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Bulletins of American Paleontology

Number 380, March 2011



BULLETINS OF AMERICAN PALEONTOLOGY

Established 1895

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Bulletins of American Paleontology

Number 380, March 2011

ISSN 0007-5779 ISBN 978-0-87710-493-3

Library of Congress Catalog Card Number 2011920734 © 2011, Paleontological Research Institution, 1259 Trumansburg Road, Ithaca, New York 14850, U. S. A.

THE NORTH AMERICAN HOLOCYSTITES FAUNA (ECHINODERMATA, BLASTOZOA: DIPLOPORITA): PALEOBIOLOGY AND SYSTEMATICS

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ABSTRACT

The Holocystites fauna of central North America includes most known Silurian Diploporita (Echinodermata: Blastozoa). This distinctive diploporite association, widespread in the Wenlockian of Wisconsin, Illinois, Indiana, Kentucky, Ohio, and Tennessee, consists of eight genera in the Aristocystitidae, Sphaeronitidae, and Holocystitidae. Species of Holocystites Hall, 1864, and Triamara Tillman, 1967, are particularly characteristic. The fauna is best known from the Osgood Member, Salamonie Dolomite (late Llandoverian-early Wenlockian) of southeastern Indiana. Expanded quarrying operations near Napoleon, Ripley County, Indiana, add materially to knowledge of the Holocystites fauna. Thousands of specimens were recovered, including some in life position. Information from this and other localities allows formulation of a paleoecological model for the Holocystites fauna, which is tested against previously known distributional information. Most Silurian diploporites were low-level feeders with relatively inefficient subvective systems as compared with co-occurring camerate crinoids. In the Osgood, they required firm attachment sites in comparatively quiet, offshore, dominantly soft-bottomed environments with a moderate rate of continuous terrigenous sedimentation, conditions limited in southeastern Indiana to the Ripley Island positive area. Two major adaptive strategies are recognized: one relatively eurytopic group comprising species with free adults with elongate thecae, narrow bases, and aboral, stem-like processes, and a more stenotopic group of globular, large-based, completely sessile (attached) species. New taxa include a species of Holocystites Hall, 1864 (H. clavus n. sp.), a new genus (Paulicystis n. gen.) related to Trematocystis Jaekel, 1899, but with uniquely large ambulacral facets, and a new Pentacystis-like genus (Osgoodicystis n. gen.). The fauna also has an advanced sphaeronitid (Finitiporus n. gen.), the only Silurian sphaeronitid yet known. Both the Sphaeronitidae and Holocystitidae are revised. Subfamilies are established in both (Sphaeronitidae: Sphaeronitinae and Herpetocystinae; Holocystitidae: Holocystitinae, Pentacystinae, and Trematocystinae), based largely on peristome morphology. Holocystites is divided into three new subgenera (Holocystites, Megacystites n. sgen., and Sepulticystis n. sgen.) on the basis of pore morphology. Evolutionary trends are noted in the Holocystitidae toward reduction in number of thecal and peristomial plates, enlargement of the subvective system, elevation of the theca. Humatipore morphology becomes more specialized and efficient, but average size decreased. Detailed specific and generic phylogenies are constructed, using both traditional and quantitative phenetic methods. All produced similar results. Osgood diploporite biostratigraphy is revised and a zonal scheme presented. Osgood diploporites are strongly endemic.

³Corresponding author, whose contribution (since September 2009) has been almost entirely confined to proofing, indexing, and editorial matters necessary to correct minor typographical errors introduced when the original typescript was scanned using OCR software. As a result, some of the sections, especially those dealing with phylogeny, will seem dated now. New taxa introduced here are to be referred to as "Frest & Strimple in Frest *et al.*, 2011."

