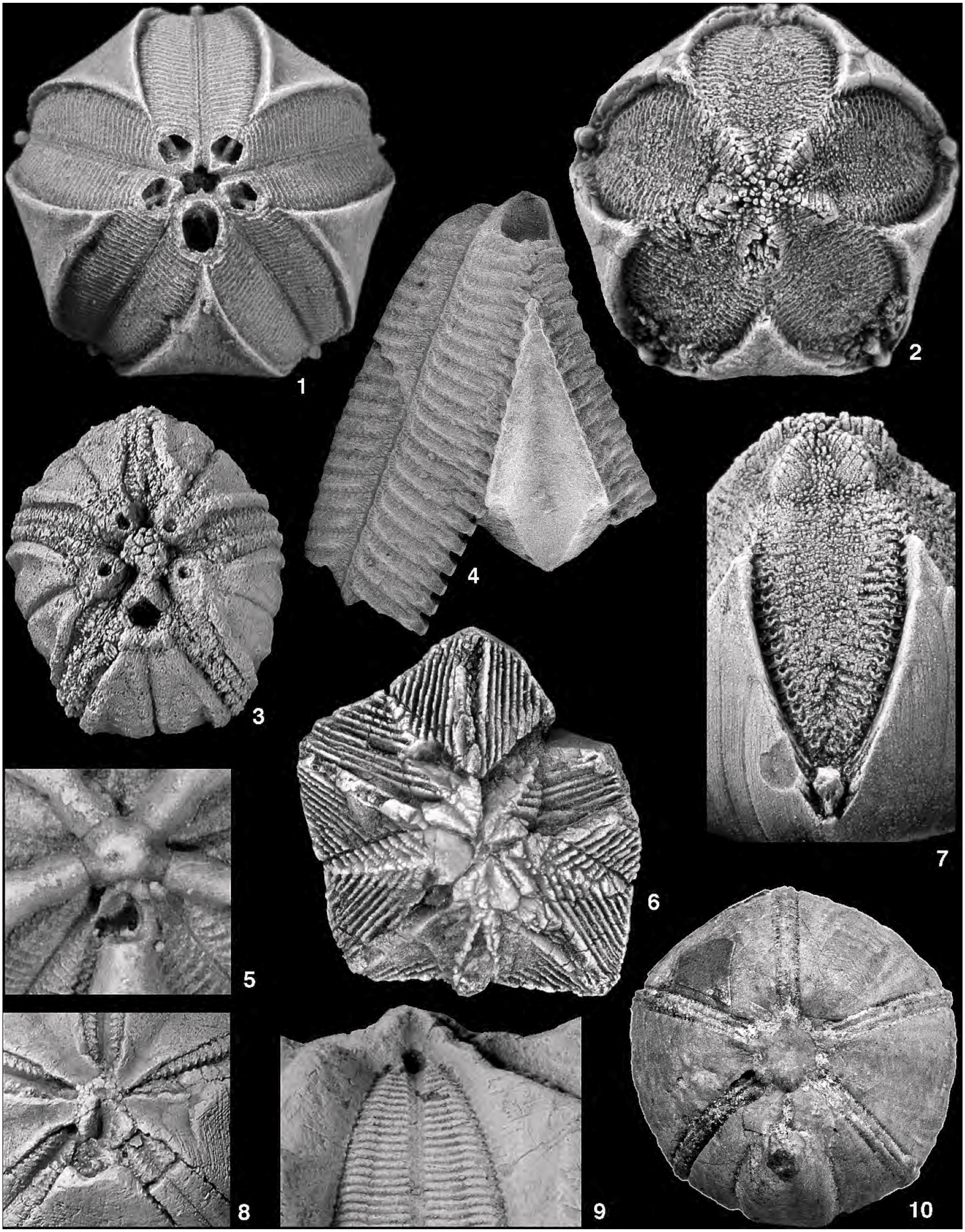


FIGURE 2—Comparative ambulacral systems of stemmed echinoderms; *1*, the glyptocystitoid *Lepadocystis moorei*; *2*, the diploporan *Tristomiacystis*; *3*, the hemicosmitoid *Hemicosmities*; *4*, the diploporan *Protocrinites*; *5*, the coronoid *Stephanocrinus*; *6*, the blastoid *Pentremites*. *1*, *3*, and *4* modified from Sumrall (2008); *2* is modified from Sumrall and Deline (2009); *5* modified from Brett et al. (1983); *6*, CMC IP 66825.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the CD interray, the position of the hydropore/gonopore and the position of the anus. Furthermore, the position of the first incorporated secondary floor plates for brachiole facets into the summit of the theca is consistent with Lovén's law as described for glyptocystitoids (Sumrall, 2008). One hemicosmitoid genus, *Thomacystis*, differs from this model. Here, the B–E ambulacra are present whereas the A ambulacrum is absent. We view this taxon as bearing an aberrant apomorphic ambulacral condition that is difficult to reconcile with UEH (see thecal plate homology below).

Blastoids.—In blastoids, the 2-1-2 symmetry is reduced into what Sumrall and Wray (2007) called pseudo five-fold symmetry. The peristome is wider than high consistent with 2-1-2 symmetry (Figs. 2.6, 3.1) and in some taxa, notably *Nucleocrinus,* the primary peristomial cover plates (see below) are arranged into 2-1-2 symmetry (Fig. 3.10). Where known, the gonopore opening lies proximally within the CD interray (Breimer and Macurda, 1972). The deltoid plates of blastoids, homologues of orals (see below), are single elements in all interambulacra except for the CD interray where there are between two and six elements (Beaver et al., 1967; Sprinkle, 1973; Breimer and Macurda, 1972; Macurda, 1983). The periproct uniformly lies in the CD interray associated with the deltoid plates, and no vestiges of Lovén's law are noted in blastoids.

Coronoids.—Coronoids are very similar to blastoids in the symmetry of the ambulacral system. The 2-1-2 symmetry is reduced into pseudo five-fold symmetry but the peristome remains pentamerally symmetric (Figs. 2.5, 4.1, 4.11). Where known, the primary peristomial cover plates (see below) are arranged with a 2-1-2 symmetry (Figs. 2.5, 4.1). The deltoid plates of coronoids, homologues of orals (see below), are single elements in all interambulacra except for the CD interray where there are two elements (Brett et al., 1983) (Figs. 2.5, 4.11). The gonopore opening lies proximally within the CD interray positioned between the two CD oral plates here termed O1 and O7 (Brett et al., 1983). The periproct uniformly lies in the CD interray between O7 and the coronal processes of two radial plates (Fig. 2.5). No vestiges of Lovén's law are noted in coronoids.

Lysocystites.—The ambulacral system of *Lysocystites* is poorly documented but the basic structure and ambulacral identities are clear. The ambulacra are arranged in a pseudo five-fold symmetry (Sumrall and Wray, 2007). The ambulacra can be identified by the placement of the periproct, hydropore and gonopore within a complex of poorly documented compound oral plates presumed to be on the CD side of the theca (Sprinkle, 1973). No vestiges of Lovén's law are noted in *Lysocystites*.

HOMOLOGY OF THECAL PLATES

General features.—Nowhere is the need for clear assessment of homology more greatly needed than in the plating of the theca. Determining homology of thecal plates in related clades can be a daunting proposition. Plesiomorphic taxa of many echinoderm clades have irregular plating and increased numbers of plates in the theca compared to derived taxa (Sprinkle and Wahlman, 1994; Guensburg and Sprinkle, 2003). Because many clades have independently acquired a reduced thecal plating formula, these reductions in thecal plating are non-homologous (Sumrall, 1997). If we assume that plate circlets in similar position of the theca in different clades are homologues, we run the risk of them being analogues, a type 1 error in which character data unite false clades. If, however, we reject the homology of plate circlets by similarity, congruence, or conjunction, but incorrectly infer no homology, we will make a type 2 error by rejecting character data that unite a true clade. Given these options we prefer to err on the side of type 2 error. It may weaken the nodal statistics for clades, or even fail to recognize some, but the data will not be positively misleading.

For the purposes of this discussion, thecal plates will include those between the stem facet and the oral plates. The oral plates are treated separately below and the basal plates are functionally constrained to attach to the stem. Because of this functional constraint, it is likely that basal plates are homologous to derived blastozoans or that basal plates have been derived only a few different times. Sumrall (1997) suggested that the number and symmetry of basal plates could be used to reject hypotheses of basal plate homology and similar arguments are used here.

