

NEW RECUMBENT ECHINODERM GENERA FROM THE BOIS D'ARC FORMATION: LOWER DEVONIAN (LOCHKOVIAN) OF COAL COUNTY, OKLAHOMA

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ABSTRACT—An echinoderm fauna from the Lower Devonian (Lochkovian) Cravatt Member of the Bois d'Arc Formation near Clarita, Oklahoma, has yielded specimens of recumbent, essentially bilaterally symmetrical taxa which are similar to Ordovician genera but absent or sparsely represented in Silurian strata. *Claritacarpus smithi* n. gen. and sp., is a dendrocystitid homoiostele with morphology similar to the Late Ordovician *Dendrocystoides* Jaekel, 1918; the anomalocystitid stylophoran *Victoriacystis* aff. *holmesorum* Ruta and Jell, 1999 shows strong affinities to *Victoriacystis holmesorum* Ruta and Jell, 1999, Humevale Formation, of Victoria, Australia; and the pleurocystitid rhombiferan, *Turgidacystis graffhami* n. gen. and sp., has close affinities to the Middle Ordovician *Coopericystis* Parsley, 1970 of West Virginia and *Henicocystis* Jell, 1983 of Victoria, Australia. *Claritacarpus* and *Turgidacystis* are North American range extensions for homoiosteles and pleurocystitids, respectively, being previously unknown from rocks younger than Upper Ordovician. Globally, Silurian homoiosteles and pleurocystitids are unknown although both occur in the Lower Devonian of Germany and Australia; additionally, Early Devonian pleurocystitids are known from Great Britain and Bohemia. These genera illustrate a pseudoextinction pattern suggesting a significant unsampled Silurian “homalozoan” and pleurocystitid history.

INTRODUCTION

A SMALL collection of echinoderms made by Allen Graffham, Ardmore, Oklahoma, from the Cravatt Member (Lochkovian) of the Bois d'Arc Formation near Clarita, Oklahoma, includes specimens of several atypical echinoderm lineages: homoiostele and ankyroid “Homalozoa” (see Parsley, 1999), and flattened Rhombifera (Pleurocystitidae) that are more commonly found in earlier Ordovician faunas. Homoiosteles and ankyroids are each represented by a single adult specimen. The homoiostele, *Claritacarpus smithi* n. gen. and sp., has strong affinities to *Dendrocystoides* Jaekel, 1918 known from the Upper Ordovician of Europe (Fig. 1). The only other post-Ordovician homoiostele species are *Rutroclipeus junori* Withers, 1933, *R. victoriae* Gill and Caster, 1960, and the problematical *R. (?)withersi* Gill and Caster, 1960, all from the Lower Devonian of Australia, and the poorly known *Dehmicystis globulus* Caster, 1968 from the Lower Devonian Hunsrückschiefer of Germany. The ankyroid *Victoriacystis* aff. *holmesorum*, has strong affinities with *Victoriacystis holmesorum* Ruta and Jell, 1999a from the Lower Devonian of Victoria, Australia and also to *Rhenocystis latipedunculata* Dehm, 1932 from the Lower Devonian Hunsrückschiefer of Germany. The pleurocystitid *Turgidacystis graffhami* n. gen. and sp., shows strong affinities to *Coopericystis* Parsley, 1970, Middle Ordovician of North America, and to *Regulaecystis* Dehm, 1932, Lower Devonian of Europe and *Henicocystis* Jell, 1983 from the Lower Devonian of Victoria, Australia (Fig. 2).

All of these genera are vagile, recumbent echinoderms and quite different from typical pentamerid taxa, i.e., they are forms belonging to groups that are essentially bilaterally symmetrical, with a flattened face of the theca resting on the seafloor. An elongated appendage (either a non-anchoring column or feeding aulacophore) is used for locomotion by generating waves that move down the structure to propel the animal across the seafloor (Caster, 1968; Parsley, 1988). None of these groups are closely related, but all are adapted for living “snowshoe” style on soft sediments and feeding at or near the sediment-water interface.

Globally, homoiosteles and pleurocystitids are unsampled in the Silurian, and ankyroids are known from only a few localities (Gill and Caster, 1960; Jefferies and Lewis, 1978; Ruta and Jell, 1999b, 1999c). The global occurrence of these taxa post-Silurian suggests a slight resurgence in diversity by the Early Devonian (at least with limited examples from North America, Europe, and Australia), and ankyroids at least are known in strata as young as Lower Pennsylvanian (Stanley, 1979; Kolata et al., 1991; Smith, 1994).

STRATIGRAPHIC POSITION

Both lithostratigraphy and biostratigraphy of the Silurian/Devonian Hunton Group of Oklahoma have been intensively studied since the 1950s. Amsden and Boucot (1958) and Amsden (1960) thoroughly documented the lithostratigraphy of the Hunton Group. It consists of three formations, the Henryhouse Formation (Ludlow), the Haragan Formation (Lochkovian), and the Bois d'Arc Formation (Lochkovian). Lithostratigraphically, the Henryhouse Formation and the Haragan Formation are indistinguishable, but share virtually no faunal elements, suggesting that they are disconformable. This is further supported by local evidence of an erosional contact (Amsden, 1962, 1988). Regionally, the Henryhouse Formation is truncated by the Haragan Formation but the contact is typically indistinguishable on lithological grounds.

The overlying Bois d'Arc Formation consists of siliceous carbonate mudstones interbedded in the middle and upper portions with skeletal wackestones and packstones of the Cravatt Member which in turn grades into the skeletal grainstones of the Fittstown Member. The Bois d'Arc fauna has been thoroughly described; especially well documented are the brachiopods (Amsden, 1958, 1988; Amsden and Ventress, 1963), ostracodes (Lundin, 1968), trilobites (Campbell, 1977; Adrain and Kloc, 1997), crinoids (Strimple, 1963), and conodonts (Barrick and Klapper, 1992). These studies indicate a Lochkovian age for the Bois d'Arc Formation. The contact with the underlying Haragan Formation is locally gradational and the two units are gradational laterally.