INTRODUCTION

The late Llandoverian-early Wenlockian Osgood (Osgood Member, Salamonie Dolomite of Pinsak & Shaver, 1964) of Indiana, Kentucky, and Tennessee has long been a focus of paleontological interest because of its extraordinary diploporite fauna. It served as the *exemplar nonpareil* of the *Holocystites* fauna (Paul, 1971), reported from six horizons in the Wenlockian of eastern North America. The *Holocystites* fauna includes all known Silurian Diploporita (Echinodermata, Blastozoa), with the exception of the more cosmopolitan Gomphocystitidae, common to Europe and North America (Bockelie, 1979).

¹Deceased 10 April 2008. Because Harrell Strimple was unable to contribute to the present manuscript beyond the first draft (Frest, 1983), any remaining errors of fact or judgement are solely the responsibility of the senior author.

²Deceased 21 August 1983.

Major impetus for the present work was provided by the discovery of an important new Osgood diploporite locality in Ripley County, Indiana. Expanded quarrying operations at the New Point Stone Company's Napoleon quarry [SW 1/4 sec. 21 and NW 1/4 sec. 28, T9N, R11E, Osgood 71/2' quadrangle; this is the same as Paul's (1971: 164) Locality 12; Text-fig. 1], due to the discovery of an unusually thick Brassfield and largely limestone Osgood section, led to the stripping off and dumping as waste of large quantities of very fossiliferous upper Osgood shales. This material contained thousands of diploporite thecae and other echinoderms, as well as a rich normal marine invertebrate fauna. Prior to the Napoleon discovery, only ca. 200 diploporites had been recovered in over a century of collecting. Extensive collecting by several Cincinnati, Ohio, area collectors, notably W. Bruce Gibson, D. Cooper, and D. Bissett salvaged much of the available material. Aside from our own collections, we were able to examine some of their material, and all three generously donated numerous critical specimens.

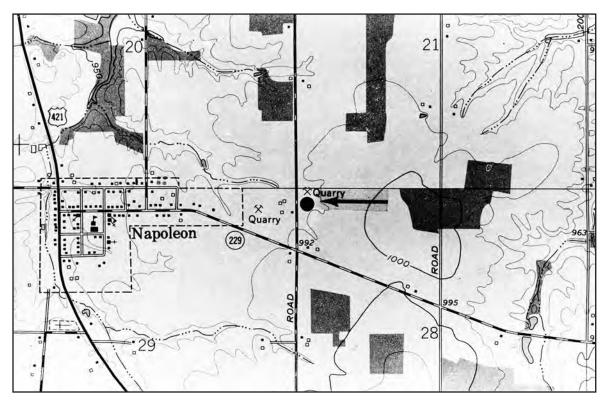
Most Osgood localities lack macrofossils, and all but a handful of specimens previously found were from a dozen sites in southeastern Indiana (Paul, 1971; Frest *et al.*, 1977). Descriptions of diploporite localities are included as an Appendix herein. Osgood fossil localities in this area generally conform stratigraphically to the four-part Osgood subdivision established by Foerste (1897), *i.e.*, basal Osgood Limestone, Lower Shales, Middle Osgood Limestone, and Upper Shales. Diploporites occur only in the upper half of the Osgood

Member and are only known from the American and European echinoderm Providences (Text-fig. 2). The *Holocystites* fauna is endemic to the Eastern North American Province.

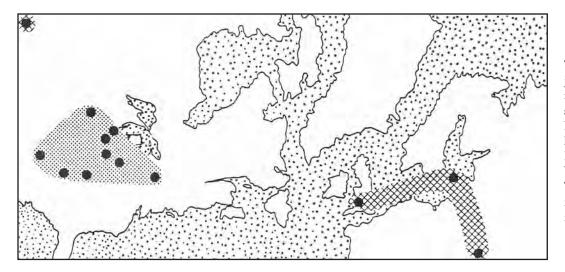
Previous Studies

The initial taxonomic phase of work on the *Holocystites* fauna dates to Hall (1861, 1864, 1868) and Winchell & Marcy (1865), who described internal molds from the Racine Dolomite and Manistique Formation and equivalents of Wisconsin and Illinois. The much richer Osgood diploporite fauna was a later discovery, with early taxonomy largely the work of S. A. Miller (see Miller, 1878, 1879, 1880, 1882, 1889, 1891, 1892a-b, 1894; Miller & Faber, 1892; Miller & Gurley, 1894, 1895). One more species was described by Foerste (1917) from Ohio. By 1920, over 50 nominal species had been established, all in the genus *Holocystites* Hall, 1864. Much of the early work was overly typological by modern standards. The total number of Osgood diploporite specimens Miller had, for example, appears to have been roughly equivalent to the number of species that he established.

