

THE ECHINODERM CLASSES STYLOPHORA AND HOMOIOSTELEA: NON CALCICHORDATA

R. L. PARSLEY

Department of Geology, Tulane University, New Orleans, Louisiana, 70118, USA

ABSTRACT—Styphora and Homoiosteia are the largest classes of the subphylum Homalozoa. They have also been placed in the Calcichordata but that position is herein rejected. Styphorans are divided into two orders the Cornuta and Ankyroidea: cornutes have asymmetrical thecae, aulacophores with stylocones and cover plates over the food groove that open widely; ankyroids have essentially bilaterally symmetrical thecae, aulacophores with styloids and in most the cover plates do not open widely. Epispines, cothurnopores, and lamellipores in cornutes are respiratory structures not atypical of early echinoderms and are only superficially similar to chordate gill slits. The superior and inferior faces of cornute and ankyroid thecae and the aulacophores are homologous. There is no evidence that ‘mitrates’ (most ankyroids) are inverted or their aulacophores (calcichordate tail) have been lost and re-evolved.

Homoiosteles are superficially similar to styphorans: the column or stele resembles the aulacophore and the theca in younger genera develop distinct marginal and somatic plate patterns. The earliest homoiosteles are attached by a holdfast, at least in juvenile stages, and this fixation may have imprinted some morphological features on steles of vagile genera. Earliest homoiosteles share significant characters with coeval species of the eocrinoid *Gogia* and it serves as outgroup.

Cladograms for Styphora and Homoiosteia were generated by NONA, a phylogenetic program for personal computers.

INTRODUCTION

HOMALOZOANS ARE the most atypical of the morphologically diverse phylum Echinodermata. They have flattened thecae which are asymmetrical to nearly bilaterally symmetrical. Most homalozoans have long flexible appendages. Homalozoans were recumbent on the sea floor most had limited vagility. There is little evidence that the four classes that comprise this subphylum are closely related. Each class appears to be a clade that evolved from mostly unknown ancestors. At least one class, the Homoiosteia, evolved from sessile stalked ancestors in the Eocrinoidea. The two smaller classes Homosteia (Middle Cambrian) and Ctenoctoidea (Middle Cambrian) will not be discussed further and attention will focus totally on the two larger classes Styphora (Middle Cambrian to Lower Pennsylvanian) and the Homoiosteia (Upper Cambrian to Lower Devonian). The two latter classes have a superficially similar appendage. Proximally it has, with few exceptions, polymerous or tetramerous segments or ‘slip rings’ and distally the appendage is typically di- or trimerous. Ubags (1961) reversed the orientation of the styphoran appendage by demonstrating that it was not a column as

it is in the Homioosteolea, but a feeding structure. Although this orientation is not universally accepted by all echinoderm workers, it is by most, and is herein termed *echinoderm model* or (echinoderm). In cornutes, the basal clade of stylophorans, the large flexible proximal aulacophore enhanced feeding by wagging the distal subvective end with its widely opening cover plates through the water column. (Parsley, 1988). Most cornutes have markedly asymmetrical thecae and were essentially sessile. Ankyroids (=Mitrata plus cornute-like bilaterally symmetrical genera without respiratory pores) are derived from cornutes. Their distal aulacophores commonly have tightly sutured cover plates that apparently did not open widely. In this clade the aulacophore also served as a locomotor structure and propelled the essentially bilaterally symmetrical theca, anal end first, in short bursts along the sea bottom.

Calcichordates.—Similarities between cornutes and ‘protochordates’ have been noted for some years. Gislén (1930) proposed that cornutes were ancestral to cephalochordates. Gregory (1946) commented on the similarity in plate patterns between ostracoderms and carpoids and opined that a remote relationship existed between the two groups. Certainly there is a relationship between homalozoans and early chordates. Both are deuterostomes and both appear in the fossil record (Middle Cambrian) at about the same time.

Jefferies (1967, 1981, 1986, 1990) has developed the concept that homioosteoles and stylophorans are more properly placed in the Chordata, subphylum Calcichordata, and they are ancestral to the craniates (see Gee, 1996, p. 277). In the echinoderm model homologies advocated by Jefferies, cothurnopores as gill slits, lamellapores and peripores as eyes, and anal structures as mouth structures, are superficial similarities and cannot support the calcichordate argument. Jefferies (1981, 1986) calcichordate model orients stylophorans differently and views their method of locomotion differently as well. His views are termed the *calcichordate model* or (calcichordate). Jefferies orients stylophorans with the appendage posterior (as a tail) and the theca (as a head) anteriorly. In cornutes both echinoderm and calcichordate orientations agree that the face with sutural pores, cothurnopores and lamellipores (echinoderm) or gill slits (calcichordate) is the superior or dorsal. In ‘mitrates’ (most ankyroids) Jefferies reverses the thecal faces and the upper (echinoderm) is the lower (calcichordate) face, which rested on the substrate. Inversion is necessary in the calcichordate model because in it the distal aulacophore ossicles in mitrates are dorsal to the notochord. In order to explain the structural similarity of the distal appendage, Jefferies hypothesized that the distal elements of cornutes are lost and re-evolved with similar morphology in the mitrates. Consistent with the calcichordate model is Jefferies interpretation that peripores and lamellipores on the inferior (echinoderm) surface of some early mitrates serve as openings for eye structures.

In the echinoderm model mitrates are not inverted and distal aulacophores of mitrates and cornutes are homologous. Lefebvre and others, (in press), have analyzed both thecal and aulacophore characters of mitrates and cornutes and on basis of morphological similarity established that inversion has not occurred. For a critical discussion of the calcichordate theory from the chordate point of view, Gee (1996) is highly recommended.

SYSTEMATICS

Class STYLOPHORA Gill and Caster, 1960.—Cladistic analysis of homalozoan class Stylophora as calcichordates is well entrenched in the literature (see

Jefferies 1986; Cripps, 1991; Cripps and Daley, 1994). Until recently, however, no cladistic study had been completed on Stylophora as echinoderms based wholly on fossil material (see Peterson, 1995; Parsley, in press).

Approximately 60 stylophoran genera are known, 42 of which are used in this analysis. Those omitted are poorly or incompletely known; many are quite similar to well-known genera. Omission of these genera has little effect on the resultant study.

Character selection.—Morphological characters of Stylophora are well known and are easily obtained from the literature (see Ubags, 1967, 1969, 1979; Caster 1952; Kolata and Guensburg, 1979; Kolata and Jollie, 1982; Parsley, 1991), and the same is true for the calcichordate literature (see Jefferies 1973, 1986; Jefferies and Prokop, 1972; Cripps 1989, 1990, 1991). All morphological attributes, orientation, and terminology are presented here in echinodermal terminology (Ubags, 1967). [Numbers in brackets refer to the character and its arguments in the character set and data matrix (see Appendices).] The following narrative is not comprehensive but is to briefly explain the character set.

Stylophorans have a theca that is commonly flattened and composed of marginal framework plates [3] with superior and inferior surfaces covered by somatic plates [3, 5]. Marginal symmetry varies in the Stylophora [4, 5] from being asymmetrical to evenly bilateral. Marginal plates are regularized in predictable sequences starting adjacent to the aulacophore with the M1, M'1 pair [18] (Figure 1). A reoccurring problem is determining the marginal plate homologies at the distal end of the theca. Various authors have assigned plate identities to distal-most marginals that differ from mine. My assignments are easily read from the character set and data matrix (Appendix 1 and 2). When position of the anal pyramid, septum (internal ridge that presumably underlaid or was adjacent to the gut), and spine articulations are considered, plate assignments of problematic distal marginals are more assured (e.g., *Phyllocystis*, *Peltocystis*, *Anatiferocystis*). The anal pyramid and septum are commonly closely linked with M4 and/or M5 series of marginal plates and their position is useful in identifying these and, when present, more distal marginals.

Order CORNUTA Jaekel, 1901.—Cornutes are generally asymmetrical-boot shaped [4] but the several species of *Phyllocystis* have marginals arranged in a (symmetrical) heart-shaped pattern [5] (Figure 1). An essentially diagonal element, the zygial, formed by extensions of M'1 and M4 or M5 divides the theca into two somatic areas [8, 9]. Presumably the zygial served as a buttress and in part, may have supported the gut. In the right somatic area most cornutes have respiratory pore structures arranged in an arcuate pattern parallel to the right proximal end of the theca [38]. These pores range from simple sutural pores (*Ceratocystis*) [16], to complex sutural pores (pores involving more than two adjacent plates) [16] (e.g., *Phyllocystis crassmarginata*), cothurnopores [36] (e.g., *Cothurnocystis*, *Nevadacystis*, *Phyllocystis blacyi*), and lamellipores [37] (e.g., *Scotiacystis* and *Bohemiacystis*).

Most cornutes have fixed or only slightly movable spines that suture with the marginals. The spinal spine [7] is commonly an extension of M3 or M4, but the digital and glossal spines [13, 14] which are located at the distal margins of the left somatic area [6] are not distinctly part of the marginal series. Several genera, including *Chauvelicystis* and *Prochauvelicystis*, have numerous small spines attached to one or both lateral sides of the marginals [15].

Most cornutes have tessellated somatic surfaces [32, 34]. *Nevadacystis* has stellate superior-surface somatic plates; presumably the genus had epispires in addition to cothurnopores.