The specimens described herein are from a 30 cm thick band of fine-grained calcareous shale in the Lower Devonian (Lochkovian) Cravatt Member of the Bois d'Arc Formation near Clarita, Coal County, Oklahoma (NW1/4 SW1/4 NW1/4 Section 33, T1S, R8E, Wapanucka 7.5' Quadrangle). The outcrop, artificially created by bulldozer and backhoe to collect fossils from this layer, was excavated by Geological Enterprises of Ardmore, Oklahoma, and was approximately 200 m long and 2–2.5 m wide. The echinoderm assemblage was first noted by Strimple (1963), who gave a brief account of the unusual disparid crinoid *Myelodactylus* Hall, 1852. Frest et al. (1999, p. 747) gave a succinct discussion of the overall fauna and its environmental setting as part of what they called the *Edriocrinus* - *Pygmaeocrinus* Association. This community association occupies the Lower Haragan Formation and the overlying Cravatt Member of the Bois d'Arc Formation. The community is dominated by 34 genera of brachiopods, which are commonly found articulated, 48 species of ostracodes, and 18 species of trilobites (Amsden and Boucot, 1958; Lundin, 1968;

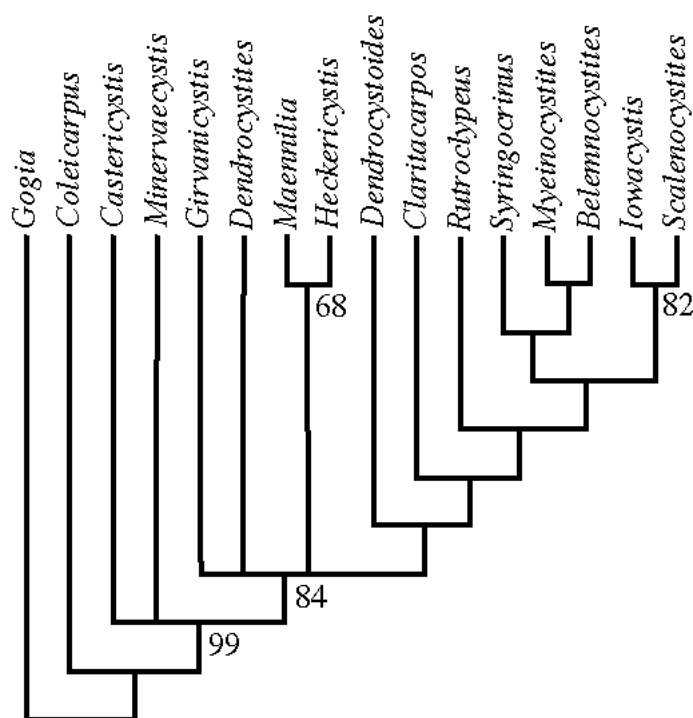


FIGURE 1—Strict consensus of the four most parsimonious trees of 41 steps found by the phylogenetic analysis of homoiosteles based on the data matrix in Table 1. Numbers at nodes are bootstrap proportions and unlabeled nodes have bootstrap support of less than 50%.

Campbell, 1977). Corals are common but not diverse according to Frest et al. (1999), *Favosites* Lamark, 1816 being the most abundant. *Machaeridia* and bryozoans are also fairly common, according to these authors. Crinoid remains are locally abundant but are by no means uniformly distributed throughout these formations. *Edriocrinus* Hall, 1859 attached to brachiopods are common throughout the section, as are disarticulated thecal plates and columns belonging to *Scyphocrinites* Zenker, 1833 (Frest et al., 1999). However, in the approximately 30 cm thick unit from which the echinoderms described herein were collected, crinoids and most other invertebrate groups, except brachiopods, are rare (A. Graffham, personal commun. 2003). The specimens of “primitive” (essentially bilaterally symmetrical rather than pentameral) echinoderms appear to have come from the lower subtidal zone [benthic assemblage 4–5 as defined by Boucot (1981) and Frest et al. (1999)] but still within the photic zone with quiet water deposition.

Specimens from the Cravatt Member are preserved as calcite in soft, buff-colored marly claystones. Early diagenetic compaction of the fine-grained sediments has resulted in considerable fracturing of the thin thecal plates (Fig. 3.5). A number of unfigured pleurocystid specimens are simply preserved as jumbles of plates with a column extending from them.

Because most recumbent echinoderms are found in obrution deposits of interbedded shale and limestone, in a broad sense their discontinuous distribution can, in part, be attributed to habitation in deeper, quieter waters (middle to outer shelf). The *Clarita* specimens, following this reasoning, would represent their incursion into shallow waters.

ECHINODERM SAMPLING

Both *Claritacarpus* n. gen. and *Turgidacystis* n. gen. are extensions of higher taxon ranges in North America. Previously, North American homoiosteles and pleurocystitids were unknown from rocks younger than Upper Ordovician. Globally, no Silurian

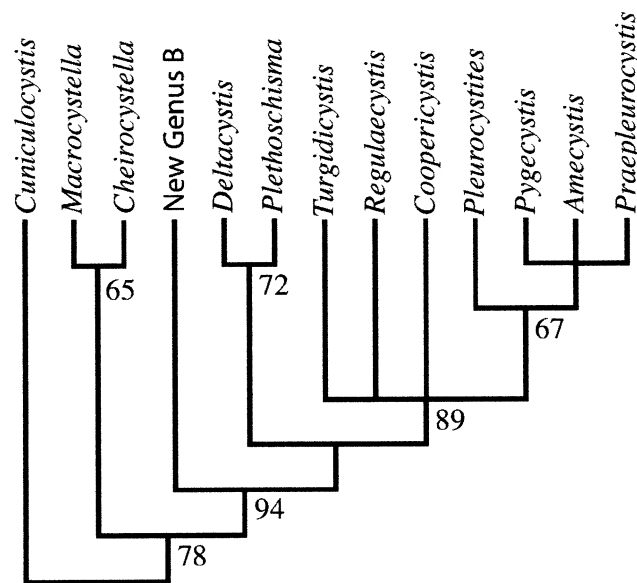


FIGURE 2—Strict consensus of the 12 most parsimonious trees of 39 steps found by the phylogenetic analysis of pleurocystitids based on the data matrix in Table 2. Numbers at nodes are bootstrap proportions and unlabeled nodes have bootstrap support of less than 50%.

homoiosteles or pleurocystitids are known although both occur in the Lower Devonian of Germany and Australia and pleurocystitids are known from the Lower Devonian of Great Britain and Bohemia (Prokop and Petr, 2004). The *Clarita* genera show a distinct pseudoextinction pattern and indicate a significant unsampled Silurian history.