As with crinoids (Ausich, 1996, 1998a, 1998b) we do not believe that basals are always homologous among clades. Above the basal plates various plate circlets have been identified in the clades under consideration (Fig. 5; Table 1). Here, different names have been assigned to circlets based on position relative to ambulacra (i.e., radial, lateral, infralateral) and shape (i.e., deltoids and lancet). Because different workers created clade-based anatomical nomenclature (Fig. 5; Table 1) situations exist in which name usage reveals little about the hypotheses of plate homology among clades. Indeed, for most clades, plate circlet homology can be rejected by similarity in terms of numbers of plates, numbers of plate circlets, symmetry, and their relative positional relationships to one another (Sumrall, 1997). Consequently, little commonality of plate names among clades can be drawn and generating phylogenetic characters based on these names can be highly misleading rather than yielding the supportable underlying homologous relationships.

Glyptocystitoids.—In glyptocystitoid rhombiferans, the stem attaches to four basals: three small azygous basals and a fourth larger zygous basal positioned in the BC interray (Fig. 6.4). Plesiomorphically, five infralaterals, five laterals, and a variable number of radials lie adoral to the basals (Sprinkle and Wahlman, 1994). Derived taxa standardize the radials between four and six depending on subclade and five oral fields of which the CD is composed of three plates.

Hemicosmitoids.—In hemicosmitoids, the stem attaches to four basals: two zygous basals symmetrically placed across the CD interray and two azygous basals symmetrical across the A ray (Fig. 6.2). These basals alternate with a circlet of six infralaterals, eight to nine laterals and a complex series of oral plates, and floor plates that form the thecal summit and facets for arms and proximal brachioles (Bockelie, 1979; Sumrall, 2008). These

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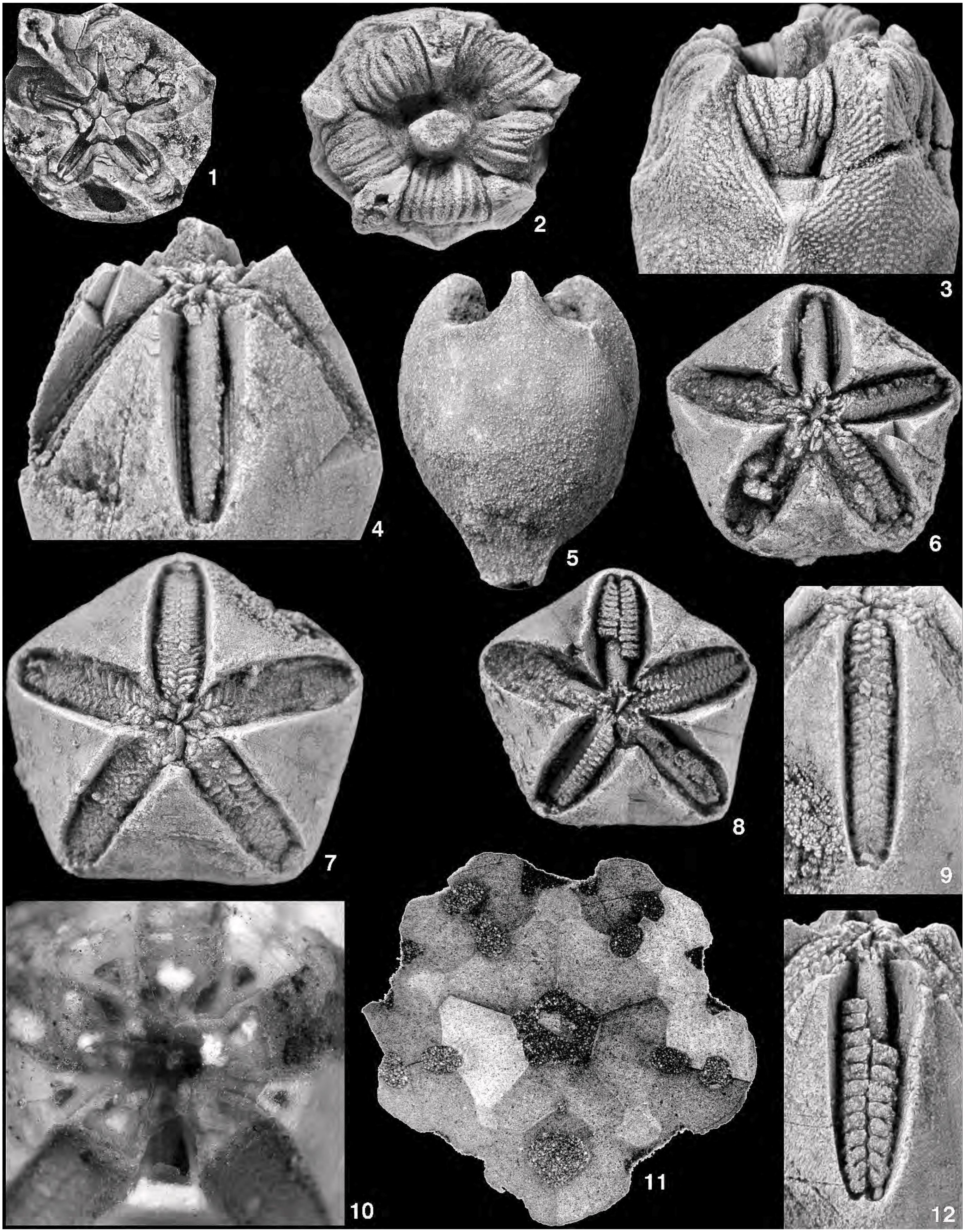
FIGURE 3—Photographs of blastoids. *1*, *Pentremites tulipiformis* CMC IP 66825, summit view of theca with cover plates missing, oral plates (deltoids) can be seen bisecting the spiracles and forming the edge of the mouth frame, ×6.5; *2*, *Pentremites tulipiformis*, CMC IP 66827, summit view of theca with cover plates, ×8; *3*, *Globoblastus norwoodi*, SUI 102902 with peristome partially covered by small polygonal oral cover plates, ×5.0; *4*, *Pentremites godoni*, CMC IP 67716 SEM of partial specimen showing deltoid, spiracle, and portions of two ambulacra, details of the ambulacrum include the lancet, side plates, outer side plates, brachiolar attachment scars, hydrospire pores, medial and lateral food grooves; radiodeltoid suture at aboral end of deltoid shows radial overlapped deltoid; spiracle formed by adoral tip of deltoid, ×27; *5*, *Deltoblastus ellipticus*, specimen figured in Wanner (1924), pl. 202, figs. 3–5, showing primary peristomial cover plates arranged in 2-1-2 symmetry, ×15; *6*, *Hadroblastus liaoi*, holotype NIGP 148832; *7*, *Pentremites tulipiformis* CMC IP B, B ambulacral view showing cover plates over the lancet and ambulacral floor plates (side plates), ×8; *8*, *Deltoblastus molengraffi*, RGM 345632, oral cover consisting of numerous small polygonal plates including PPCPs and shared cover that abut aboral tips of deltoids to form hood over the peristome, ×6.0; *9*, *Deltoblastus delta*, RGM 297385, lateral view showing ambulacral medial food groove traveling underneath two of the five large oral covering plates, ×5.3; *10*, *Nucleocrinus lucina*, AMNH 24058 showing five large PPCPs covering peristome in 2-1-2 arrangement, ambulacral food grooves converge underneath oral covering plates, ×3.5.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circlets show variable numbers of plates among taxa of the same clade, and the names used refer to position on the theca rather than on any expectation of homology. Furthermore, the plating of the theca has six-fold symmetry reflecting the triradiate ambulacral system, whereas other taxa with pentaradiate ambulacra tend to reduce thecal plating to a five-fold pattern (Sumrall, 2008).

Blastoids, coronoids, and Lysocystites.—Unlike other clades considered here, thecal plating of blastoids, coronoids, and *Lysocystites* cannot be rejected as homologous. The arrangement of the basals, two large zygous basals and one small azygous basal typically placed in the AB interray (Fig. 6.1, 6.3, 6.5), is identical in these groups. Five radially positioned radial plates form the plate circlet adoral to the basals. Radials are aligned with five radially positioned lancet plates. The lancet plates alternate with and are separated from the mouth by the oral plate circlet. The configuration of the lancet plates is differently expressed among blastoids, coronoids and *Lysocystites*. In coronoids, the lancet is expressed as a small circular to half moon-shaped plate upon which the distal erect ambulacra and the first left brachiole are mounted if viewed proximally to distally as is typical for stemmed echinoderms (Brett et al., 1983) (Figs. 4.1, 4.3, 6.1). In *Lysocystites* the lancet is radially elongate but lies topologically between the oral plates (Sprinkle, 1973). In the vast majority of blastoids, the lancet plate extends into a cleft in the radial (Beaver et al., 1967) (Fig. 6.4, 6.12). Regardless of shape, however, lancet plates in all three groups topologically lie in the same position, radially between the oral plates and the radial plates.