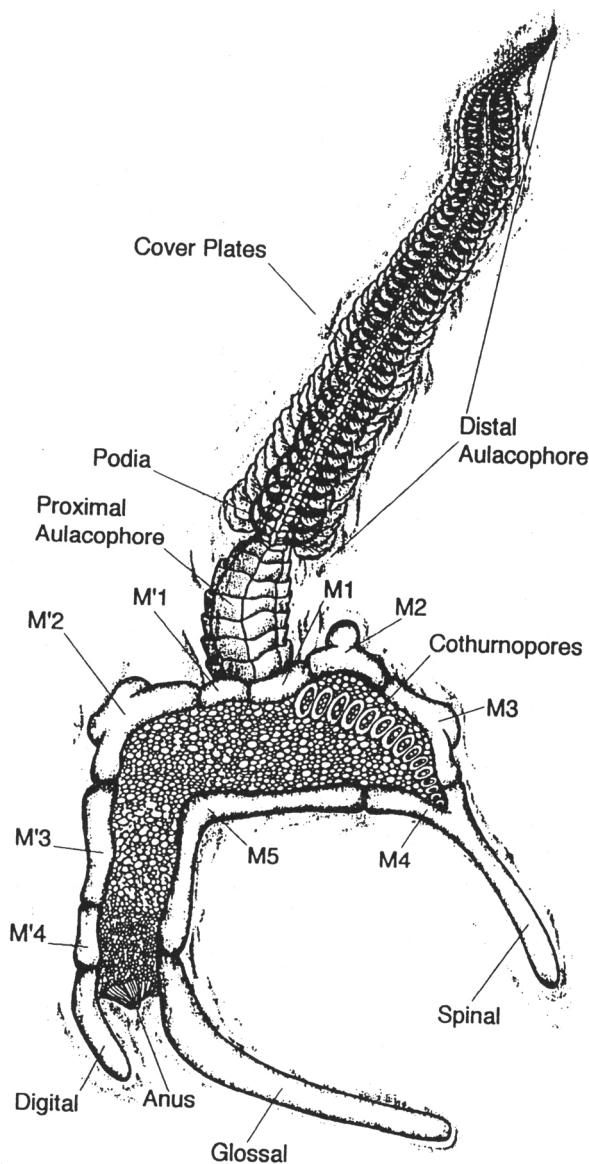


FIGURE 1—*Cothurnocystis*. Superior face of the theca, with aulacophore cover plates open exposing podia and food groove (after Parsley, 1988).

All stylophorans have an aulacophore [1], which is interpreted to be the feeding structure. In cornutes, with the exception of *Ceratocystis*, the proximal aulacophore is tetramerous [40]. Distal to the tetrameres is a stylocone [17] without flanges or excrescences. The stylocone is followed by the uniserial, arm-like, distal aulacophore with tall and loosely articulated cover plates [2]. Under the cover plates impressions of what appears to be the water vascular system are commonly found. They are on the superior surface of the distal aulacophore ossicles—a central axial groove with lateral ampullae pits and grooves connecting the pits to the axial groove.

Order ANKYROIDA Parsley, in press.—A second group, the Ankyroidea (Greek, *Ankyra*—anchor, in reference to the styloid), has been defined by Parsley (in press). It includes genera commonly placed in the Mitrata plus a number of genera with symmetrically or near symmetrically [41] arranged marginals [5] and with a zygal where the distal element is *not* part of the marginal plate series (Figure 2). It is a somatic plate [10]. This element is homologous with the central somatic (CS) plate on the inferior surface and present in many genera. Ankyroids range from having seven pairs (e.g., *Amygdalotheca*), to as few as a single pair (e.g., *Jaekelocarpus* and *Anatiferocystis*) of symmetrically arranged marginals [18]. Some early ankyroids (e.g., *Hanusia*, *Reticulocarpus*, and *Prokopocystis*) have a dorsal bar made of interconnecting extensions of M4 and M'4.

Apparently, shortening by loss of distal pairs [18] is the rule. The development of paired articulated spines at the distal-lateral margins is coupled with shortening [19]. In all cases paired spines articulate with M4/M'4 at the distal end of the theca and the spines are interpreted to be homologous with M5/M'5 (Kirk, 1911). There is strong possibility that this relationship is also true in genera with only one spine [20] (e.g., *Diamphidiocystis*, *Lagynocystis*, and *Peltocystis*), and may also hold in genera where extreme thecal shorting has taken place (e.g., *Anatiferocystis* and *Jaekelocarpus*). A small thecal plate (M4? series) provides the base and articulation for the spine in these latter cases. The single articulating spine condition may not be linked to the loss of a paired spine in all cases.

In most ankyroids a ridge, the septum, is present on the interior of the inferior surface: it is the probable supporting ridge for the gut. The normal course is across M'1, CS, and M4 [12]. However, in some genera with one spine the normal course is M'1–M4 [11] (e.g., *Anatiferocystis*(?) and *Jaekelocarpus*(?), and *Peltocystis*). In these genera the central somatic (CS) is omitted and there is a subanal plate (SA) [29] (Figure 3). *Chinianocarpus* is similar to *Peltocystis* in character regarding septum and subanal plate, but it does not have an articulating spine. *Diamphidiocystis* and *Lagynocystis* have one spine and are exceptions in that they don't have a subanal plate and the septum crosses M'1, and CS, plates.

Some ankyroid genera have a transversely placed azygous marginal plate at the distal end of the theca ("closed" theca); otherwise, the distal end is bounded by (inferior surface) somatic plates [39]. In some genera these distal somatics are regularized [22, 23]. The extension of M'1 across the inferior surface shortens in most more advanced ankyroids and is essentially equalized in size with M1; *Peltocystis*, *Mitrocystites*, and *Anatiferocystis* are exceptions [35].

Many primitive ankyroids have tessellate somatic surfaces similar to cornutes. Secondarily, distally overlapping platelets evolved on the superior surfaces of some genera (e.g., *Anomalocystites* and *Lagnocystis*), and most advanced genera have regularized superior [34] and inferior [32, 42] somatic plate sequences.

More advanced ankyroids have a conservative inferior somatic plate pattern. The central somatic (CS), anomalocystitid (A), and distal somatic (DS) plates commonly are found in many advanced genera [32]. In genera with paired spines, five or fewer plates of somatic origin form the inferior distal margin [23].

Somatic plates on the superior surface are more variable. Primitive ankyroids commonly have paired adaulacophoral plates, some with a slit-like hydropore [30]. More advanced genera may have a large somatic (MA) plate partly intercalated but not reaching the aulacophore margin and genera most advanced have three adaulacophoral plates [33]. Some genera in the upper branches of the cladogram have an axial central somatic plate,

the placocystid plate, [25] at approximately thecal mid-length. Somatic plates on the superior surface are generally arranged in arcuate patterns and the distal margin is formed by regularized somatics [22] (Figure 4). Some genera also have a dorsal bar or transverse connection between M4 and M'4 on the superior surface [21] (e.g., *Reticulocarpus*, *Prokopicystis* and *Hanusia*).

Respiratory pore structures are absent in ankyroids and those reported in *Ruticulocarpus* (Jefferies and Prokop, 1972) and *Prokopicystis* (Cripps 1989) are misinterpretations of missing somatic plates on the superior surfaces of those genera.

Most cornutes have a rounded anal pyramid, but in ankyroids it tends to become a linear value (platelets against a larger plate or line of plates; e.g., *Lagynocystis*, *Enoploura*), or it is lost all together (e.g., *Anomalocystites*). Genera with anal plates or flaps do not have any sort of valvular structure of small platelets [31].

Some rather primitive ankyroids (mitrocystitids) have one or two pairs of pores on the inferior surface—peripores and lateripores. Their function is not clearly understood. Parsley, 1994 suggested they might be multiple gonopores. These apomorphic structures evolved in early ankyroids and were subsequently lost. Vestigial pores can be seen in some specimens of *Mitrocystella* [26, 27] (Parsley, 1994).

Two genera, *Lagynocystis* and *Jaekelocarpus*, possess ctenoid organs. These thin folded sheets of stereom are of unknown function. Because of their proximity to the aulacophore in the proximal end of the theca they may have had respiratory and/or food sorting functions [28].

The aulacophore in ankyroids is similar to that in cornutes except that the stylocone is a styloid [1, 17]: it is the same structure except it has anchoring spines or flanges that project into the substrate. Primitive ankyroids have tall loosely articulated cover plates, as cornutes do, but more advanced genera have shorter and tightly sutured cover plates [2] and thereby are more commonly preserved.

In primitive ankyroids the styloid normally has a single spike projection and the adjacent distal aulacophorals are spiked with nearly equal length projections. More advanced genera commonly have multicupid styloids that range from spike-like projections to large subrounded plowshare-like flanges (Figure 5). In these genera the distal aulacophorals have much shorter projections.

Aulacophore length is commonly about 1.5 times the length of the theca; in some genera they are abnormally long (e.g., *Lagynocystis*), or abnormally short (e.g., *Jaekelocarpus*) [24]. Only *Lagynocystis* among ankyroids lacks a tetramerous proximal aulacophore; it is polymorous and resembles that of *Ceratocystis*.

Discussion.—Evolutionary taxonomists recognize at least twelve stylophoran families that collectively contain approximately 55 genera. Some groupings of genera on the consensus tree conform to traditional (evolutionary taxonomy) families. With the exception of recognizing two orders, Cornuta and Ankyroidea, the classification herein is rankless.