However, such gaps and range extensions are not uncommon for echinoderm clades. In recent years, the stratigraphic range of isorophinid edrioasteroids, previously unknown from rocks younger than Upper Mississippian (Regnéll, 1966), were extended by new discoveries to the Early Middle Pennsylvanian in North America and the Permian of Russia (Bell, 1976; Arendt, 1983; Sumrall and Bowsher, 1996; Sumrall et al., 2000). The discovery of stylophorans in the Lower Pennsylvanian (Morrowan) of Oklahoma (Kolata et al., 1991) extended the range of this clade from the Middle Devonian. Although some have argued for a relatively adequate fossil record for echinoderms (Bodenbender and Fisher, 2001), given the fragility of the echinoderm skeleton (Brett et al., 1997) and the general indistinctiveness of most isolated echinoderm thecal plates at the clade level, such range extensions suggest a much lower confidence in our understanding of echinoderm temporal patterns.

PHYLOGENETIC POSITION

To place *Claritacarpus* n. gen. and *Turgidacystis* n. gen. into a phylogenetic context, two separate phylogenetic analyses were performed. *Claritacarpus* was scored for the characters of Parsley (1997, p. 235, 241, Table 1 in Appendix), and the new matrix was reanalyzed using PAUP* (Swofford, 2002) and using parsimony and a branch-and-bound search to assure that the complete set of most parsimonious trees was recovered (Fig. 1). All characters were unordered and equally weighted. The analysis recovered four trees (TL = 41, CI = 0.68, RI = 0.79). To assess nodal support, a bootstrap analysis was performed on the matrix using a branch-and-bound search and 1,000 pseudoreplicate matrices.

This analysis recovered a tree structure largely congruent with the single tree presented by Parsley (1997), though with less precise placements of *Minervaecystis* Ubahgs and Caster, 1968, the clade *Maennilia* Rozhnov and Jefferies, 1996, *Heckericystis* Gill and Caster, 1960, and *Dendrocystites*, owing to the presentation herein of a consensus of the complete set of most parsimonious