Following the first burst of taxonomic interest was a lull of several decades duration. A separate genus, *Triamara* Tillman, 1967, was established for one Osgood form. More substantially, Paul (1971) monographed the North American *Holocystites* fauna. As well as producing an exceptionally thorough and careful taxonomic revision (reducing the fauna to 18 species distributed among five genera), he also considerably refined the



Text-fig. 1. Enlargement of a portion of the Osgood 71/2' quadrangle, Ripley County, Indiana, showing locathe tion of the Napoleon Quarry, New Point Company, the major source of diploporites described in this work.



Text-fig. 2. Localities with major Wenlockian echinoderm faunas (large dots). Smallscale dotting indicates Eastern North American Province; cross hatching indicates European Province. Modified from Witzke *et al.* (1979: fig. 1). The base map is not intended to reflect actual Wenlockian continental positions.

biostratigraphy of the Osgood Member, Salamonie Dolomite Formation, a thin (average 4-5 m) unit. Most previously collected specimens are from a thin (15 cm) layer, 7-8 cm below the top of the "Lower Shales" (actually siltstones: the "main cystoid layer" of Foerste, 1897), and from the lower unit of the Middle Osgood Limestone. As described by Hubbard (1892), the preferred collection method was to wander up the creek valleys, scanning the underside of the bottom ledge of the prominent limestone (lower unit, Middle Osgood Limestone). Only a half-dozen species and a total of *ca.* 50 specimens were reported from the Upper Shales, largely because this bed is seldom exposed. However, the Napoleon specimens are mostly from this unit. With over a dozen diploporite species, the Osgood Upper Shales now have the most diverse Silurian diploporite fauna yet reported.

SCOPE

We recognize three new genera and five new species from the Napoleon locality. Several other new taxa are as yet too incompletely known to justify description. Among the new taxa is the only Silurian sphaeronitid (*Finitiporus* n. gen.), an advanced form with peculiar peristomial morphology and considerably reduced diplopores. New holocystitids include *Paulicystis* n. gen., an Upper Shales relative of the Lower Shales *Trematocystis* Jaekel, 1899, and another new form, *Osgoodicystis* n. gen., closely related to the previously described *Pentacystis* Paul, 1971. Large numbers of specimens of previously described holocystitid taxa enable us to supplement Paul (1971) in many details. More importantly, the much-enlarged database suggests the propriety of subdivision of the Holocystitidae into subfamilies. Although the aristocystitid *Triamara* is abundant at Napoleon, we have nothing to add to Paul's taxonomic treatment.

The existence of a relatively completely collected, stratigraphically and geographically limited, and phylogenetically closely related diploporite fauna allows construction of the first detailed

phylogeny for any diploporite family. Both traditional intuitive phyletic and quantitative phyletic (phenetic) approaches were utilized: interestingly, both yielded similar results. Large sample sizes have enabled accurate determination of species variation, and suggest some criteria for distinguishing evolutionary trends and mutations from normal variation and abnormalities due to physical injury. Detected trends seem to parallel the evolution of the Diploporita as a whole, but particularly that of the Sphaeronitida, as deduced by previous authors from abundant and diverse Ordovician occurrences (see especially Paul, 1984; Paul & Bockelie, 1983; Bockelie, 1984).