Cornuta Jaekel, 1901, is retained as emended by Ubags, 1967. The order *Mitrata* Jaekel, 1918 and emended by Ubags, 1967 is not retained. Some genera previously placed in the *Cornuta* (see Cripps, 1991; e.g., *Amygdalotheca*, *Nanocarpus*, *Hanusia*, *Beryllia*, *Domfrontia*?, *Milonicystis*, *Reticulocarpus*, and *Prokopicystis*) fit in neither traditional order. Each of these genera has a zygala and in most genera it is complete. The distal element of the zygala is *not* part of the marginal plate series but is a somatic plate and is homologous with the central somatic (CS) plate.

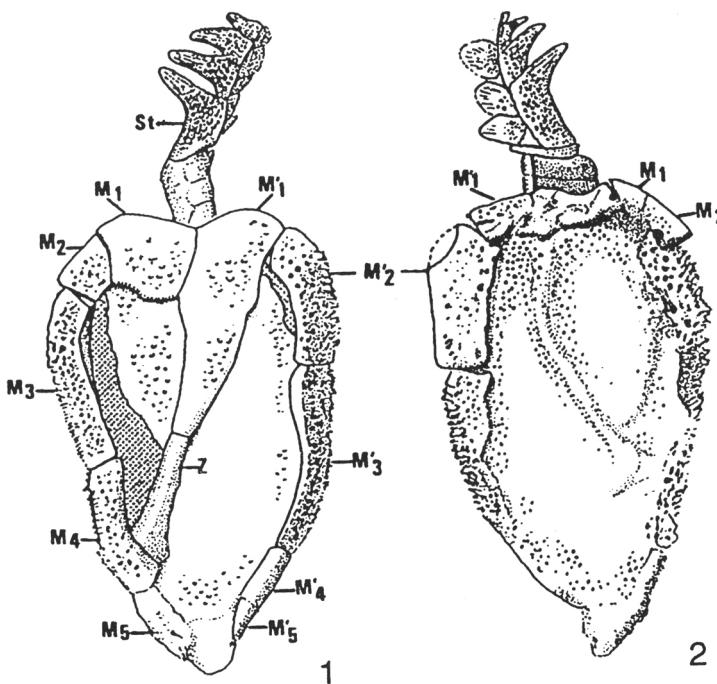


FIGURE 2—*Nanocarpus*; a cornute-like ankyroid. The z plate is not part of the marginal sequence and is homologous with the central somatic plate of most ankyroids. Another cornute-like feature is the loosely articulated cover plates on the aulacophore; 1, inferior face; 2, superior face (after Ubaghs, 1991).

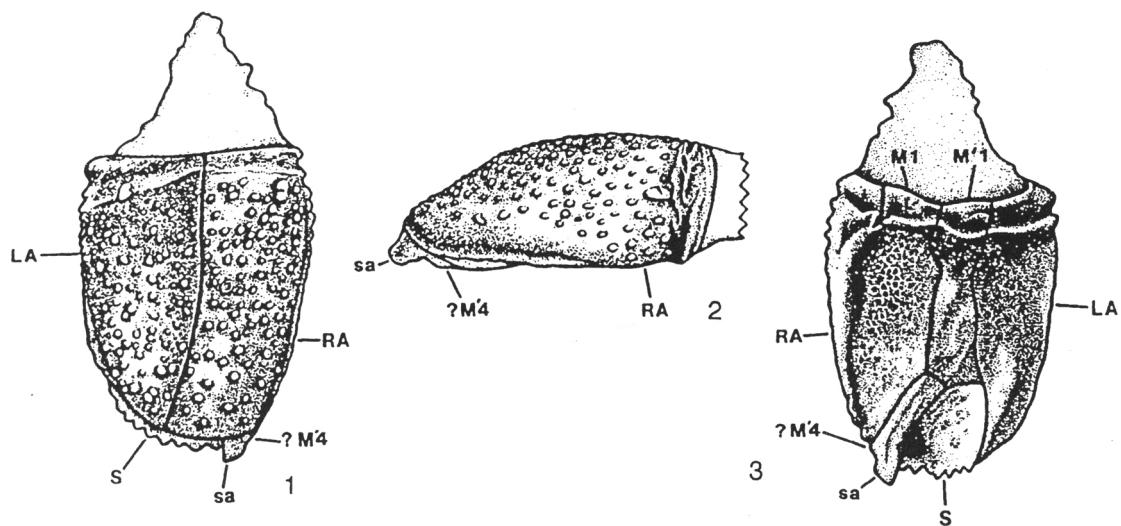


FIGURE 3—*Anatiferocystis*. 1, Superior face; 2, lateral view; 3, inferior face of an ankyroid with greatly reduced plating. S, subanal plate; sa, spine articulation surface (after Parsley, 1991).

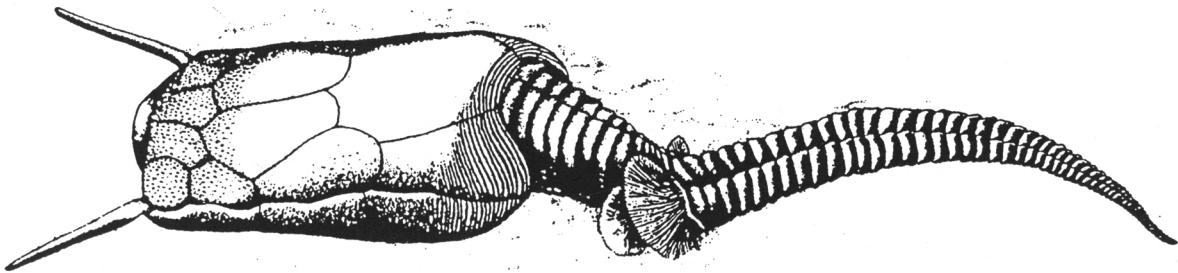


FIGURE 4—Oblique view of *Enoploura*. The animal is anchored by large flange-like styloid blades against a current moving right to left. The distal articulating spines buttressed the animal against the current (after, Parsley, 1988).

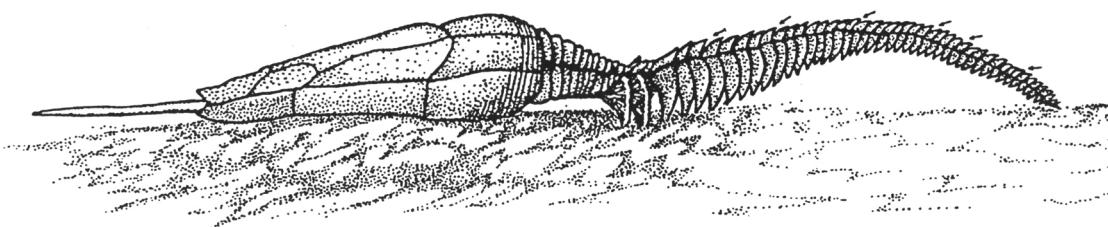


FIGURE 5—Lateral view of *Enoploura*; the arched aulacophore faced into the current. The tightly attached cover plates probably did not open widely (after Parsley, 1988).

These non-conforming genera also have a styloid and not a stylocone. These genera are not cornutes nor can they be included in the Mitrata without considerable revision to the ordinal definition. Parsley (in press) placed the nonconforming genera into the same group as the mitrata and redefined it as the Ankyroidea (see Figure 6).

The strict consensus tree was processed by NONA (Goloboff, 1993) using the command: whennig40; max*, nelsen; tplot. Processing the command resulted in 478,526 trees examined, six trees were found; fit=169 (C=52; Ci=52; R=86) (Figure 6).

Forty two taxa were studied and 42, mostly multistate characters were used. If the character set is expanded to 65 mostly binary characters the results are almost the same. The multistate character set saves considerable space. Comparison of the cladogram to the evolutionary taxonomic groupings shows that the genera clump with a high degree of concurrence to their traditional familial groupings. Cornutes and ankyroids together are clearly a monophyletic clade. Ankyroids probably originated in the late Cambrian from cornutes closely related to *Phyllocystis*. Ubags, 1963, illustrated a phyllocystid similar to *Phyllocystis crassmarginata* from the Upper Cambrian of Nevada. Phyllocystids have a bilateral theca (heart shaped), and a distal theca similar to early ankyroids such as *Nanocarpus* and *Milonicystis*. The earliest ankyroids in the fossil record are from the Montage Noir, Aranigian of France. Shared plesiomorphic structures such as extensions of M'1 across the inferior somatic surface and aulacophores with tall, loosely articulated, overlapping cover plates (in primitive ankyroids) clearly demonstrate that ankyroids are derived from cornutes.

The most vexing problem in the phylogenetic study of stylophorans is the choice of outgroup. In the echinoderm model there are no clear cut, closely related, candidates (i.e., non-stylophoran echinoderms) that share enough meaningful characters. Therefore, the cladogram is based on the earliest genus *Ceratocystis*.