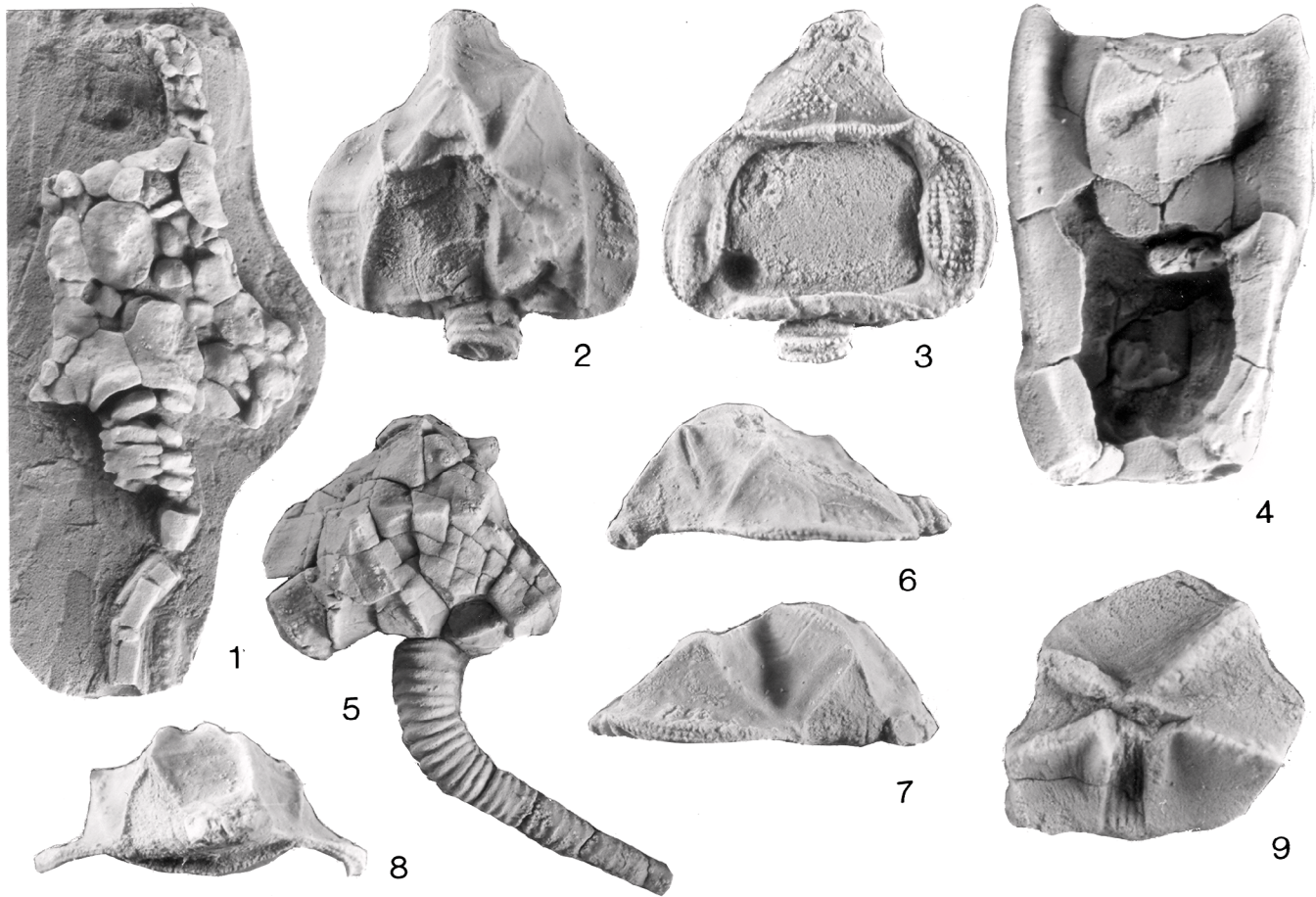


FIGURE 3—1, Holotype CMCP 50660 of *Claritacarpus smithi* n. gen. and sp. ventral face, whitened with NH_4Cl . Note the shape of the theca, and the plating of the brachiole and stele, $\times 3.5$. 2, 3, 6–8, Abanal, anal, left lateral, right lateral, and summit views of holotype CMCP 50662 of *Turgidacystis graffhami* n. gen. and sp. Note the highly inflated theca and the rectangular periproctal opening, $\times 3.5$. 5, Paratype CMCP 50663 of *Turgidacystis graffhami*. Note the shape of the stem, $\times 3$. 9, Paratype CMCP 50666, L3 plate of *Turgidacystis graffhami*, $\times 6$. Note the nature of the halfrhomb. 4, CMCP 50661, theca, ventral face, of *Victoriacystis* aff. *holmesorum*, $\times 5$.

trees. Although the analysis recovered only four trees, much of the tree structure is weakly supported, as shown by low nodal bootstrap proportions (Fig. 1). *Claritacarpus* is derived relative to the similarly shaped *Dendrocystoides* as the sister taxon to *Iowacystis* Thomas and Ladd, 1926, *Scalenocystites* Kolata 1973, *Myeinocystites* Strimble, 1953, *Belemnocystites* Miller and Gurlley, 1894, *Syringocrinus* Billings, 1859, *Rutroclypeus* Withers, 1933. *Dehmicystis* Caster, 1968 is now known to be very similar to *Rutroclypeus* (Fig. 1). This placement is supported by character 12, a distal stele with alternating dimers. *Claritacarpus* and *Rutroclypeus* (Early Devonian) along with *Dehmicystis* Emsian (Middle Devonian) are the youngest dendrocystitids as well as the youngest known solutes. Dendrocystitids remain unknown from Silurian aged rocks.

Turgidacystis was scored for the characters of Sumrall and Sprinkle (1995, p. 778) (Table 2 in Appendix), and the new matrix using the same search settings was reanalyzed using PAUP* (Swofford, 2002). All characters were unordered and equally weighted except character 7 which concerns the plating of the periproctal border. For this character a step matrix was coded to better express this complex series of transformations (see Sumrall and Sprinkle, 1995 for further details on the treatment of this character). The analysis recovered 12 trees (TL = 39, CI = 0.75, RI = 0.80, excluding the step matrix). To assess nodal support, a bootstrap analysis was performed on the matrix using a branch-and-bound search and 1,000 pseudoreplicate matrices (Fig. 2).

The tree topology was completely congruent with the phylogeny recovered by Sumrall and Sprinkle (1995) though with more equally most parsimonious trees owing to uncertainty associated with the placement of the largely incomplete *Coopericystis*, known only from a single abanal face. *Turgidacystis* was placed in a polytomy with the morphologically similar *Regulaecystis* Dehm, 1932, *Coopericystis*, and *Pleurocystitinae* (sensu Sumrall and Sprinkle, 1995) based upon characters 5 (absence of a pectinirhomb on the L3-L4 suture), 7 (the border of the periproct), 8 (B1 crossing the thecal ambitus), 9 (lateral thecal margin formed by IL5 and L1), 12 (an elongation of L1), 20 (a small L5), and 23 (presence of vestibule rims on the pectinirhombs) (Fig. 3). It is thought that with a more complete understanding of *Coopericystis*, higher phylogenetic precision can be recovered for derived pleurocystitids.

SYSTEMATIC PALEONTOLOGY

Class HOMIOOSTELEA Gill and Caster, 1960

Order SOLUTA Jaekel, 1901

Family DENDROCYSTITIDAE Bassler, 1938

Discussion.—This solutan family is characterized by an asymmetrical theca made up of numerous platelets. Two exceptions, apparently independently derived to this, are *Girvanicystis* Caster, 1968 from the Upper Ordovician of Scotland and the new genus *Claritacarpus* from the Lower Devonian of Oklahoma. In both genera, the theca is in part covered with large, mostly irregularly

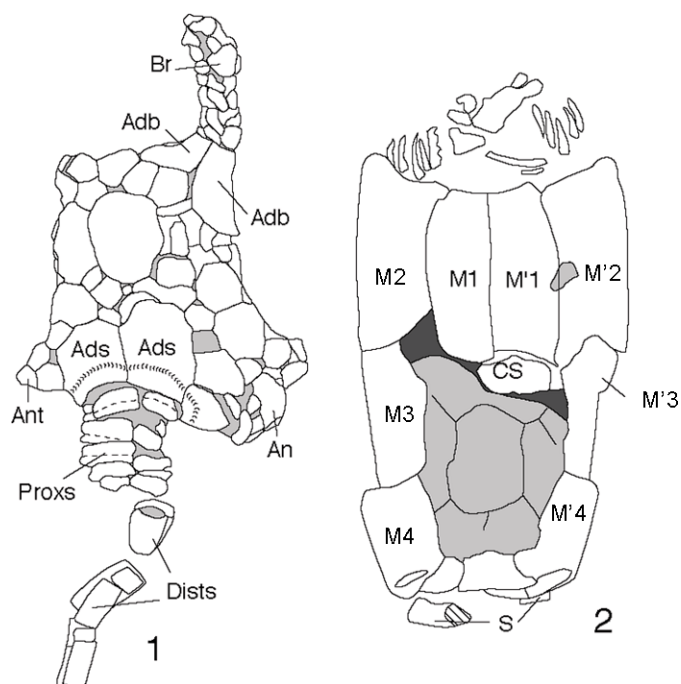


FIGURE 4—Camera lucida drawings of the homalozoans from the Bois d'Arc fauna. 1, The holotype of *Claritacarpus smithi* n. gen. and sp. CMCP 50660. Note the slightly disrupted dorsal face of the theca and stele and the general thecal outline, $\times 3.5$. 2, Theca, ventral face, of *Victoriacystis* aff. *holmesorum* CMCP 50661. Stippled area is plates showing through from the dorsal side, $\times 3$. Adb = adbrachiole; Ads = adsetel; An = anal lobe; Ant = anterior lobe; Br = brachiole; Dists = dististele; CS = central somatic; M = right marginal series; M' = left marginal series; Proxs = proxistele; S = spine.