Remarks.—Although blastoids, coronoids and *Lysocystites* show extreme conservatism in their thecal plating, phylogenetically, as well as morphologically, these plate reductions cannot be reconciled with those of glyptocystitoids and hemicosmitoids. Radial plates are called radials because of their position on the theca rather than any implication of homology. Indeed the lancet plates in blastoid-like taxa are in the same topological position as hemicosmitoid and glyptocystitoid radials (radially positioned, immediately distal to the oral plates). Blastoid radials are one circlet more distal than the lancets in the radial position. Furthermore, the number of radial plates is variable within glyptocystitoids (Kesling, 1968; Sprinkle and Wahlman, 1994; Broadhead and Sumrall, 2003) and changes ontogenetically (Sumrall and Sprinkle, 1998). Furthermore, hemicosmitoid radials (*sensu* Bockelie, 1979) consist of a combination of oral plates and ambulacral floor plates (Sumrall, 2008). Although the generalized plating of glyptocystitoids is pentaradiate as in blastoids, that of hemicosmitoids is hexaradiate probably reflecting the triradial ambulacral symmetry. On the basis of Patterson's test of congruence, we can, therefore, reject the hypothesis that these taxa share a homologous thecal reduction.

The puzzling morphology of *Thomacystis* is difficult to reconcile with UEH or indeed with paedomorphic ambulacral reduction (Sumrall and Wray, 2007). Four ambulacra, likely B through E with A missing, bear one or two erect ambulacra that arise from plates bordering the peristome (Paul, 1984). This condition is highly derived from other hemicosmitoids, likely representing an apomorphic condition. Because UEH speaks to the plesiomorphic condition underlying homology in blastozoan echinoderms, such radical transformations are difficult to reconcile with the UEH model.

HOMOLOGY OF RESPIRATORY STRUCTURES

General features.—Glyptocystitoids, hemicosmitoids, blastoids, coronoids, and *Lysocystites* have respiratory structures that are markedly different in their construction. Respiratory structures in blastozoans can be delimitated into two functional groups. Endothecal respiratory structures are characterized by external pores connecting internal thin stereom folds through which water circulates (Paul, 1968b). These include pectinirhombs, cryptorhombs, and hydrospires. Exothecal respiratory structures are characterized by internal pores connecting canals within the thecal plates through which coelomic fluids circulate (Paul, 1972). These include epispires, diplopores, and coronal canals.

Glyptocystitoids.—Glyptocystitoids have several different types of respiratory structures including exothecal covered sutural pores or thin corrugated plates in the most plesiomorphic taxa (Paul, 1968a; Sprinkle and Wahlman, 1994) and pectinirhombs in more derived forms (Paul, 1968b, 1972). In the latter, external dichopores are connected via thin folds of stereom called dichopore canals across plate sutures. Gas is exchanged within the theca between the ambient seawater in the dichopore canals and the coleomic fluid.

Hemicosmitoids.—Cryptorhombs are very similar in construction to pectinirhombs. Pores are connected via thin folds of stereom called canals across plate sutures (Paul, 1972). Here gas is exchanged within the theca between ambient seawater in the canals to the coelomic fluid within the theca. The primary constructional difference is the differentiation of incurrent and excurrent pores. The incurrent pores are located along the upper and lower portion of the theca and have a sieve-like mesh of small pores covering the surface. A single excurrent pore is often elevated slightly with a spout located along the mid portion of the theca. The separation is thought to keep incurrent and excurrent water separate for higher efficiency. Cryptorhombs are a synapomorphy of all hemicosmitoids.

Blastoids.—Blastoids all have endothecal respiratory structures called hydrospires (Beaver et al., 1967). Incurrent pores located along the edge of the ambulacra connect to hydrospire canals that exit through slits or spiracles near the thecal summit (Fig. 3.1, 3.4). The hydrospire canals are thin folds of stereom that are positioned symmetrically about each ambulacrum through which gas is exchanged between the ambient seawater in the hydrospire and the coelomic fluid. All blastoid taxa have this structure, which is a synapomorphy for the clade.

Coronoids.—Coronoids uniformly have exothecal respiratory structures in the form of coelomic canals (Fig. 4.11). These canals are in the coronal crests of the radials and deltoid plates (Fig. 4.3, 4.5). In *Stephanocrinus* two main canals are connected by a series of network-like canals through which colomic fluids are passed (Brett et al., 1983). Interestingly, these canals are present in all coronoids, but also in a modified form in the Silurian blastoid

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FIGURE 4—Photographs of coronoids and blastoids. *1*, summit of the coronoid *Stephanocrinus angulatus*, SUI 49758, showing articulated primary peristomial cover plates and radially elongate cover plates, ×4.5; *2, 3*, summit and lateral radial views of *Stepahnocrinus angulatus*, SUI 49743, with erect ambulacrum and brachioles, whitened, ×7.5 and ×10; *4*, *Troosticrinus reinwardti*, CMC IP 67717, A ambulacral view stripped of floor plates showing underlying lancet plate and hydrospire slits and short coronal processes between ambulacra, ×10; *5*, *Cupulocorona* sp., SUI 97615, lateral view of theca, whitened, ×7.5; *6*, summit view of *Troosticrinus reinwardti*, CMC IP 67717, ×7.5; *7*, summit view of *Troosticrinus reinwardti*, CMC IP 67718, with well-preserved ambulacra, note the lack of deltoid bodies on the side of the theca, ×7.5; *8*, summit view of *Troosticrinus reinwardti*, CMC IP 67719, showing partly stripped ambulacral floor plates, ×7.5; *9*, view of well preserved A ambulacrum of *Troosticrinus reinwardti*, CMC IP 67718, ×7.5; *10*, ground summit view of *Troosticrinus reinwardti*, CMC IP 67720, showing coronal canals penetrating short coronal crests of theca, ×10; *11*, thin section through the summit of *Stephanocrinus angulatus*, CMC IP 67721, in cross polarized light showing the coronal canals and gonopore opening, ×10; *12*, view of well preserved A ambulacrum of *Troosticrinus reinwardti*, CMC IP 67719, ×10.