All characters are clearly echinodermal and given the apomorphic nature of many, the Stylophora must be considered well within the echinoderm ingroup; they are not a basal or an early offshoot clade. A recent cladistic analysis of the Echinodermata based on fossil taxa (Sumrall, 1996) supports this view. Echinoderm characters of Stylophora include the following:

1. All skeletal elements are made of typical echinoderm stereom structure. All elements are high Mg-rich calcite.
2. Sutural pores (epispires) are present in *Ceratocystis* and subsequently evolved into elaborate structures (cothurnopores and lamellipores) in younger cornutes. They are covered by flaps made of small pavements of platelets. Similar structures are present in *Rhopalocystis destombesi* Ubags 1963, an eocrinoid from the Lower Ordovician. Cothurnopores and lamellipores are only superficially similar to chordate gill slits.
3. The aulacophore with its internal lumen and (probable) imprint of the water vascular system is an echinodermal arm, a structure unique to the phylum.
4. The well developed anal pyramid in most cornutes is similar to that of many echinoderms.
5. The presence of a hydropore in some genera, such as *Ceratocystis* (Cornuta) and *Mitrocystites* (Ankyroidea).
6. The theca in many is differentiated into marginal and somatic plates. This character is independently derived in eocrinoids, homosteles, homoiosteles, ctenocystoids, and pleurocystitids. I argue that somewhat similar (echinodermal) organisms independently adapted to living recumbently on the sea floor, and acquired morphologically similar thecal plate character.

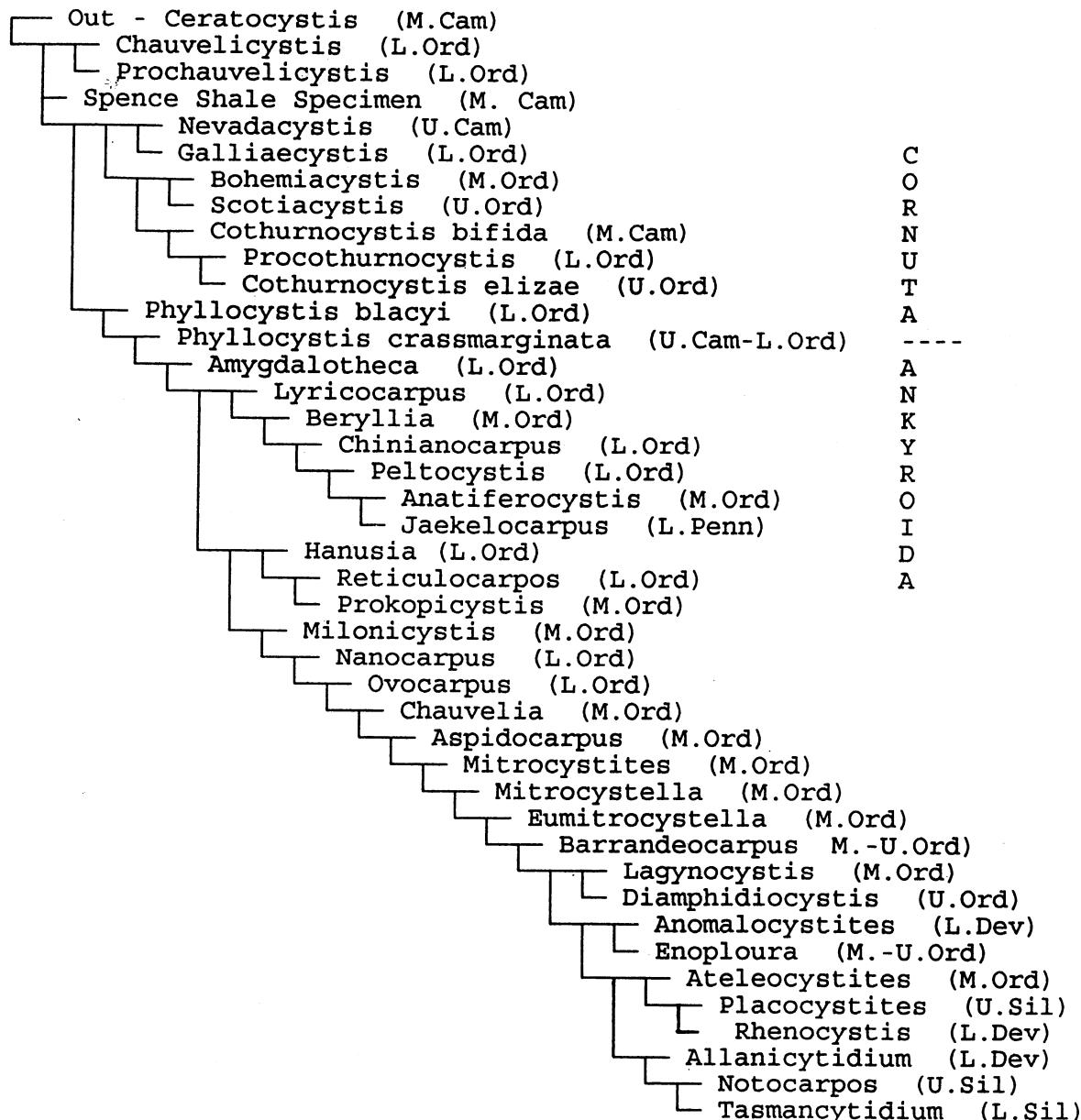


FIGURE 6—Consensus tree—Stylophora, processed by NONA (from Parsley, in press).

Class HOMOIOSTELEA Gill and Caster, 1960; *Order SOLUTA* Jaekel, 1901.—In his study of *Dendrocystoides scoticus*, Jefferies (1990) extended the scope of the calcichordates to include the solutes. Papers by Rozhnov and Jefferies (1966) and Daley (1992, 1995, 1996) also included solutes in the Calcichordata. These authors agree with the echinoderm model on oral-aboral orientation but invert the organism so that the cover plates and food groove on the feeding appendage are facing the substrate.

Character selection.—Solute morphology is widely described and illustrated (as echinoderms: Barrande, 1887; Jaekel, 1901, 1921; Bather, 1913; Dehm, 1934; Hecker, 1940; Thomas and Ladd, 1926; Kolata, 1973; Kolata et al., 1977; Parsley and Caster, 1965; Parsley, 1972; Caster, 1968; as calcichordates: Jefferies, 1990; Rozhnov and Jefferies, 1996; Daley, 1995, 1996). The following narrative briefly explains the character set and data matrix (Appendices 3 and 4).

When compared to the outgroup (the eocrinoid *Gogia*, especially *Gogia* sp. from the Middle Cambrian Spence Shale of Utah), solutes have a greatly reduced ambulacrinal system [1, 2] (Figure 7). The single biserial feeding appendage, commonly called an arm in the literature, is structurally a robust brachiole. The brachiole base varies considerably from where it extends from the theca: from anterior-most, in the axial plane (e.g., *Coleicarpus*, *Castericystis*), to slightly offset (e.g., *Rutrocycleus*, *Iowacystis*), to offset to a lateral or near lateral position (e.g., *Minervaecystis*, *Maennilia*) [3]. An aboral lobe is commonly present on genera with a markedly offset brachiole (e.g., *Girvanicystis*) [4].

Most thecae are flattened and basal genera are polyplated. Earliest occurring genera have an oval shaped theca (e.g., *Coleicystis*, *Castericystis*, *Minervaecystis*; Figure 8) and later-occurring genera develop triangular or circular outlines (e.g., *Dendrocystites*, *Rutrocycleus*; Figure 9). In the Middle Ordovician genera evolved with differentiated marginal and somatic plates (e.g., *Scalenocystites*, *Syringocrinus*) [8] (Figure 10). Several genera evolved regularized somatics (e.g., *Belemnocystites*) [8] (Figure 11).

Several small clades are probably present among those genera with regularized marginals. Based on the number and position of adstèle marginals on the inferior face and a median adstèle on the superior face, at least two clades are present: 1) *Scalenocystites*, *Iowacystis*, and *Syringocrinus*; and 2) *Belemnocystites*, and *Myeinocystites* [14, 16, 17, 18].

Considerable variation is present in the solute stèle. The earliest known genera *Coleicarpus* and *Castericystis* have distal most holdfasts that are very similar to that of the coeval eocrinoid *Gogia* sp. (Spence Shale species). In *Castericystis* the holdfast is found only in juvenile specimens [13]. All other solutes are without holdfasts and are viewed as vagile benthonic organisms [13]. *Coleicystis* and *Castericystis* are irregularly plated in the proximal stèle and are not organized into segmented rings. All other solutes have a well organized proxistèle of polymerous or tetramerous rings [9].

A median stèle or mesistèle is present in some genera which ranges from two to six plates in length [10]. Caster (1967) suggested that this is a zone of transformation from a fundamentally tetramerous structure to one that is essentially dimerous and accompanied with axial rotation (e.g., *Dendrocystites*, *Minervaecystis*) [10]. With the discovery of the Middle Cambrian genera *Coleicarpus* and *Castericystis* this interpretation can be strongly questioned. The proxistèle is not fundamentally tetramerous and there is little evidence of rotation.