shaped plates. Some of the plates in these genera may be regularized in number and position but are variable in outline. *Girvanicystis* more closely approximates *Dendrocystites* Barrande, 1887 from the Middle Ordovician of Bohemia in thecal outline, while that of *Claritacarpus* is closer to *Dendrocystoides* Jaekel, 1918 from the Late Ordovician of Scotland. The tetramerous proxistele of *Claritacystis* is very similar to that of *Dendrocystoides*. Both of these genera also have a large, squared anal lobe instead of one that is rounded, as is commonly the case in *Dendrocystites* and *Girvanicystis*. The proxistele of *Dendrocystites* is composed of numerous, 1) small elongated, and 2) more equidimensional platelets that are organized into circlets in mature specimens. In *Girvanicystis* the circlets are better organized; tetramerous with intercalated equidimensional platelets between tetrameres. Thecal and stele characters are sufficiently distinct to differentiate each of these genera and to closely group *Dendrocystoides* with *Claritacystis* and *Dendrocystites* with *Girvanicystis* (Fig. 1).

Genus CLARITACARPUS new genus

Type species.—*Claritacarpus smithi* n. sp.

Diagnosis.—The genus is monotypic; the diagnosis is the same as for *Claritacarpus smithi*.

Etymology.—The genus is named for Clarita, Oklahoma, which is close to the commercial fossil quarry where the type specimen was collected.

CLARITACARPUS *Smithi* new species

Figures 3.1, 4.1

Diagnosis.—Dendrocystitid with irregularly pentagonal thecal outline; theca with small number of relatively large plates; anal lobe large, somewhat squared in profile; antanal lobe small, pointed laterally; large paired adsteals present on dorsal face; adorals on dorsal face large, paired, curve onto the ventral face; brachiole

robust; proxistele with five tetrameres, mesistele with single pair of plates, tapered distally; dististele with two series of irregularly alternating plates, with alternating elongate rectangular plate juxtaposed with short squared plate.

Description.—Description based on single known specimen that exposes only dorsal face (obverse face; see Caster, 1968), brachiole, and stele. Theca irregularly pentagonal in outline, lateral sides slightly concave, anterior side straight. Plating irregular except for three enlarged adsteals, single pair of adbrachials which curve onto ventral (reverse face; see Caster, 1968), and large somatic plate located near anterior margin; large plates interspersed with smaller plates up to one-fourth diameter of largest plates; all plating relatively larger (to size of theca) than that found on closely related dendrocystitids of Ordovician age and consequently, theca has fewer plates. Total number of plates on dorsal surface about 45, areas of missing plates few, but indicating total of about 50 plates. Missing plates and taphonomic separations gives some view of ventral surface and plating there appears similar to that of dorsal face. In general, plates do not curve onto ventral face to produce incipient "marginals." Plates near thecal edges tend to be larger. Adsteals with prominent ridge adjacent to posterior (proxistele) margin and several of larger plates bossed. Articulation surface with proxistele deeply excavated under marginal ridges. Anal lobe large, squared in outline, multiplated; antanal lobe small, pointed, composed of three plates on ventral surface. Oral lobe cone-shaped, consisting of two plates on dorsal face and unknown number of plates on ventral surface; flattened anterior surface of adorals forms attachment base for brachiole. Only slight suggestion of an antibrachial lobe. Brachiole robust, somewhat disrupted in available material; apparently composed of paired ossicles with paired cover plates over food groove. Preservation precludes detection of lumen in brachiole. Brachiole incomplete but rate of taper suggests length nearly equal to that of theca.

Proxistele tetramerous, transversely broadly oval in cross section, composed of five gently distally tapering segments. Segments insert into excavated circular socket formed by proximal tetramerous circlet with large internal lumen. Mesistele comprised of two tapering plates, forming conelike segment. Proximal end of segment hollowed but distal end without lumen. Dististele dimmerous, plane separating each series horizontal, each series composed of short, nearly square, profiled plate adjacent to elongated rectangular plate about four times length of square plate, each series offset with the suture between short and long plate occurring at about mid-length of long plate of opposing series. Total length of dististele unknown but rate of taper suggests total length of two to two-and-a-half times that of theca.

Etymology.—Species is named in honor of David Smith, an employee of Geological Enterprises, Ardmore, Oklahoma, who collected the single known specimen.

Type.—Holotype CMCP 50660 preserves the dorsal face of the theca, the proximal end of the brachiole, and the proxistele, mesistele, and several elements of the dististele.

Discussion.—Terminology used in this description and discussion is that of Caster (1968). The disposition of thecal plates indicates that the ventral face was axially convex in life. We propose that the theca in *Claritacarpus* was biconvex and similar in this respect to *Girvanicystis batheri* Caster, 1968 (see Daley, 1992). Contact with the substrate is minimized to reduce adhesion either by a protruding axial ridge or protruding marginal plates that rest on the substrate. This enhances locomotor function made by the stele to lift the animal off the bottom and propel it short distances. This wriggling, but apparently inefficient, mode of locomotion is commonly accepted for homoiosteles (Gill and Caster, 1960; Caster, 1968; Kolata, 1973; Parsley and Caster, 1975; Kolata et al., 1977; Parsley, 1980, 1997).

Class STYLOPHORA Gill and Caster, 1960

Order ANKYROIDA Parsley, 1998

Suborder ANOMALOCYSTITIDA Caster, 1952

Family ANOMALOCYSTITIDAE Bassler, 1938

Genus VICTORIACYSTIS Gill and Caster, 1960

VICTORIACYSTIS aff. HOLMESORUM Ruta and Jell, 1999a

Figures 3.4, 4.2

Victoriacystis holmesorum RUTA AND JELL 1999a, pp. 399–422, figs. 1–12.

Material examined.—Single specimen CMCP 50661 is an incomplete specimen of an exposed ventral thecal face with greatly disrupted proximal aulacophore segments attached.