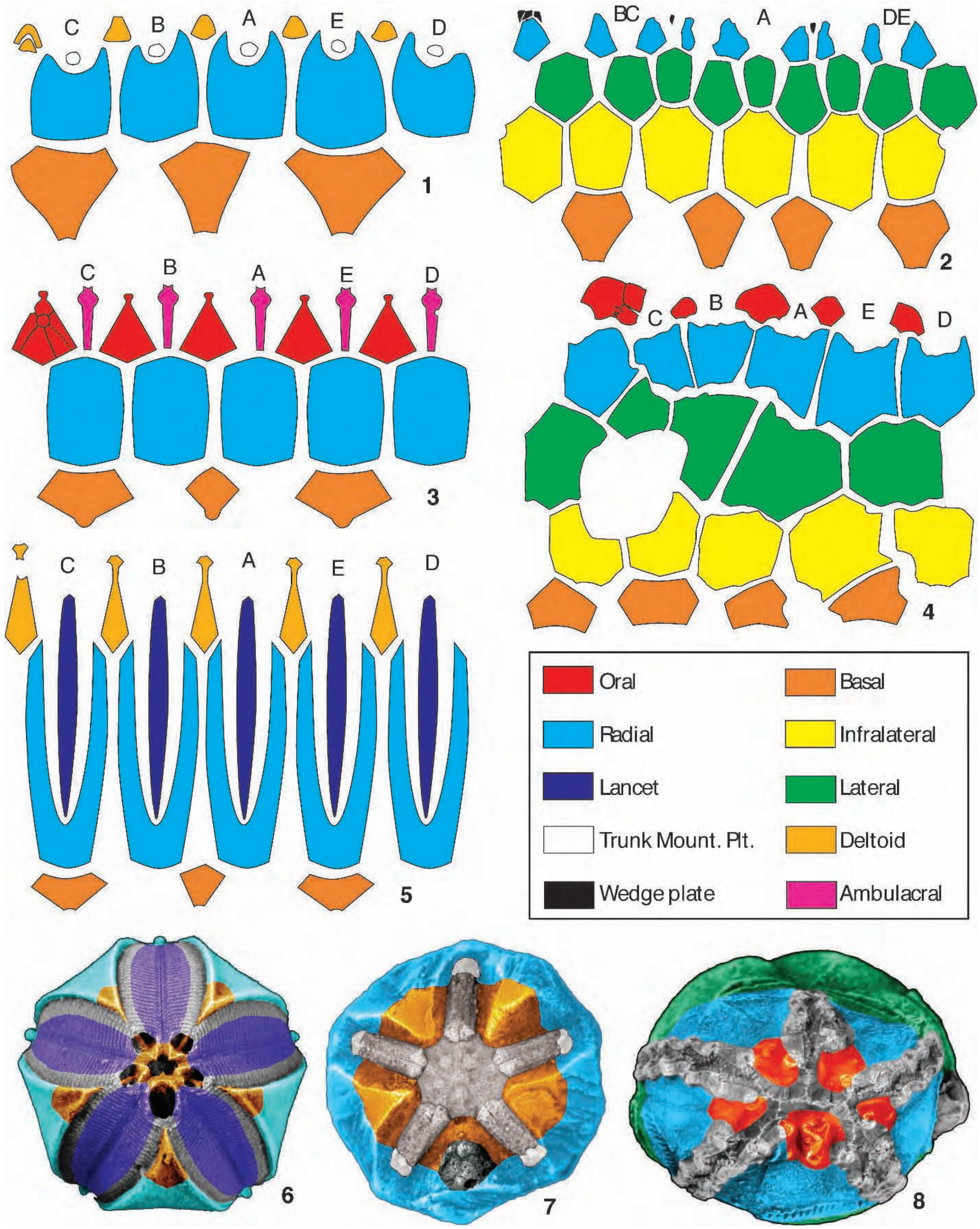


FIGURE 5—Plate diagrams and false color specimens illustrating thecal plate names as typically used in their respective clades (compare to *Fig. 6*): *1*, the coronoid *Cupulocorona*; *2*, the hemicosmitoid *Hemicosmites*; *3*, *Lysocystites*; *4*, the glyptocystitoid *Cheirocystis*; *5*, the blastoid *Hydroblastus*; *6*, the blastoid *Pentremites tulipiformis*; *7*, the coronoid *Stephanocrinus angulatus*; *8*, the glyptocystitoid *Lepadocystis moorei*. A–E are the ambulacral designations in Carpenter's system.

Troosticrinus providing further phylogenetic evidence for a close relationship between blastoids and coronoids (Fig. 4.11).

Lysocystites.—In *Lysocystites* exothecal respiratory structures are expressed as covered epispires (Sprinkle, 1973). These structures take the form of sutural pores at three plate junctions of thecal plates from which internal canals radiate toward plate centers. These canals are filled with coelomic fluid with apparent circulation between incurrent and excurrent pores (Sprinkle, 1973). This flow brings the coelomic fluid to the thecal surface where gas is exchanged with ambient seawater.

Discussion.—The endothecal respiratory structures of glyptocystitoids, hemicosmitoids and blastoids are all constructed of thin folds of stereom. In each of these groups, there is a consistent pattern of pores that are clade specific (Beaver et al., 1967; Paul, 1968b; Sprinkle, 1973). Glyptocystitoids exhibit much greater variation. However, each sub clade has well defined plate sutures where respiratory structures are placed (Paul, 1968b). Because they are all positioned differently in the theca, they fail the test of similarity and are deemed non-homologous. Furthermore, because the plesiomorphic state of respiratory structures in glyptocystitoids lacks internal stereom folds, we can reject the hypothesis of homology via the test of congruence at least between derived glyptocystitoids and other taxa. That similar respiratory structures have also evolved in other taxa including Crinoidea (Sprinkle and Kolata, 1982), Stylophora (Parsley, 2000; Domingues et al., 2002), and Parablastoidea (Sprinkle, 1973; Sprinkle and Sumrall, 2008), further suggests that the evolution of endothecal respiratory structures is relatively commonplace.

Hollow ridges and covered epispires of plesiomorphic glyptocystitoids and *Lysocystites* are topologically and structurally similar (Sprinkle, 1973; Sprinkle and Wahlman, 1994) suggesting that at least as epispire-like structures they may be homologous. Because the thecal plates have no homologues between these taxa (see above), the homology of individual epispires cannot be established. Similar structures are found in many early plesiomorphic clades, i.e., eocrinoid-grade blastozoans, suggesting that these structures are plesiomorphic. The specialized coronal canals of coronoids and *Troosticrinus* are topologically and structurally similar as they occur on homologous plate junctions (Fig. 4.10, 4.11). Their homology cannot be rejected by any of the tests of homology and therefore are consistent with the hypothesis of homology.

The presence of both coronal canals and hydrospires in *Troosticrinus* rejects any suggestion that hydrospires are somehow homologous with coronal canals regardless of their dissimilarity via the test of conjunction. Although superficially similar to hydrospires and cryptorhombs, pectinirhombs bearing dichopore canals are derived in glyptocystitoids (Paul, 1968b; Sprinkle and Wahlman, 1994) and therefore are rejected as homologous to hydrospires in blastoids by the test of congruence.

HOMOLOGY OF PERISTOMIAL AND AMBULACRAL PLATES

General features.—Blastoids, crinoids and many other stemmed echinoderm clades have four types of plates associated with the ambulacra and peristome. Oral plates (OP) form the border of the peristome, primary peristomial cover plates (PPCP) cover the peristome, ambulacral cover plates (ACP) cover the ambulacral tunnel and ambulacral floor plates (AFP) form a platform for the ambulacral tunnel and carry the food groove (Sumrall, 2010) (Fig. 1). These plates are described in detail below.

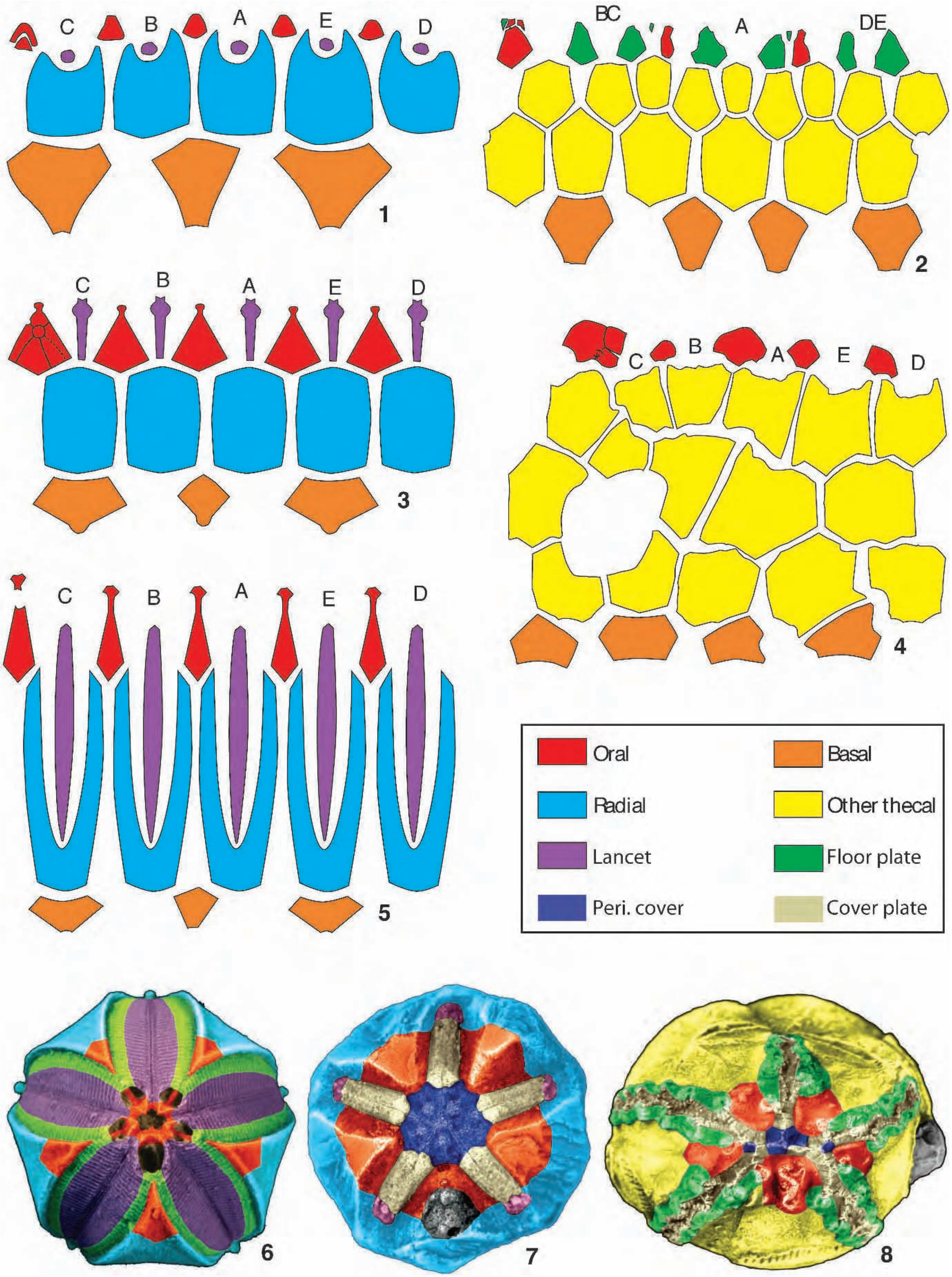
ORAL PLATES

General features.—The term "oral plates" (OP) (sensu Sumrall, 2010) is used here to include interradial plate elements that form the peristomial border, share the food groove proximally along their adjacent sutures, and lack overriding floor plates (Table 1; Fig. 1). Commonly, there are five to seven oral plates, which are typically multiple in the CD interradius in association with the hydropore and or gonopore. In a few clades some of the oral plates are secondarily lost (Sumrall, 2008) (Fig. 2.2, 2.5, 2.6). Homologues include oral plates of most blastozoans, oral plates of some Paleozoic crinoids, and deltoids of blastoids (Sumrall, 2010; Kammer et al., 2011).