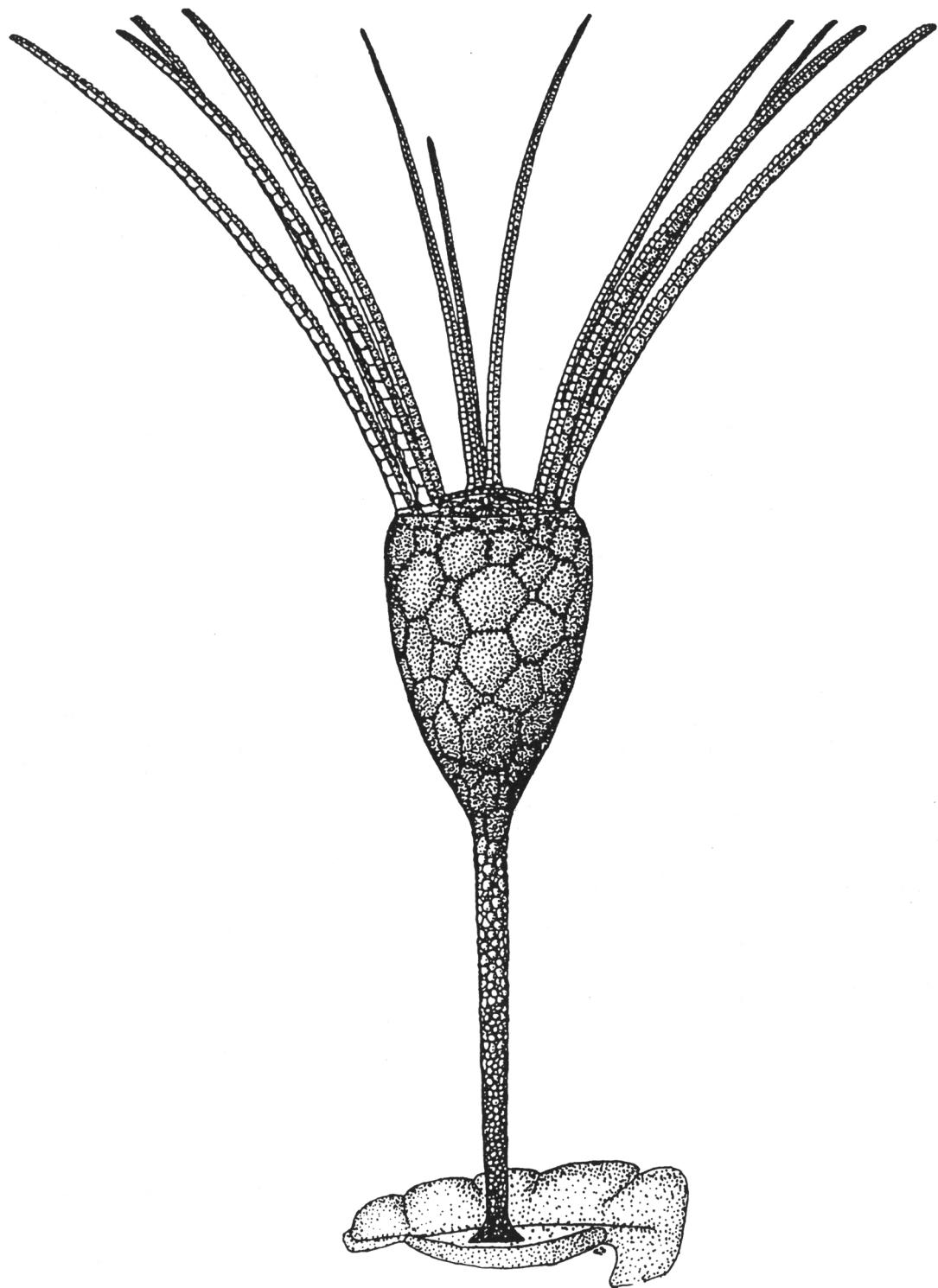


FIGURE 7—*Gogia* sp. from the Spence Shale, Utah, Middle Cambrian. Outgroup species for the Homoiosteola (from Sumrall, 1996).

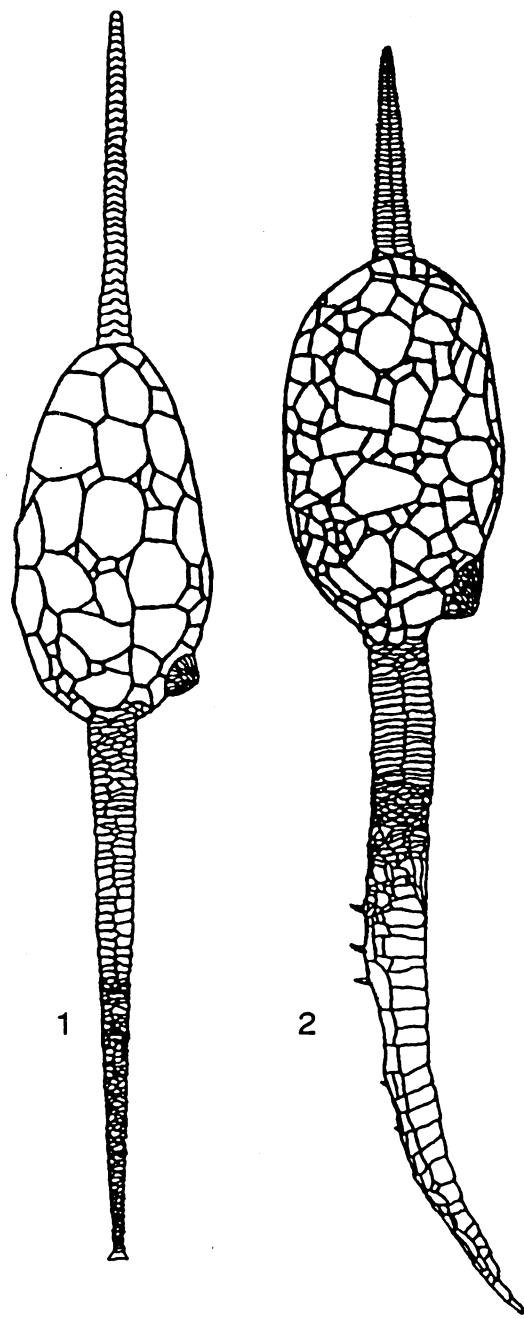


FIGURE 8—1, *Coleicarpus*, and 2, *Castericystis*. *Coleicarpus* has a stele (column) and holdfast similar to *Gogia* sp. *Castericystis* in its adult form has lost its holdfast and the dististele has modified considerably to accommodate a vagile mode of life (after Daley, 1996).

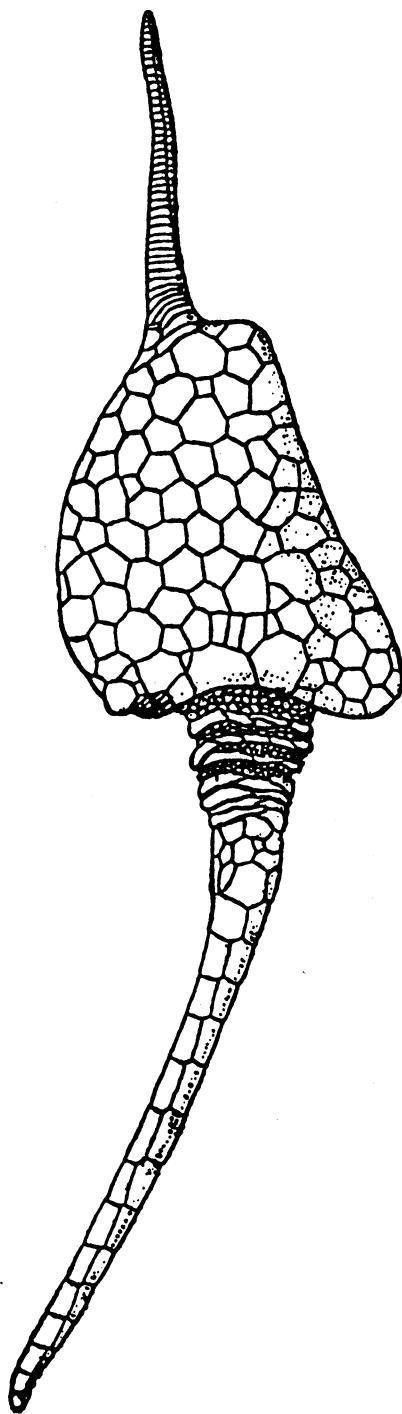


FIGURE 9—*Dendrocystites*; an early homioostelean with polyplated theca and proxistele with numerous polymerous segments. Presence of a 'sugar loaf' plate in the anal valve and a simplified dististele are apomorphic characters (after Bather, 1913).