Discussion.—This single specimen is the first occurrence of an "Australian" anomolocystitid in North America. The incomplete

ventral surface (plastron) of the theca is exposed, and where incomplete, part of the interior dorsal surface (carapace) has been exposed by excavating the matrix (Fig. 3.4). Four pair of marginals (M1-M4), movable spine articulations on the posterior ends of the M4 marginal pair, and three plastron distal marginal plates indicate that it is an anomalocystitid ankyroid (Figs. 3.4, 4.2). The size and shape of the M1 pair is consistent with that of *Victoriacystis holmesorum* from the Lower Devonian Humevale Formation, Central Victoria, Australia. However, the thecal proportions are somewhat different in the Oklahoma specimen, being slightly narrower on the distal margin. The ventral plating of the Oklahoma specimen is also similar to *Rhenocystis latipedunculata* Dehm, 1932 from the Hunsrückschiefer (also compare to *R. latipedunculata* specimens in Ruta and Bartels, 1998 and the type species of *Victoriacystis*, *V. wilkinsi*, in Ruta and Jell, 1999b). Differences between the German and Australian genera are minor and the assignment of a name to the Clarita specimen is subjective, (*Rhenocystis* specimens in the highly metamorphosed Hunsrückschiefer have lost much detail). Significantly, the Clarita specimen expands the geographic range and facies preference of the wide-ranging Lower Devonian anomalocystitids. Commonly, anomalocystitids are found in silty carbonate settings that suggest offshore or deeper, quiet water conditions. The Clarita specimen was deposited in a less silty, shallow water carbonate setting. The only other coeval anomalocystitid known from North America is *Anomalocystites cornutus* Hall, 1858 (see Parsley, 1991 for clarification of both genus and species). In this species, the M1 pair is relatively shorter than the Oklahoma specimen and the plastron distal marginal plates are differently shaped. The posterior carapace plates of the Oklahoma specimen are large and similar to those of *V. holmesorum*.

Class RHOMBIFERA Zittel, 1879

Order DICHOPORITA Jaekel, 1899

Superfamily GLYPTOCYSTITIDA Bather, 1899

Discussion.—Glyptocystitoid rhombiferans are known from several Early Devonian faunas worldwide, including those in the Keuper Formation of West Virginia (Schuchert, 1904), the Hunsrückschiefer of Germany (Dehm, 1932), and the Humevale Formation of Victoria, Australia (Jell, 1983). However, these faunas include two very different glyptocystitoid clades that have radically different life modes. Callocystitid glyptocystitoids are found in association with hard or firm substrates or large bioclasts to which they are permanently attached (Kesling and Mintz, 1961; Koch and Strimple, 1968). These taxa are typically gregarious and found in large numbers (Schuchert, 1904; Koch and Strimple, 1968). Pleurocystitid glyptocystitids are motile, either wriggling upon the substrate or swimming for short distances (Parsley, 1970), and are suitably adapted to soft substrates. These two different clades do not co-occur in deposits younger than Late Ordovician, where both types are present in the Brainard Shale of central Illinois (Sumrall and Carlson, 2000). In the Early Devonian, only pleurocystitids were associated with other free-living echinoderm groups.

Family PLEUROCYSTITIDAE Neumayr, 1889

Subfamily PLEUROCYSTITINAE Sumrall and Sprinkle, 1995

Genus TURGIDACYSTIS new genus

Type species.—*Turgidacystis graffhami* n. gen. and sp.

Diagnosis.—Pleurocystitid with six plates around periproct; periproct somewhat rectangular; theca inflated; single pectinirhomb on L3/L4.

Description.—Genus is monotypic and description is the same as for species.

Etymology.—From Latin, *turgidus*, meaning inflated, swollen.

Discussion.—This genus is similar to Ordovician and Devonian pleurocystitids with a single L3/L4 rhomb, but its plating is distinct. The well-known *Regulaecystis pleurocystoides* Dehm, 1932

from the Lower Devonian Hunsrückschiefer is a distinct genus, being larger, less inflated, and bearing a wider single pectinirhomb, but sufficiently similar to be placed in the same subfamily. Paul (1984) placed several similar Ordovician species *Cooperi-cystis pyriformis* Parsley, 1970 and *Regulaecystis inconstans* Paul, 1984, into the genus *Regulaecystis*, but the morphology of the oral and anal areas and degree of thecal flattening precludes synonymizing any of these species pending more detailed, species-level, phylogenetic analysis.

The Clarita specimens are also similar to *Henicocystis darraghi* Jell, 1983 from the Lower Devonian of Australia; both share the inflated theca, similar elevated ribbing, and the lateral winglike projections. In addition to variations in relative plate sizes and other minor differences, *Henicocystis* has a larger, better developed, L3/L4 pectinirhomb with at least 10 dichopores and uniserial brachioles (Jell, 1983).

Based on the pectinirhomb morphology, and ridging on the anal surface and the oral area, *Turgidacystis* seems closely related to *Cooperi-cystis pyriformis*, and in general all of the Ordovician near-homeomorphs are closely related to the Devonian species (Sumrall and Sprinkle, 1995).

TURGIDACYSTIS GRAFFHAMI new species

Figures 3.2, 3.3, 3.5–3.9, 5

Diagnosis.—Same as for genus.