Glyptocystitoids.—Glyptocystitoids form the model upon which UEH was developed. The oral plates of this clade include interradial elements that plesiomorphically form the edge of the peristomial border, are interradially positioned and bear the proximal food grooves along their sutures without underlying ambulacral floor plates. In this clade, there are seven oral plates that are interradially positioned including three in the CD interray (Fig. 2.1). The peristome typically is bordered by four plates O1, O3, O4, and O6. The broad sutures between O1/O3 and O4/O6 define the projection of the shared ambulacral grooves. Orals O2 and O5 are added later in ontogeny associated with the bifurcation of the lateral ambulacra and therefore are not typically in contact with the peristome (Sumrall and Sprinkle, 1998; Sumrall, 2008). Plate O7 is a small plate of the distal CD interray associated with the hydropore and likewise does not contact the peristome (Fig. 1). These plates can be identified in nearly all other taxa and the O1–O7 numbering system is used throughout.

Hemicosmitoids.—The oral area of hemicosmitoids was recently reviewed by Sumrall (2008) wherein plates O2 and O5 were interpreted as missing via paedomorphic ambulacral reduction (Sumrall and Wray, 2007). In the CD interray, O1 and O6 are small plates, termed wedge plates by Bockelie (1979), bordering the peristome whereas O7 is large, occupying most of the interray (Fig. 2.3). Plates O3 and O4 are large and occupy the interrays on either side of the A ambulacrum and adjacent shared ambulacra. Three small wedge plates (sensu Bockelie, 1979) were interpreted as being the first left secondary floor plates of the shared and A ambulacra (Fig. 2.3). Large paired perradial plates were interpreted as fused ambulacral floor plates or else enlarged floor plates where erect ambulacra mount (Sumrall, 2008). In later taxa such as *Caryocrinites*, the summit is covered by a tegmen-like covering of thick heavy plates that may in part be primary peristomial cover plates and ambulacral cover plates. No oral plates are seen externally but may exist internally.

Blastoids.—The oral plates of blastoids are the deltoid plates (Sumrall, 2010). These plates, though unusual for oral plates, fit all three of the plesiomorphic criteria, forming the peristomial border, being multiple only in the CD interray, and bearing the proximal most ambulacral food grooves without underlying floor plates (Figs. 2.6, 3.1, 3.6, 4.10). They are arranged into a pseudo-five-fold arrangement (sensu Sumrall and Wray, 2007) completely lacking shared food grooves. As the result, O2 and O5 are in contact with the peristomial opening (Fig. 2.6). Often the peristomial opening is pentagonal and slightly wider than high reflecting a remnant of the plesiomorphic 2-1-2 symmetry (Fig. 3.1). In most taxa oral plates are partly internal leading to many misconceptions about their true nature. In *Pentremites*, for example, the most proximal portions of the deltoids are the deltoid lips that form the peristomial opening. Distally, the deltoids extend internally forming an internal septum in the spiracles, underneath the most proximal side plates and emerge again distally as the deltoid body forming part of the thecal wall. Thin sections of blastoid summits confirm that the deltoid lips connect to the deltoid bodies and that these structures are in optical continuity throughout (Fig. 7.1). In some cases such as *Troosticrinus* the deltoid is extremely small, whereas in other cases such as *Nucleocrinus* the deltoid plates can comprise the majority of the theca wall. On the CD interray of the theca, multiple deltoids occur as in other derived blastozoans, but the presence of the anal opening within the oral complex makes it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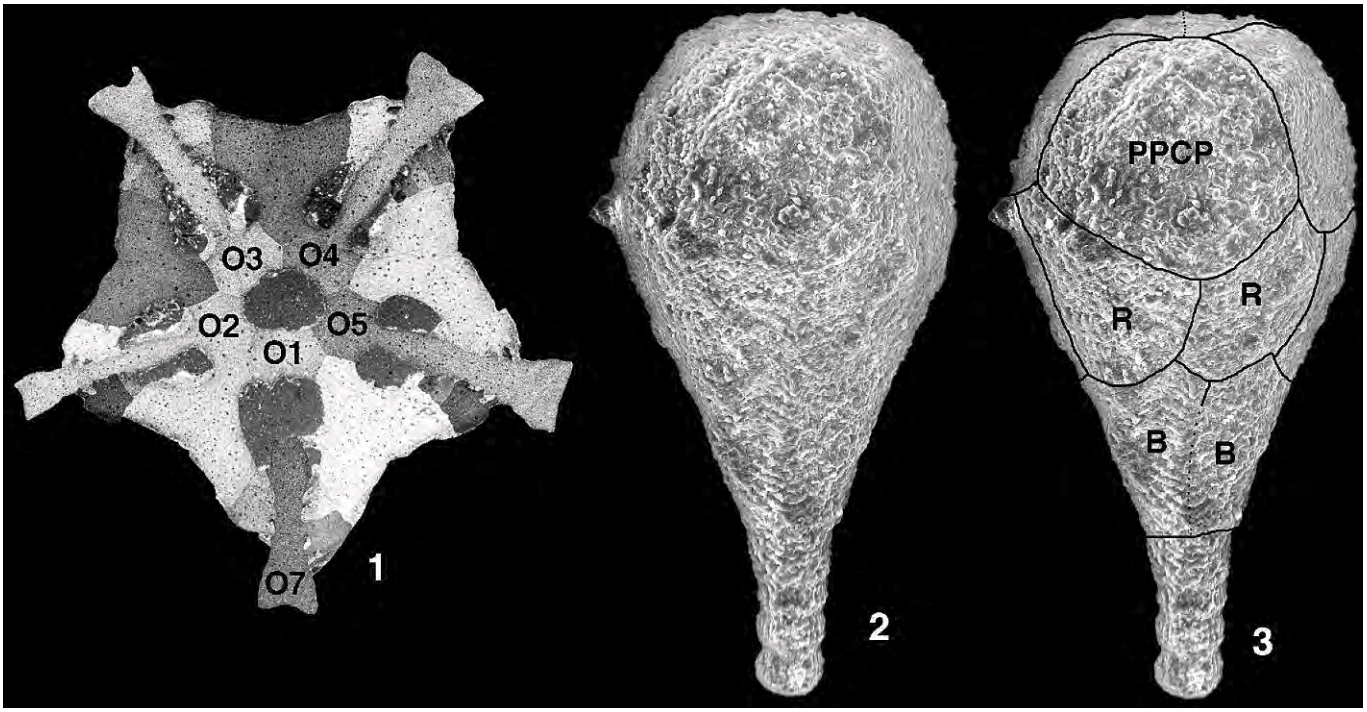

FIGURE 7—*1*, thin section through the summit of the blastoid *Pentremites* sp., CMC IP 67722, with oral plates labeled. Note that the orals (deltoids) are in optical continuity proximally to distally, ×5; *2, 3,* the larval blastoid *Passalocrinus*, CMC IP 67723, showing plate relationships, ×170.

difficult to interpret plate homology. It seems reasonable to assume that the hypodeltoid is O7 because this large plate does not form the edge of the mouth frame in other blastozoans, but is associated with the gonopore in some (Breimer and Macurda, 1972). Cryptodeltoids may have resulted from neomorphism, or potentially descend from proximal side plates incorporated into the anal side deltoid complex. Whether the epideltoid is O1 or O6 is not clear, but a very similar arrangement of plates is seen in coronoids (see below). Here we interpret the epideltoid as O1 (Figs. 2.6, 7.1).

Coronoids.—The deltoid plates of coronoids are homologous with the orals of other stemmed echinoderms. As in blastoids, coronoid oral plates are arranged with pseudo five-fold symmetry lacking shared ambulacra. Here, however, the peristomial opening is large and circular and the contact between adjacent oral plates is relatively elongate (Fig. 4.11). The CD interray is composed of two plates that include either O1 or O6 along the peristomial border and O7 distally (Fig. 2.5). The hydropore is positioned between these plates as a slit and the anus is positioned between O7 and two radial plates.