PARSLEY—STYLOPHORA AND MONOIOSTELEA: NON CALCICHORDATA

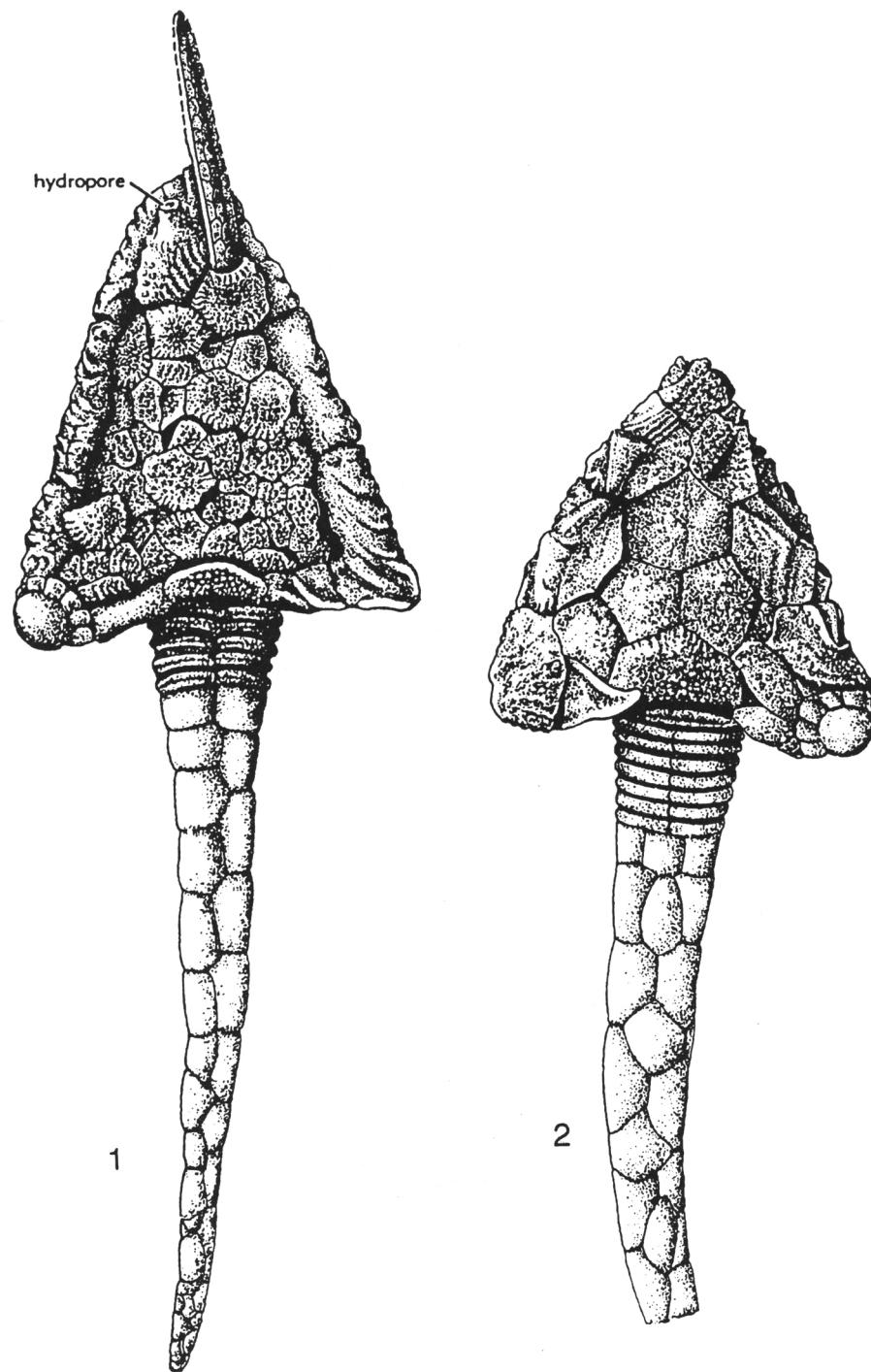


FIGURE 10—*Iowacystis*; a somewhat advanced (Upper Ordovician) homoiostelean with well defined marginal and somatic plates. Somatic plates on superior surface (1) are not regularized, those on the inferior surface (2) are regularized (after Parsley and Caster, 1965).

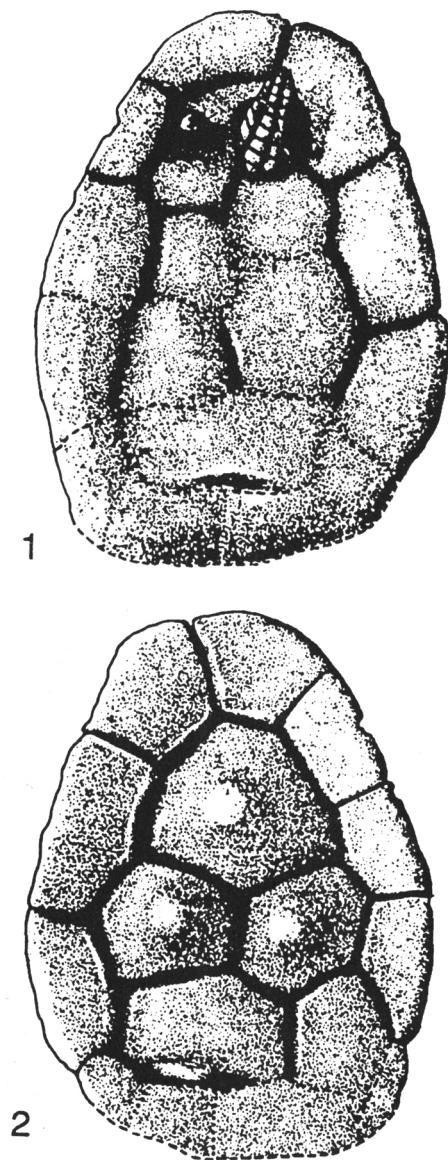


FIGURE 11—*Belemnocystites*; a homioostelean with regularized marginal and somatic plates. 1, Superior surface; 2, inferior surface (after Parsley, 1972).

PARSLEY—STYLOPHORA AND MONOIOSTELEA: NON CALCICHORDATA

The distal stele or dististele is variously organized along a dimerous plan. Some or unevenly paired in size and shape of the plates, others are quite evenly paired (e.g., *Dendrocystites*, *Rutrocyptes*) [11, 12].

Indication that the distal stele may have rotated in life is based on the presence of laterally produced spines. Rotation of the spines into the substrate may have resulted in a stylophoran-like styloid function (e.g., *Castericystis*, *Minervaecystis*, *Syringocrinus*) [15].

Discussion.—As in the Stylophora, the homoiostelean cladogram clumps genera closely with their traditional (evolutionary taxonomy) familial groupings (Ubags, 1967). The classification herein is rankless.

In addition to *Gogia* as outgroup, fourteen genera were studied using eighteen multistate characters. The consensus tree was processed by a phylogenetic program for personal computers (PCs), NONA (Goloboff, 1993). The command whennig40; max*; tplot; resulted in 2488 trees examined; two trees were found. (Figure 12); fit=44 (C=63; Ci=60; R=77).

Derivation of the Homoiostelea.—*Gogia* from the Middle Cambrian Spence Shale of Utah has a polyplated column that is remarkably similar to that of the sessile Middle Cambrian solutan *Coleicarpus* Daley, 1996 (Wheeler Formation, central House Range, Utah). Daley (1996) argued that *Coleitalcarpus* wagged the theca and feeding structure in order to move the subvective area through the nutrient bearing water mass. To take his argument one step farther, it is logical to assume that most of the movement occurred close to the theca and it would have been advantageous to organize the area into holomerous and subsequently tetramerous segments. The onset of this organization occurred in *Coleicarpus* or similar sessile species and was enhanced and co-opted for locomotion in younger genera. This transition from sessility to vagility, expressed in stele morphology, is clearly observed in *Castericystis*. This transition is paralleled in glyptocystitid rhombiferans where the adthecal column has well developed ‘slip ring’ segments. In the vagile family Pleurocystitidae these segments are especially well developed and were used to propel the greatly flattened theca along the bottom.

The dististele in younger genera is greatly simplified from that of *Coleicarpus* and appears to function as a flexible buttressing rod to both hold the animal in place (into prevailing currents), as well as, provide a tail surface for locomotion.

ACKNOWLEDGMENTS

Special thanks are extended to Colin Sumrall, Tulane University, for the use of an illustration and assistance in computer drafting of most of the illustrations. Paul Daley, The Natural History Museum, London, allowed the use of several illustrations. Joan Hughes, Tulane University, ably processed the manuscript.

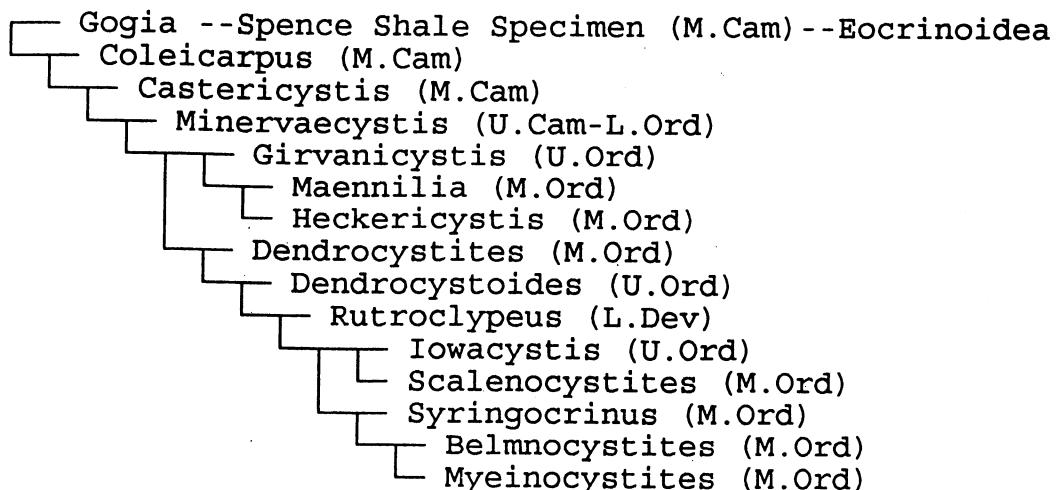


FIGURE 12—Consensus tree: Homoiostelea, processed by NONA.