Description.—Theca small, with greatly arched rhomb (upper) face and nearly planar anal (lower) face, broadly triangular outline; lateral sides of theca modified by broadly curved winglike structures. Basals four, forming stem facet; B1 small and triangular on rhomb face, wide and short on anal side, forms lower margin of periproct; B2 confined to rhomb face generally pentagonal; B3 developed on rhomb face, pentagonal; B4 very small, irregularly quadrangular, narrowly in contact with the column on anal surface, forming posterior right portion of periproctal border. Infralaterals five in broad arc on the rhomb face, form closed circlet except between IL4 and IL5, where interrupted by periproct; IL1, IL2, and IL3 confined to rhomb face, form the center of the rhomb face and highest point on theca; IL1 generally smaller than other two; IL4 large, straddles thecal edge forming posterior left corner and posterior right corner of rhomb face and anal face respectively, forms posterior right corner of periproctal border; IL5 medium-sized, straddles thecal edge, forming posterior right corner and posterior left corner of rhomb face and anal face, respectively, forms posterior left corner of periproctal border. Laterals four, placed in broad arc across rhomb face; L1 very large, straddles thecal margin forming right edge and anterior left margins of rhomb face and periproctal face, respectively; L2, mostly on rhomb face, forms anterior right thecal margin; L3 confined to rhomb face, located along thecal midline; L4 extremely large, straddles thecal margin, forms anterior left margin of theca and anterior right corner of periproctal border, shares small vertical suture with L1 (Fig. 5.2). Radial circlet open with three, perhaps four plates, R1 largest, straddling right edge of theca from rhomb side; R2, slightly larger than R1, along midline of rhomb face; R3 straddles left edge of theca of rhomb face; hints of sutures along thecal edge separating R1 and R3 into two plates cannot be confirmed in present material. Orals surround laterally elongate peristome. O1 relatively large, transversely elongate, bearing slitlike hydropore and small circular gonopore with O7. O2 and O3 cannot be clearly distinguished in present material. O4 and O5 very small, form brachiole facet for BC brachiole. O6 small, borders O1 and O7 as in other glyptocystitids. O7 relatively large, does not share in periproctal border, shares hydropore and gonopore with O1. Two brachioles attaching to thecal along laterally shared ambulacra, incompletely preserved in holotype; brachioles robust with stout biserial brachiolar plates and much smaller cover plates over narrow food groove (Fig. 5.1). Single equal, symmetrical, compressed, and extremely narrow pectinirhomb present on L3/L4 suture (L/W ratio about 7:1); four confluent dichopores present in holotype. Ornament on rhomb face distinctive, manifested as prominent ridge systems that radiate from centers of IL1, IL2, IL3, L2, and L3 (Fig. 5.1). Ridges pass through plate edges rather than plate corners. Ornament on anal face expressed as series of parallel beaded ridges on right and left sides of periproct (Fig. 3.3). Periproct very large, rectangular with rounded corners, centered on anal face, sunken, bordered by B1, B4, IL4, IL5, L1, and L4, bordered proximally and distally by high beaded ridges (Fig. 3.3). Partially preserved periproctal membrane of extremely small platelets in distal right edge of periproct (Fig. 5.2). Anal pyramid unknown. Several specimens known with partial columns (Fig. 3.5). Proximal stem plated with thin holomeric inner and outer columnals. Distal columnals barrel-shaped holomeric, much narrower and longer than proximal stem, apparently lacking holdfast as do other pleurocystitids.

Etymology.—The species is named in honor of Allen Graffham, who provided the material.

Types.—The holotype CMCP 50662 is a small theca with both faces exposed; paratype CMCP 50663 is a rhomb face of a theca with a nearly complete stem attached; paratype CMCP 50664 is a juvenile with the anal face of the theca exposed and several segments of the column attached; paratype CMCP 50665 is a partly preserved anal face of a theca; paratype CMCP 50666 is a disarticulated L3 plate.

Discussion.—Even though specimens are imperfectly preserved, they impart a great deal of information. This species appears to have close affinities to the Late Ordovician single rhomb genus *Coopericystis*. The surficial topography and pattern of ridges on the rhomb face and morphology of the rhomb are remarkably similar. The Late Ordovician *Praepleurocystis* Paul, 1967 also has large and wide L1 and L4 laterals and a prominent radiating ornament ridge system. Thecal plate patterns and convexity are somewhat different in the type species of *Pleurocystites*, *P. squamosus* Billings, 1854.

Regulaecystis pleurocystoides from the Lower Devonian Hunsrückschiefer is similar to *Turgidacystis* n. gen. but its preservation precludes close comparisons. *Regulaecystis* does not seem to be as inflated, the ornament ridge system on the rhomb face is different, and the plate outlines do not correspond closely. Caution in making close comparisons between the two genera is necessary because plate outlines in *Regulaecystis* are distorted by preservation. The broad similarities between the two genera suggest that both were adapted for living in a similar environment. Paul (1984) discussed *Regulaecystis devonica* Paul, 1974, Meadfoot Beds, Triangle Point, Devonshire, and reassigned them to the Middle Devonian (Givetian) rather than the Lower Devonian (Siegenian-Emsian), as he did in his original description. This species, based on a single weathered specimen, is elongated, oval in outline, and has a single, but large, L3/L4 rhomb with numerous dichopores. Its similarities to *Regulaecystis* are somewhat vague, and the species cannot be assigned with confidence to the genus.

The bowed transverse ridge on laterals L1 and L4 and similar bowing on the extensions of B1 and B4 strongly indicate the polyplated periproct bowed along the sagittal axis of *Turgidacystis*. There is a distinct narrow facet just below the crest of each ridge, which is probably the attachment area for the polyplated surface. Bowing the polyplated field would have increased the surface area and possibly enhanced its flexibility.

All pleurocystitids have between zero and three respiratory pectinirhomb. However, Ordovician taxa show the highest disparity with taxa bearing between zero and three rhombs whereas Devonian taxa all have either zero or one rhomb. It is clear that with this general decrease in respiratory structures through time, an increase in reliance upon other respiratory mechanisms must take place. Paul (1967), Parsley (1970), Broadhead and Strimple (1975), and Brower (1999) have all proposed that the large flexible periprocts of pleurocystitids were associated with respiratory exchange occurring in the gut. Brower further argued for the presence of a water vascular system in the brachioles to aid in respiration. However, Parsley (1970, 1982), Sprinkle, (1973), and Haugh and Bell (1980) have argued that brachioles lacked extensions of the water vascular system.