Lysocystites.—The oral plating of *Lysocystites* is less clear than for other taxa under discussion. There are five obvious oral areas, each bearing one large plate except for the CD interray. Here, plate sutures bound the hydropore and/or gonopore as well as the periproct. After studying several specimens, Sprinkle (1973) concluded that *Lysocystites* has a variable number of CD oral plates. Although this seems unlikely, poor preservation contributes to the difficulty in reconciling the oral plates of this taxon with those of other blastozoans.

PRIMARY PERISTOMIAL COVER PLATES

General features.—Primary peristomial cover plates (PPCP) are plates that cover the peristome but do not demarcate its periphery as do oral plates (Fig. 1). These plates are interradially positioned at the bifurcation points of the ambulacra, and form the cover over the peristome. Here PPCPs are designated 1–5 in correspondence with the oral plate with which they articulate (Fig. 1). Primary peristomial cover plates are the earliest plates of the ambulacral system developed in edrioasteroids (Bell, 1976b). Similarly, they are the first plates in the cover plate series to form in blastoids (Fig. 7.2, 7.3) and are identifiable in nearly all derived blastozoans (Sumrall, 2010). In taxa with a well-developed 2-1-2 symmetry, PPCPs mark the bifurcation points of the A, shared BC and DE ambulacra at the junction of PPCPs 1, 3, and 4 and the bifurcation points of the shared ambulacra at PPCPs 2 and 5 (Fig. 1). In taxa with pseudo-five-fold symmetry, the PPCPs often cover the peristomial opening, suturing in a 2-1-2 pattern (Brett et al., 1983) (Fig. 2.5). Even here PPCPs 2 and 5 do not meet, being separated by PPCPs 1, 3, and 4 (Fig. 2.5). Homologues for these plates (Table 1) include the summit plates of blastoids, the oral plates of several blastozoan clades, the primary orals and lateral bifurcation plates of edrioasteroids, and oral plates in some crinoids such as the microcrinoids.

Glyptocystitoids.—Primary peristomial cover plates in glyptocystitoids tend to be poorly differentiated from other plates in the cover plate series (Fig. 1). Three (PPCPs 1, 3, and 4) are positioned directly over the peristome marking the splitting points of the A and shared ambulacra. The other two (PPCPs 2 and 5) are laterally positioned at the ends of the shared ambulacra marking the bifurcation points of the distal B–E ambulacra.

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FIGURE 6—Plate diagrams and false color specimens illustrating thecal plates using the universal elemental homology scheme (compare to *Fig. 5*). *1*, the coronoid *Cupulocorona*; *2*, the hemicosmitid *Hemicosmites*; *3*, *Lysocystites*; *4*, the glyptocystitoid *Cheirocystis*; *5*, the blastoid *Hydroblastus*; *6*, the blastoid *Pentremites tulipiformis*; *7*, the coronoid *Stephanocrinus angulatus*; *8*, the glyptocystitoid *Lepadocystis moorei*. A–E are the ambulacral designations in Carpenter's system.

Hemicosmitoids.—Primary peristomial cover plates in hemicosmitoids are poorly known. In plesiomorphic taxa such as *Hemicosmites*, three (PPCPs 1, 3, and 4) meet over the peristome in a manner consistent with that of the three proximal plates in glyptocystitoids (Bockelie, 1979). Because the lateral bifurcation of the shared ambulacra fails to develop, the lateral PPCPs 2 and 5 also fail to develop (Sumrall, 2008). In later taxa such as *Caryocrinites*, the summit is covered by a tegmen of thick heavy plates that may in part be PPCPs and ambulacral cover plates. The homology here is not certain at this time.

Blastoids.—Primary peristomial cover plates in blastoids show several different expressions that are highly variable even within genera. The simplest expression is enlarged PPCPs with other proximal cover plates lost as in *Nucleocrinus* (Fig. 3.10). Here the PPCPs articulate with the deltoid plates and form a distinct, but greatly reduced 2-1-2 symmetry over the mouth in which PPCPs 1, 3, and 4 meet over the peristome and PPCPs 2 and 5 articulate slightly distally to the peristome. Other taxa such as *Globoblastus* are less derived and suggest the plesiomorphic condition. The PPCPs are only slightly enlarged and are placed at the bifurcation points of the ambulacra (Fig. 3.3). Secondary peristomial plates are positioned along greatly reduced shared ambulacra showing pseudo five-fold symmetry (Sumrall and Wray, 2007) and ambulacral cover plates begin just distally to the PPCPs. Similar to this is a condition found in some species of *Pentremites* in which all peristomial covering plates and proximal ambulacral cover plates form a conical structure of spine-shaped plates forming an oral cone (Beaver et al., 2000). In this condition, the PPCPs are present but undifferentiated and unrecognizable among the myriad of small cover plates (Fig. 3.2).

Coronoids.—Primary peristomial cover plates in coronoids are similar to the condition in *Nucleocrinus*. The PPCPs articulate with the oral plates and form a distinct, but greatly reduced 2-1-2 symmetry over the mouth in which the PPCPs 1, 3, and 4 meet over the peristome and the PPCPs 2 and 5 articulate slightly distally to the peristome (Brett et al., 1983) (Figs. 2.5, 4.1).

Lysocystites.—Primary peristomial cover plates in *Lysocystites* are unknown at this time.

AMBULACRAL PLATES

General features.—In most blastozoan echinoderms the ambulacral system is composed of three different elements: floor plates that form the food groove, cover plates that cover the food groove and brachioles. In this discussion we will examine ambulacral floor plates (AFP) and cover plates (ACP). In all cases the brachioles are similar in construction (Sprinkle, 1973) and we offer no new insights.

Ambulacral floor plates.—Ambulacral floor plates (AFP) are radial or perradial plate series forming the food groove and brachiole facets (Sumrall, 2008, 2010). Although these plates can be uniserial, biserial, or double biserial, all of the taxa detailed in this discussion have double biserial floor plates bearing primary and secondary floor plates bearing brachiole facets between them. In blastozoans these plates are fitted with brachiole facets that can be borne on single plates, borne between undifferentiated adjacent plates, or borne on pairs of primary and secondary plates (Sumrall, 1997). Furthermore in different clades, floor plates can be epithecal lying atop plates of the theca as in blastoids and some glyptocystitoids, incorporated into the theca where they form portions of the thecal wall itself as in some glyptocystitoids, or erect where they are free of the theca as in hemicosmitoids and coronoids (Sprinkle, 1975; Brett et al., 1983; Sumrall, 1997, 2008, 2010). In some cases such as *Eumorphocystis* and *Coronocystis* the floor plates transition between these expressions proximally to distally (Parsley, 1982; Sumrall, 2010).

In the vast majority of stemmed echinoderm clades, the floor plate series begins on the left if viewed proximally to distally (Sumrall, 2008) (Figs. 1, 2.1–2.4). This has not been directly observed in blastoids or coronoids because of difficulty in seeing these small plate relationships. Furthermore, in many taxa the first brachiole facet is borne across the suture between the oral plate and these first left floor plates (Fig. 2.1–2.3).

Ambulacral cover plates.—Ambulacral cover plates (ACP) cover the ambulacral tunnel. In forms with a well-developed 2-1-2 symmetry separate cover plate series between the PPCPs form shared cover plates (Bell, 1976a, 1976b). In most blastozoans the proximal cover plates lie on oral plates because the food groove lies along the sutures of adjacent oral plates. Distally in most blastozoan taxa, ACPs lie atop for food groove on the floor plates. Often the food groove branches such that cover plates extend along the side branch to the brachiole facet on the floor plate(s) and continue up the brachioles. In rare cases, food grooves lie atop the thecal plating without underlying floor plates as in many blastoids (Fig. 3.9). Here cover plates over these food grooves are still thought to be homologous. A similar situation is thought to exist in some diploporans such as *Glyptosphaerites*.

Brachioles.—Brachioles are generally thin long feeding appendages that arise from the ambulacral floor plates that carry a small food groove (Sprinkle, 1973). They are constructed of two plate types: brachiolar plates, analogous to ambulacral floor plates and cover plates, covering the food groove.

Glyptocystitoids.—The ambulacral system of glyptocystitoids is similar to that of most blastozoans. Ambulacral floor plates are arranged into a double biseries with primary and secondary floor plates forming brachiole facets (Fig. 1). In glyptocystitoids, the AFPs can either form the thecal wall, lie epithecally upon the thecal plates, or in some combination thereof. Generally the first floor plates are added to the left side of each ambulacrum including the shared ambulacra (Sumrall, 2008). The main food groove runs along the perradial suture of the floor plates. A smaller side food groove extends from the main food grove along the common suture between primary and secondary floor plates to the brachiole facet (Fig. 6.8). In some taxa distal branching of the ambulacra occurs.