REFERENCES

- BARRANDE, J. 1887. Système Silurien de centre de la Bohême. Part 1: recherches paléontologiques, vol. 7, classe des echinodermes, sec. 1, ordre des cystidées. Rivař, Prague and Gerhard, Leipzig, 233 p.
- BATHER, F. A. 1913. Caradocian Cystidea from Girvan. Transactions of the Royal Society of Edinburgh, 49:359–529.
- CASTER, K. E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology, 34:1–47.
- . 1967. Homoiostelea, p. S581–S627. In R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part S, Echinodermata 1. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- CRIPPS, A. P. 1989. A new genus of stem chordate (Cornuta) from the lower and Middle Ordovician of Czechoslovakia and the origin of bilateral symmetry in the chordates. Geobios, 22(2): 215–245.
- . 1989. A new stem-group chordate (Cornuta) from the Llandeilo of Czechoslovakia and the cornute mitrate transition. Zoological Journal Linnean Society, 96:49–85.
- . 1990. A new stem craniate from the Ordovician of Morocco and the search for the sister group of the craniata. Zoological Journal Linnean Society, 100:27–71.

PARSLEY—STYLOPHORA AND MONOIOSTELEA: NON CALCICHORDATA

- sister group of the craniata. *Zoological Journal of the Linnean Society*, 100:27–71.
- . 1991. A cladistic analysis of the cornutes (stem chordates). *Zoological Journal of the Linnean Society*, 102:333–366.
- AND P. DALEY. 1994. Two chordates from the Middle Ordovician (Llandeilo) of Normandy, France and a reinterpretation of *Milonicystis kerfornei*. *Palaeontographica, Abhandlungen A*, 232:99–132.
- DALEY, P. E. J. 1992. The anatomy of the solute *Girvanicystis batheri* (?Chordate) from the Upper Ordovician of Scotland and a new species of *Girvanicystis*, from the Upper Ordovician of South Wales. *Zoological Journal of the Linnean Society*, 105:353–375.
- . 1995. Anatomy, locomotion and ontogeny of the solute *Castericystis vali* from the Middle Cambrian of Utah. *Geobios* 28, 5:585–615.
- . 1996. The first solute which is attached as an adult: a mid-Cambrian fossil from Utah with echinoderm and chordate affinities. *Zoological Journal of the Linnean Society*, 117:405–440.
- DEHM, T. 1934. Untersuchungen über Cystoideen des rheinischen Unterdevons. *Sitzungberichte der bayerischen Akademie der Wissenschaften*, 1934, 19–43.
- GEE, H. 1996. Before the Backbone, Views on the Origin of the Vertebrates. Chapman and Hall, London.
- GILL, E. D., AND K. E. CASTER 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. *Bulletin of American Paleontology*, 41:1–71.
- HECKER, R. 1940. Carpoidea, Eocrinoidea i Ophiocistia nizhnego silura Leningradskoi oblasti i Estonii. *Trudy Paleontologicheskogo Instituta Akademii Nauk*, 9:5–82.
- JAEKEL, O. 1901. Über Carpoideen, eine neue klasse von Pelmatozoen. *Zeitschrift der deutschen geologischen Gesellschaft*, 52:661–677.
- . 1918 (1921). Phylogenie und system der peltatozoen. *Paläontologische Zeitschrift* 3, 1–128.
- JEFFRIES, R. P. S. 1973. The Ordovician fossil *Lagynocystis pyramidalis* and the ancestry of amphioxus. *Philosophical Transactions of the Royal Society*, B265:409–469.
- . 1981. In defence of calcichordates. *Zoological Journal Linnean Society*. 73:351–396.
- . 1986. The Ancestry of the Vertebrates. British Museum (Natural History) and Cambridge University Press, London and Cambridge.
- . 1990. The solute *Dendrocystoides scoticus* from the Upper Ordovician of Scotland and the ancestry of chordates and echinoderms. *Palaeontology*, 33:631–679.
- , AND R. J. PROKOP. 1972. A new calcichordate from the Ordovician of Bohemia and its anatomy, adaptations, and relationships. *Biological Journal of the Linnean Society*, 4:69–115.
- GOLOBOFF, P. A. 1993. Estimating character weights during tree search. *Cladistics*, 9:83–91.
- KIRK, E. 1911. The structure and relationships of certain eleutherozoic Pelmatozoa. *Proceedings of the U.S. National Museum*, 41:1–137.
- KOLATA, D. R. 1973. *Scalenocystites strimplei*, a new Ordovician belemnocystitid from Minnesota. *Journal of Paleontology*, 47:969–974.
- , H. L. STRIMPLE, AND C. O. LEVORSON. 1977. Revision of the carpoid family Iowacystidae. *Palaeontology*, 20:529–557.
- , AND T. E. GUENSBURG. 1979. *Diamphidiocystis*, a new mitrate "carpoid" from the Cincinnati (Upper Ordovician) Maquoketa Group in Southern Illinois. *Journal of*

- Paleontology, 53:1121–1135.
- , AND M. JOLLIE. 1982. Anomalocystitid mitrates (Stylophora—Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley region. *Journal of Paleontology*, 56:631–653.
 - LEFEBVRE, B., P. RACHEBOEUF, AND B. DAVID. In press. Homologies in stylophoran echinoderms. *In* R. Mooi (ed.), *Echinoderms: San Francisco*. A. A. Balkema, Rotterdam.
 - PARSLEY, R. L. 1972. The Belemnocystitidae: solutan homeomorphs of the Anomalocystitidae. *Journal of Paleontology*, 46:341–347.
 - . 1988. Feeding and respiratory strategies in stylophora, p. 347–361. *In* C. R. C. Paul and A. B. Smith (eds.), *Echinoderm Phylogeny and Evolutionary Biology*. Oxford Science Publications and Liverpool Geological Society, Oxford and Liverpool.
 - . 1991. Review of selected North American mitrates stylophorans (Homalozoa: Echinodermata). *Bulletins of American Paleontology*, 100:1–57.
 - . 1994. Mitrocystitid functional morphology, evolution and their relationships with other primitive echinoderm classes, p. 167–172. *In* B. David, B. Guille, J.-P. Féral, and M. Roux (eds.), *Echinoderms Through Time*. A. A. Balkema, Rotterdam.
 - . In press. Taxonomic Revisions of the Stylophora. *In* R. Mooi (ed.), *Echinoderms: San Francisco*. A. A. Balkema, Rotterdam.
 - , AND K. E. CASTER. 1965. North American Soluta (Carpoidea, Echinodermata). *Bulletins of American Paleontology*, 49:109–174.
 - PETERSON, K. J. 1995. A phylogenetic test of the calcichordate scenario. *Lethaia*, 28:25–38.
 - ROZHNOV, S. V., AND R. P. S. JEFFERIES. 1996. A new stem-chordate solute from the Middle Ordovician of Estonia. *Geobios*, 29:1:91–109.
 - SUMRALL, C. 1996. A phylogenetic analysis of Echinodermata based in primitive fossil taxa. Unpublished Ph.D. Dissertation, University of Texas at Austin.
 - THOMAS, A. O., AND H. S. LADD. 1926. Additional cystoids and crinoids from the Maquoketa shale of Iowa. *University of Iowa Studies, Natural History, Papers on Geology*, 2:8:5–18.
 - UBAGHS, G. 1961. Sur la nature de l'organe appelé Fig C ou pedoncale chez les carpoides Cornuta et Mitrata. *Academie Sciences, Paris, Comptes Rendus Séances*, 253:2738–2740.
 - . 1963. *Cothurnocystis* Bather, *Phyllocystis* Thoral and an undetermined member of the order Soluta (Echinodermata:Carpoidea) in the uppermost Cambrian of Nevada. *Journal of Paleontology*, 37:1133–1142.
 - . 1963. *Rhopalocystis destombesi* n.g. n.sp. Eocrinöide de l'Ordovicien inférieur (Tremadocien supérieur) de Sud marocain. *Servis Geologic Marocain*, 23:172:25–44.
 - . 1967. Stylophora, p. S495–S565. *In* R. C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part S., Echinodermata 1. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
 - . 1969. Les échinodermes carpoides de l'Ordovicien inférieur de la Montagne Noire (France). *Cahiers de Paléontologie*, Paris, Centre National de la Recherche Scientifique, 112 p.
 - . 1979. Trois Mitrata (Echinodermata:Stylophora) nouveaux de l'Ordovician de Tchécoslovaquie. *Paläontologische Zeitschrift*, 53:98–119.

- . 1991. Deux Stylophora (Homalozoa, Echinodermata) nouveaux pour l'Ordovician inferior de la Montagne Noir (France Meridionale). *Paläontologische Zeitschrift*, 65:157–171.