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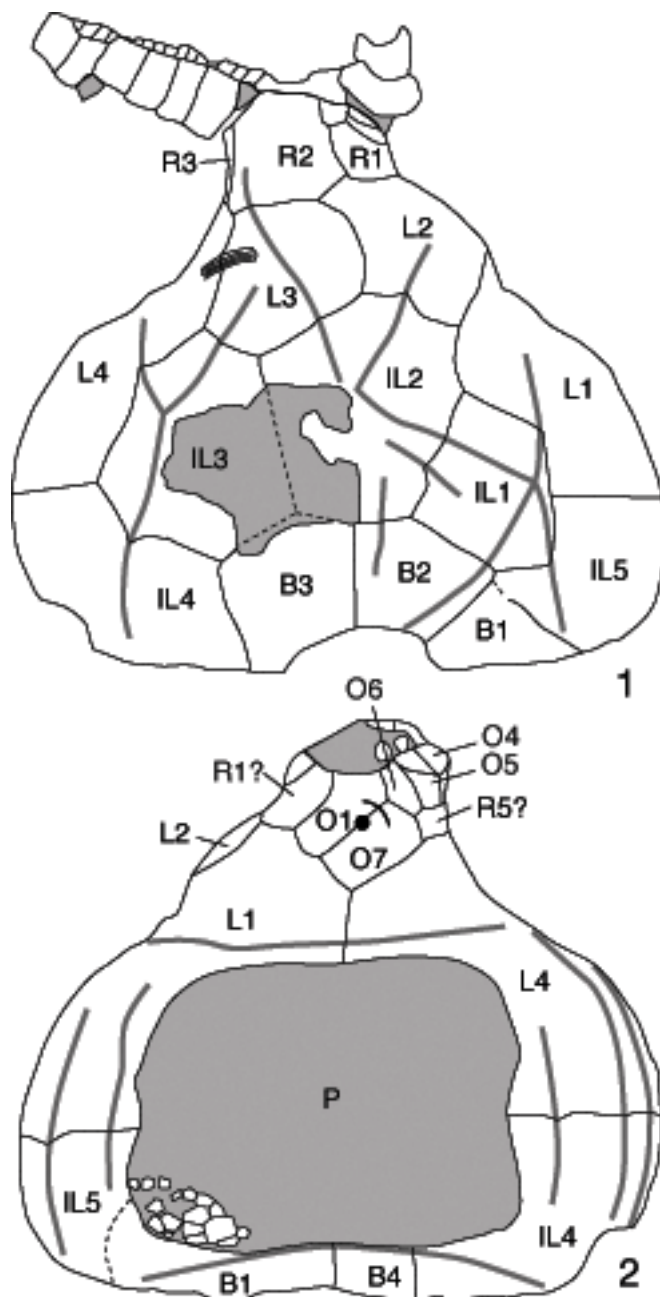


FIGURE 5—*Turgidacystis graffhami* n. gen. and sp., CMCP 50662. 1, The nonperiproctal face. Note the shifting of most of the thecal plates to this face and the presence of a single small pectinirhomb on the L4/L3 suture. Stippled area between IL2 and IL3 is a hole through the specimen. 2, Anal side of specimen, showing the enlarged periproct and position of the hydropore and gonopore between O1 and O7.

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APPENDIX 1—Data set for homoiosteles. Based on and modified from character set in Parsley (1997, p. 235, 241).

<i>Gogia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coleicarpus</i>	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Castericystis</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
<i>Minervacystis</i>	1	1	2	0	0	1	0	0	2	1	1	1	1	0	1	0	0	0
<i>Dendrocystites</i>	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	1	0	1
<i>Maemilia</i>	1	1	2	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0
<i>Heckericystis</i>	1	1	2	1	1	?	1	0	1	1	1	1	1	0	0	0	0	0
<i>Dendrocystoides</i>	1	1	2	1	1	1	1	0	2	1	1	1	1	1	0	1	0	1
<i>Girvanicystis</i>	1	1	1	1	1	2	1	0	2	3	1	3	1	0	0	0	1	0
<i>Rutroclipeus</i>	1	1	1	0	0	1	2	0	2	3	1	3	1	1	0	1	?	1
<i>Syringocrinus</i>	1	1	1	0	1	1	3	1	2	2	1	2	1	1	1	1	0	0
<i>Iowacystis</i>	1	1	1	0	1	1	3	1	2	2	1	2	1	1	0	0	1	1
<i>Myeinocystites</i>	1	1	1	0	1	1	3	2	2	?	1	?	1	1	0	1	0	0
<i>Belemnocystites</i>	1	1	1	0	1	1	3	2	2	?	1	?	1	1	0	1	0	0
<i>Scalenocystites</i>	1	1	1	0	1	1	3	1	2	2	1	2	1	1	0	0	1	1
<i>Claritacarpus</i>	1	1	2	1	1	?	?	?	2	2	1	2	?	1	0	1	0	?

APPENDIX 2—Data set for pleurocystitid rhombiferans. Based on and modified from character set in Sumrall and Sprinkle (1995, p. 778).

<i>Macrocystella</i>	0	0	0	0	0	1	?	?	0	0	0	0	0	0	1	0	0	0	?	?
<i>Cuniculocystis</i>	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	?	?
<i>Cheirocystella</i>	0	0	0	1	0	0	1	?	?	1	0	0	0	0	1	1	0	?	0	?
New Genus B	0	1	0	0	0	0	0	?	?	0	0	0	0	?	0	3	1	0	?	?
<i>Deltacystis</i>	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	2	1	1	0	?
<i>Plethoschisma</i>	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	2	1	?	0	?
<i>Pleurocystites</i>	1	1	0	{01}	1	1	2	1	1	1	{01}	1	1	0	1	0	2	1	1	1
<i>Pygocystis</i>	1	1	0	{01}	1	1	3	1	1	1	1	1	1	0	1	0	2	1	1	1
<i>Amecystis</i>	1	1	0	0	0	0	3	1	1	1	0	1	1	0	1	0	2	1	1	?
<i>Regulaecystis</i>	1	1	0	0	1	0	2	1	1	1	0	1	0	0	1	0	2	1	?	?
<i>Coopericystis</i>	1	1	0	0	1	0	?	?	1	1	?	1	0	0	?	?	?	?	?	?
<i>Praepleurocystis</i>	1	1	0	1	1	1	3	1	1	1	0	1	1	0	1	0	2	1	1	1
<i>Turgidacystis</i>	1	1	0	0	1	0	2	1	1	1	0	1	0	1	1	0	2	1	1	1