Cover plates are present on the shared ambulacra as well as the proximal portions of the food groves upon the oral plates (Fig. 1). Ambulacral cover plates continue down the main food groove of the ambulacra and onto the side food grooves to the brachiole facets (Fig. 6.8). These cover plates are generally biserial, but in some cases they may be in a double biseries.

The brachioles are typical and generally unmodified except in a few cases where enlarged brachioles have evolved as in pleurocystitids and some derived callocystitids (Koch and Strimple, 1968; Parsley, 1970; Paul, 1984).

Hemicosmitoids.—The ambulacra of hemicosmitoids are highly modified and include both incorporated floor plates and erect ambulacra bearing brachioles (Sprinkle, 1975; Bockelie, 1979; Sumrall, 2008). In *Hemicosmites*, erect ambulacra are mounted on paired fused or enlarged floor plates that lie perradially at the tips of each of the three ambulacra (Fig. 2.3). A smaller facet on the left side of each of these plates mounted at the junction of an oral plate and a secondary floor plate (three of the wedge plates of Bockelie [1979]) represent the first brachiole of the shared ambulacra and the A ambulacrum. The floor plates of the distal ambulacrum are arranged into a double biseries with primary and secondary floor plates with brachioles mounted between (Sprinkle, 1975). These erect ambulacra form a well-developed filtration fan.

The cover plates are quite variable. In *Hemicosmites* the proximal ambulacra are covered by simple biserial cover plates and are similar to other blastozoans (Bockelie, 1979). In *Hemicosmites* the typical biserial cover plates extend up the erect ambulacra covering the food groove. In *Caryocrinites* the proximal ambulacral cover plates are greatly thickened and form a tegmen that covers the oral surface. The exact homologies of these plates have yet to be established. In the erect ambulacra, cover plates are modified into thick T-shaped plates over the food groove (Sprinkle, 1975). In both genera, brachioles are mounted at the junction between primary and secondary floor plates in the erect ambulacra.

Blastoids.—In blastoids the ambulacra are recumbent epithecally and are highly derived. The floor plates (termed side plates in blastoid nomenclature) form a double biseries in which brachiole facets are shared across sutures between primary and secondary floor plates (Beaver et al., 1967; Sprinkle, 1973). In many taxa, proximally they cover portions of the oral plates between the deltoid lips and the deltoid bodies (Fig. 3.1, 3.4). Floor plates in early forms lie directly upon the lancet plates so that the latter are not visible from the outside of the theca (Fig. 4.12). The main food groove lies along the suture between right and left floor plates. Side food grooves lie along the sutures between pair of floor plates on each side of the brachiole and end distally in a small brachiole facet (Fig. 4.12). In more derived forms such as *Pentremites* the right and left floor plates are no longer in contact along the ambulacral midline exposing the lancet plate (Fig. 3.1, 3.4) (Waters and Horowitz, 1993). Here, the main food groove and proximal side food grooves lie atop the lancet without underlying floor plates. In such forms the floor plates "unzip" ontogenetically and the food groove transitions from lying on floor plate sutures to lying on thecal plates.

Ambulacral cover plates cover all of the food grooves. There are extremely short shared ambulacra in some taxa seen by the presence of shared cover plates (Fig. 3.3). In other taxa such as *Pentremites* there may be extensive cover plates on the most proximal portion of the ambulacra where the food groove lies along the suture between oral plates (Fig. 3.2, 3.7). In the distal ambulacra the main food groove and side food grooves are covered by very small biserial cover plates (Fig. 3.7). In forms where the lancet is concealed, the cover plates all lie atop floor plates. In forms with an exposed lancet, the cover plates lie directly atop the food grooves on the lancet. There is no break in morphology where the side food grooves transition from lancet plate to floor plate. In blastoids the brachioles are long, thin and numerous but otherwise typical for blastozoans.

Coronoids.—The ambulacra of coronoids are in the form of short ambulacra along the oral plates with erect distal ambulacra bearing brachioles (Brett et al., 1983). The proximal food groove extends along the sutures between adjacent floor plates and onto the lancet plate (Figs. 2.5, 4.1). Here the distal floor plates are attached to a facet forming an erect ambulacrum. In many cases a second smaller food groove is present on the left side of the main food groove for the attachment of the most proximal brachiole (Brett et al., 1983, fig. 3k). The distal ambulacrum is plated with a double biseries of AFPs from which brachioles arise at the suture of each pair of primary and secondary floor plates. Where known, these ambulacra are coiled like a closed fist (Fig. 4.1, 4.2).

Coronoids lack shared ambulacra so there are no shared cover plates. The proximal portion of the distal ambulacra has a single elongate cover plate pair covering the food groove (Brett et al., 1983) (Figs. 2.5, 4.1). Cover plates of the distal erect ambulacra are presently unknown. The brachioles are thin, curled, and biserial and otherwise unremarkable.

Lysocystites.—No floor plates and cover plates are known for *Lysocystites*.

DISCUSSION

One way to test hypotheses of echinoderm plate homology is to examine the developmental timing, and ultimate fate of plates within different lineages. Recently, Sevastopulo (2005) presented a convincing argument that *Passalocrinus* (Fig. 7.2, 7.3) is a larval blastoid, rather than a microcrinoid, based on its thecal plating and the inherent asymmetry in the blastoid basal circlet. He also concluded that the oral plates in larval blastoids were formed then later resorbed, and that blastoid deltoids and lancet plates develop later in ontogeny.

We believe that comparison of *Passalocrinus* to cystidean stage modern crinoid larvae helps unravel the homology of the oral plates and deltoid plates of blastoids. In *Passalocrinus* and embryonic crinoids the oral plates cover the peristome and are interpreted as homologous with the primary peristomial cover plates (Fig. 7.2, 7.3). At this stage of development the oral plates (deltoids in blastoid terminology) are either not yet developed, or small and not exposed on the exterior of the theca. Later expression of the deltoids forms the peristomial border and bears the most proximal ambulacra on their sutures.

The PPCPs were inferred to be later resorbed by Sevastopulo (2005) followed by the development of the deltoid plates. Here we interpret these observations differently. Numerous specimens of *Passalocrinus* were collected along with full later ontogenies of several species of *Pentremites*. Small specimens of *Pentremites* $\sim$0.5–1.5 mm high uniformly have basals and radials but lack any evidence of the oral surface whereas slightly larger specimens were nearly always fully articulated (Smith, 1906). We suggest that we are seeing a taphonomic window early in development during which loose suturing of the oral plates, ambulacral system, and lancet plates preclude preservation. Furthermore, mature blastoids are occasionally preserved with the PPCP intact (Fig. 3.2, 3.3, 3.5, 3.8, 3.10) suggesting that these plates are taphonomically removed from small specimens rather than resorbed.

Although universal elemental homology works well with stemmed echinoderms, work needs to continue to understand homology between stemmed forms and Eleutherozoa. Problems in terminology abound and indeed, there may be little in the way of plate homologues between these large echinoderm groups. Ambulacral floor plates in particular are complex because of the presence of two sets of ambulacrals and adambulacrals in sea stars whereas plesiomorphically stemmed echinoderms have a single series.

Recent discoveries may help shed light on this issue however. The edrioasteroid grade echinoderm *Kailidiscus* and the closely related taxon *Walcottidiscus* bear four rows of floor plates as well as integrated interradial plates that that are topologically interradially positioned (Zhao et al., 2010). These interradial elements are in the same series as the outer floor plates and if these plates are homologues of oral plates, then the outer floor plates may be homologues of ambulacral floor plates of stemmed forms. If all four rows of floor plates are homologous with ambulacral and adambulacral plates of sea stars then we have a link for understanding floor plate homology across Echinodermata.

PHYLOGENETIC ANALYSIS AND BLASTOID ORIGINS

To confirm the origins of blastoids within this new homology scheme, a phylogenetic analysis was conducted for nine ingroup taxa including three blastoids, two coronoids, *Lysocystites*, *Hemicosmites* and two glyptocystitoids. These taxa represent a clade diagnosed by the presence of double biserial floor plates with brachioles mounted between pairs of primary and secondary cover plates. These taxa were coded for 26 characters that were equally weighted and unordered (Tables 2, 3). Uninformative characters were removed from the analysis. The matrix was polarized using the outgroup criterion using the parablastoid *Eurekablastus* to assign character state polarity.

The matrix was analyzed using the branch and bound search algorithm to assure the complete set of most parsimonious trees

TABLE *2*—Character matrix used in the phylogenetic analysis.