APPENDIX 1
CHARACTER SET—*STYLOPHORA*

1. Tripartite aulacophore with stylocone: 0; with styloid, 1.
2. Loosely attached cover plates on distal aulacophore: 0; short; tightly attached cover plates, 1.
3. Marginal plates: somatic plates not differentiated, 0; differentiated, 1.
4. Asymmetrical theca: 0; boot-shaped, 1; loss of, 2.
5. Symmetrical theca: no, 0; yes, 1; secondary loss (u-shaped, collapsed), 2.
6. Anal lobe: none, 0; M4/M6, 1; M5/M6, 2; M5/M'5, 3; loss of anal lobe, 4.
7. Spinal: none, 0; M3, 1; M4, 2.
8. Zygal (strut): none, 0; M'1-M4, 1.
9. Zygal (strut): none, 0; M'1-M5, 1.
10. Zygal (strut): none, 0; M'1-CS or S, 1.
11. Septum: none, 0; M'1-M4, 1.
12. Septum: none, 0; M'1/CS, 1; M'1, CS, M4, 2.
13. Glossal spine: none, 0; attached to M5, 1; attached to another marginal, 2.
14. Digital spine: none 0; attached to M4, 1; attached to another marginal, 2.
15. Many small spines attached to marginals: none, 0; yes, 1; one side only, 2.
16. Sutural respiratory pores: simple, 0; compound 1; loss of pores, 2.
17. Stylocone: with, 0; styloid as “spike”, 1; flanged or multicuspied, 2.
18. Symmetrical theca marginals: none, 0; M1-M7, 1; M6 + M7, 2; M1-M6, 3; M5+M6, 4; M1-M5, 5; M4+M5, 6; M1-M4, 7; M1, 8.
19. Thecal movable spines: none, 0; with M5 plus other marginals in thecal frame 1; M5 marginals as fixed projections, 2; M5 marginals as moveable spines, 3; loss of one spine, 4.
20. Single movable spine-but with M'1-M4 septum, no CS plate: none, 0; with, 1.
21. Dorsal bar connecting M4-M'4: no, 0; yes, 1.
22. Distal superior margin with transversely arranged somatics: no, 0; multiplated, 1; five plates, 2; four plates, 3; three plates, 4; M4 marginals, 5.
23. Distal margin of inferior somatics: no, 0; multiplated, 1; M5, M6, M'5, 2; single plate, 3.
24. Aulacophore normal length (assumed to be so): 0; flagellate, 1; shortened, 2.
25. Placocystited plate: no, 0; yes, 1.
26. Lateripores: no, 0; yes, 1; loss, 2.
27. Peripores: no, 0; yes, 1.
28. Ctenoid organ: no, 0; yes, 1.
29. Subanal plate: no, 0, yes, 1.
30. Adaulacophoral plate with hydropore: no, 0; yes, 1.
31. Anal pyramid: pre-360° pyramid, 0; 360° pyramid, 1; 180° (in line or flattened pyramid), 2; loss of anal plates, 3.
32. Plastron order: ancestral, 0; tessellated, 1; S or CS, 2; CS+A, 3; CS+A+DS, 4; paired CS, 5; loss or never in the organization, 6.

33. Paired aulacophorals: none, 0; present, 1; partly inserted MAM plate, 2; three aulacophorals, 3.
34. Dorsal somatics: ancestral—massive, 0; tessellated pavement, 1; distally overlapping 2; ordered and abutting, 3; single massive plate, 4.
35. M1 marginals: ancestral subequal, 0; M'1 with distal extension, 1; reduced to equalized M1 series, 2.
36. Cothurnopores: no, 0; yes, 1.
37. Lamelliholes: no, 0; yes 1.
38. Respiratory structures: yes, 0; no, 1 set.
39. Distal end “open” or “closed” by transverse marginal plate:
non-asymmetrical genera, 0; open, 1; closed, 2; subanal or not applicable, 3.
40. Tetramerous organization of proximal aulacophore: no, 0; yes, 1.
41. Loss of marginal symmetry in symmetrical forms: not applicable, 0; no, 1; yes, 2.
42. CS in contact with 2 1/2 or more pairs of marginals: not applicable, 0; no, 1; yes 2.

PARSLEY—STYLOPHORA AND MONIOSTELEA: NON CALCICHORDATA

APPENDIX 2
DATA SET—STYLOPHORA

	10	20	30	40
	/	/	/	/
Out- <i>Ceratocystis</i>	00000000000000000000000000000000?	0000000000000000		
<i>Nevadacystis</i>	0011031100000002000000000000?	10111000100		
<i>Galliaecystis</i>	0011031100000202000100000000?	1011?000100		
<i>Procothurnocystis</i>	001102201000110200000000000001	10111000100		
<i>Cothurnocystis bifida</i>	0011011010002?02000000000000?	10111000100		
<i>Bohemiacystis</i>	001103101000??02000000000000?	10110100100		
<i>Scotiacystis</i>	001103101000100200000000000001	101110100100		
<i>Chauvelicystis</i>	0011020010000120000000000000?	10111000100		
<i>Prochauvelicystis</i>	00110200100001200000000000001	10111000100		
Spence Shale Specimen	0011020010000020000000000000?	10111000100		
<i>Cothurnocystis elizae</i>	00110220100011020000000000001	10111000100		
<i>Phyllocystis blacyi</i>	00121300100000200000000000001	10111000110		
<i>Phyllocystis crassmarginata</i>	00121300100000100000000000001	10111000110		
<i>Amygdalotheca</i>	?1214000100002?100000000000?	20110011111		
<i>Nanocarpus</i>	1012140001000021410000000000?	21110012111		
<i>Lyricocarpus</i>	1012140002000021700000000000??	1110011111		
<i>Peltocystis</i>	1112140002100021701000000010??	1210013110		
<i>Lagynocystis</i>	111224000201002274000100010022322001102?			
<i>Anatiferocystis</i>	1112140002000022841000100010361510013110			
<i>Jaekelocarpus</i>	11121400021000218410002000100361520013110			
<i>Chauvelia</i>	1112140001000022310000010001?21220012111			
<i>Ovocarpus</i>	1012140000?0002241000001000??1?2001211?			
<i>Milonicystis</i>	1?1214000100002?410000000000?20110012111			
<i>Hanusia</i>	1?1214000100002?52011000000?20110011110			
<i>Chinianocarpus</i>	11121400021000216000000001010?20110011110			
<i>Aspidocarpus</i>	10121400020100223100100010001222320012112			
<i>Mitrocystites</i>	111214000201000222100100011001241210012111			
<i>Mitrocystella</i>	11121400020100022210010000000241220012112			
<i>Eumitrocystella</i>	11121400020100022410010000000232220012112			
<i>Reticulocarpus</i>	1112140002000021520111000000?10110021111			
<i>Prokopicystis</i>	1112140002000021520111000000?10110021111			
<i>Ateleocystites</i>	11121400020200022730032010000242320011112			
<i>Placocystites</i>	11121400020200022730042010000232320011112			
<i>Anomalocystites</i>	11121400020200022730022000000333320011112			
<i>Rhenocystis</i>	11121400020200011730042010000232320011112			
<i>Barrandeocarpus</i>	11121400020100022410020010000242320012112			
<i>Enoploura</i>	11121400020200022730022000000243320011112			
<i>Allanicytidium</i>	11121400020200022730053000000253420011112			
<i>Notocarpas</i>	11121400020200022730053000000231420011112			
<i>Tasmancytidium</i>	1112140002020002?730052000000221420011112			
<i>Diamphiodiocystis</i>	11122400020?0002?740022000000241320011122			
<i>Beryllia</i>	11121400020000227000??000000?2011001?110			

APPENDIX 3
CHARACTER SET—SOLUTA

1. Reduced ambulacral system: no, 0; yes, 1.
2. Brachioles: multiple, 0; single, 1.
3. Oral opening offset: none, 0; slightly, 1; markedly 2.
4. Theca without an aboral lobe: 0, with, 1.
5. Theca with an anal lobe: 0; with, 1.
6. Anal pyramid: 0; pyramid and sugar loaf plate, 1; sugar loaf plate 2.
7. Oval polyplated theca: 0; tri-quadrangular theca, 1; circular, 2; not polyplated, 3.
8. Thecal marginals and somatics: none, 0; with, 1; regularized somatics, 2.
9. Proximal stele irregularly platted: 0; multimerous rings, 1; tetramerous rings, 2.
10. No mesistele: 0; gradual mesistele, 1; short and organized mesistele, 2; none—proxi- and sististele abutted, 3.
11. Distal stele polyplated: 0; simplified, 1.
12. Distal stele unevenly paired: no, 0; yes, 1; alternating dimeres, 2; evenly paired 3.
13. Distal stele with holdfast in some stage of ontogeny: 0; no, 1.
14. Adstielial basals: no, 0; yes, 1.
15. Distal stele with spines: no, 0; yes, 1.
16. Paired inferior face adstielials: no, 0; yes, 1.
17. Three inferior face adstielials: no, 0; yes, 1.
18. Median superior face adstielial: no, 0; yes, 1.

APPENDIX 4
DATA SET—SOLUTA

	/10
<i>Gogia</i>	000000000000000000
<i>Coleicarpus</i>	110001000000000000
<i>Castericystis</i>	110001000111101000
<i>Minervacystis</i>	112001002111101000
<i>Dendrocystites</i>	111011100111100101
<i>Maennila</i>	112111101111100000
<i>Heckericystis</i>	11211?101111100000
<i>Dendrocystoides</i>	112111102111110101
<i>Girvanicystis</i>	111112102313100010
<i>Rutroclypeus</i>	1110012023131101?1
<i>Syringocrinus</i>	111011312212111100
<i>Iowacystis</i>	111011312212110011
<i>Belmnocystites</i>	111011322?1?110100
<i>Myeinocystites</i>	111011322?1?110100
<i>Scalenocystites</i>	111011312212110011