Eurekablastus	01??0110??0???1?0?013?001?
Hemicosmites	00000000??0???0000000?0001
Cheirocrinus	11110010??0???0000011?1100
Lepadocystis	11110010??0???0000021?1100
Pentremites	00001121101111111?022?0011
Koryschisma	00001121101111111??22?0011
Troosticrinus	0???1121111111110102210011
Stephanocrinus	00001121011000110110?10020
Cupulocrinus	000?1121011000110110?10020

was recovered. Nodal support was examined through bootstrap analysis of 1000 pseudoreplicate runs of the matrix. Bremer support was also assigned for each node.

Results of the phylogenetic analysis were largely similar to those recovered by Donovan and Paul (1985) and Paul (1988) where blastoids, coronoids and *Lysocystites* form a clade. Our analysis and that of Paul (1988) differ from the results of Donovan and Paul (1985) by recovering coronoids closer to blastoids, rather than coronoids as sister to *Lysocystites* plus blastoids (Fig. 8). The analysis recovered a single most parsimonious tree of 36 steps, CI=0.86; RI=0.90; RC=0.77. This tree is shown in Figure 7 with bootstrap and Bremer support as noted. The structure of the tree is unsurprising with the three blastoids forming a clade, the coronoids forming a clade, and blastoids forming the sister taxon to coronoids. *Lysocystites* branched as sister taxon to coronoids plus blastoids. Glyptocystitoids formed a clade that was the sister taxon of *Hemicosmites*, and this clade was the sister taxon to blastoids plus coronoids plus *Lysocystites*.

The analysis strongly supports the close phylogenetic relationship among blastoids coronoids and *Lysocystites*. This relationship has a high bootstrap proportion and Bremer support. Most of the features supporting this relationship concern the plating of the theca that bears the same elements in the same position in all taxa. These taxa, however, differ greatly in terms of the respiratory structures and feeding appendages.

The support for blastoid monophyly is relatively weak in this analysis mainly because of limited taxon sampling and unusual morphological features of the early blastoid *Troosticrinus* that bears several features of coronoids that other blastoids do not (i.e., sutures between adjacent radials forming a coronal process, the lack of a deltoid body on the oral plates, and the presence of coronal canals). The position of *Lysocystites* as sister to blastoids and coronoids is also weakly supported. The position shown here is supported unequivocally by the triangular base of the theca. Other features such as the presence of an arm facet on the lancet and the elongation of the lancet serve to unite *Lysocystites* with coronoids and blastoids respectively.

EVOLUTIONARY SCENARIO

The origin of Blastoidea is intimately nested within the clade containing coronoids and *Lysocystites* (Sprinkle, 1980b; Brett et al., 1983; Donovan and Paul, 1985; Bodenbender and Fisher, 2001). Although Fay (1978) classified coronoids as an order of inadunate crinoids, they are now firmly established as blastozoans. All of the taxa under consideration here have similarities in the construction of the ambulacra bearing 1) double biserial floor plates that 2) have brachioles mounted between floor plate pairs as synapomorphies for this clade (Sumrall, 1997). Glyptocystitoids and hemicosmitoids independently evolved, generating a series of clade-specific synapomorphies in terms of thecal plating, ambulacral construction and other features that serve to unite these individual clades.

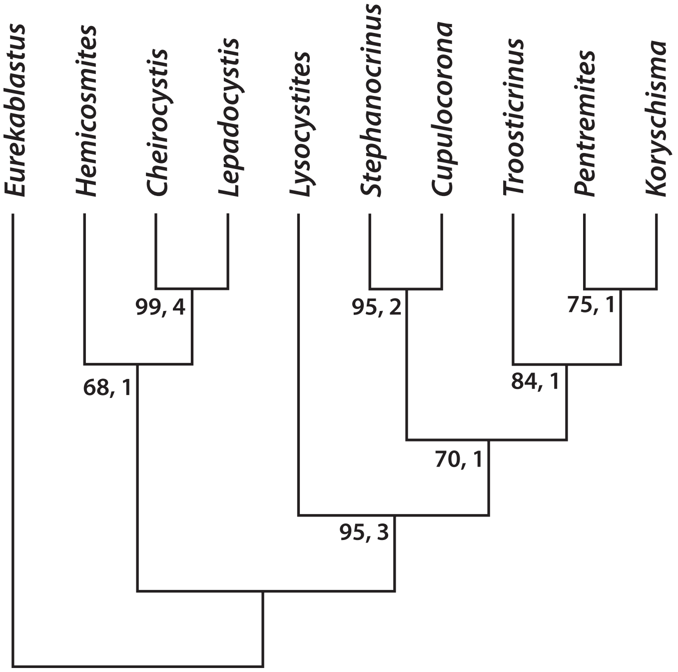

FIGURE *8*—Phylogenetic relationships among derived blastozoans. Numbers at nodes represent bootstrap proportions and decay index for each node.

Regardless of optimization, evolution of erect ambulacra, pseudo five-fold symmetry, small stem facet, and the standardization of the plating of the theca into the stereotypical blastoid model form synapomorphies for the clade including *Lysocystites*, coronoids and blastoids. Furthermore, the presence of coronal processes and coronal canals optimizes as plesiomorphic for blastoids. Synapomorphies for true blastoids include only the presence of hydrospires, the loss of the arm facet, and the recumbent ambulacra that lie atop the lancet plate. It is interesting to note that with the exception of the recumbent nature of the ambulacrum, blastoid ambulacra are plated identically to those of coronoids.

CONCLUSION

Universal elemental homology is a powerful tool that places plate homology into a testable hypothesis of homology. These homology models provide high-resolution homology identification across many lineages of stemmed echinoderms that allow high precision in character description. Thus, UEH avoids many vague characters such as counting the number of plates in circlets or the number of ambulacra present that can confound character construction. Furthermore, it provides mechanisms for rejection of homology hypotheses using the criteria of Patterson.

Universal elemental homology provides a common linguistic framework for the comparison of anatomy across stemmed echinoderms. Although it would be ideal to have a common lexicon, we readily admit that this would cause confusion within clades where a rigid stereotypy of construction and plate naming is well entrenched into the literature such as that of the Blastoidea. We recommend, however, the use of this consistent terminology across clades to facilitate meaning and eliminate confusion.

In this study case, universal elemental homology confirms that blastoids, coronoids and *Lysocystites* are closely related taxa and that hypothesized transformations and evolutionary novelties in homologous elements can be tested in a rigorous, phylogenetic framework. It allows a high degree of precision for the generation of morphologic characters that are placed into the same nomenclature regardless of clade.

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APPENDIX. Characters used in the phylogenetic analysis to generate the data matrix Table 2.

1. Stem proximally wide (0), or narrow (1)
2. Proximal stem homeomorphic (0), or heteromorphic (1)
3. Proximal lumen of stem narrow (0), or large (1)
4. Distal stem with columnals wider than high (0), or higher than wide (1)
5. Stem facet platform not triangular (0), or distinctly triangular (1)
6. Theca globular (0), or bud-shaped (1)
7. Theca with four basals (2 zygous 2 azygous) (0), four basals 1 zygous, three azygous, (1), or three 2 zygous and 1 azygous (2)
8. Blastoid type radials not present (0), or present (1)
9. Radial plates with ambulacral sinus (0), or without (1)
10. Radial plates not raised (0), or raised into coronal processes (1)
11. Lancet plates not present (0), or present (1)
12. Lancet small (0), or elongate (1)
13. Lancet not broadly bordered by radial plate (0), or broadly bordered by radial plate (1)
14. Lancet plates bearing arm facet (0), or covered by floor plates (1)
15. Ambulacra arranged in 2-1-2 symmetry (0), or with pseudo-5 fold symmetry (1)
16. CD peristomial border with O1 and O6 (0), or single oral plate (1)
17. Orals lacking deltoid body (0), or deltoid body present (1)
18. Primary peristomial cover plates form 2-1-2 pattern (0), or separated by shared cover plates (1)
19. Proximal cover plates small (0), or elongate flap (1)
20. Ambulacra floor plates raised into erect arms bearing brachioles (0), forming body wall (1), or recumbent onto theca (2)
21. Endothecal respiratory structures in the form of, cryptorhombs (0), pectinirhombs (1) or hydrospires (2), or cataspires (3)
22. Exothecal respiratory structures in the form of epispires (0), or coronal canals (1)
23. Anus located in CD interray (0), or BC interray (1)
24. Anal opening small (0), or large (1)
25. Anal opening bordered in part by oral plates (0), positioned between oral plates and radial plates (1), or bordered by thecal plates (2)
26. Peristome oval (0), or stellate (1)