Diploporita are sufficiently common in the Osgood that a tentative zonation can be suggested for southeastern Indiana. It is likely that the same zonation eventually will prove applicable to other areas. The Osgood contains several diploporite horizons, each with a high degree of endemicity. Several microniches are represented, and the *Holocystites* fauna members as a whole pursued two main adaptive strategies to compete successfully with co-existing Crinoidea and crinoid-like Rhombifera. Considerable new information on Osgood echinoderm paleoecology and functional morphology has been accumulated, and is dealt with in separate sections below. Additionally, existing information on the biogeography and distribution of the *Holocystites* fauna is synthesized and updated. Whereas summary community paleoecology is discussed herein, details are elaborated elsewhere (Frest *et al.*, 1999).

WENLOCKIAN ECHINODERM PALEOBIOGEOGRAPHY

SETTING

Ordovician echinoderms exhibit a marked degree of provinciality, more or less in line with that reported for trilobites and brachiopods. Three main provinces are recognized (Paul, 1976): North American, Baltic, and South European. These are most

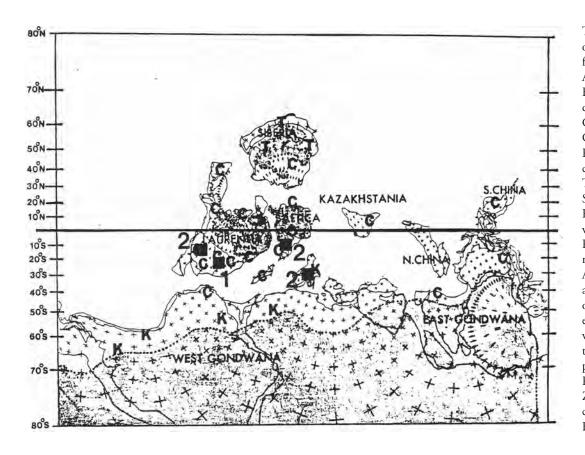
distinct in the Early Ordovician, with later faunas becoming gradually more cosmopolitan, possibly due to closure of ocean barriers. Most echinoderm localities lie within 30°N and S of the contemporary equator (Paul, 1976). The richest faunas inhabited warm shallow tropical seas. Oxygen production could have centered on shallow seas, and echinoderm respiratory pore structures reached their taxonomic and morphologic zenith during this period (Paul, 1976, 1979). An extraordinary proliferation of echinoderm classes occurred during the Early and Middle Ordovician, with as many as 17 classes being present in single units (Sprinkle, 1980). Diploporites are common and diverse in most known Ordovician tropical and polar faunas, but are sparse in North American tropical faunas for unknown reasons (Paul, 1976). On the other hand, nearly all known paracrinoids are Middle Ordovician and North American (Parsley & Mintz, 1975). Widespread glaciation and accompanying glacioeustatic regression and refrigeration at the close of the Ordovician seems to have stimulated large-scale extinction and subsequent radiation events in the early Silurian (e.g., Johnson, 1974, 1984; Brenchley, 1984; Brenchley & Newall, 1984; Stanley, 1984a-b: for a critical discussion of Late Ordovician crinoid extinctions and their possible causes, see Eckert, 1988). Llandoverian deglaciation coincided with wide scale onlap of marine waters onto broad areas of continental platforms, notably the North American and Baltoscandian (Berry & Boucot, 1973). Among the brachiopods, Ordovician New World endemics were rapidly replaced by Old World groups (Sheehan, 1975). The Silurian as a whole is characterized by cosmopolitanism, with most areas included in the huge temperate-tropical North Silurian Realm (Boucot, 1975) and only limited endemism to the north and south (Tuvaella and Clarkeia Realms of Boucot & Johnson, 1973; Malvinokaffric Realm of Boucot, 1975: text-fig. 3). As regards echinoderms, explosive evolution occurred in the crinoid subclass Camerata. Camerate diversification was initiated during the Llandoverian and continued through the Wenlockian, coinciding with continued widespread transgression (Witzke & Strimple, 1981). A similar radiation occurred in the rhombiferan family Callocystitidae at the same time. Originating from the American Upper Ordovician Lepadocystis Carpenter, 1891, this group began to diversify in the early Silurian (Anartiocystis Ausich & Schumacher, 1984, Brockocystis Foerste, 1914, and related genera) and was extraordinarily diverse and widespread during the Wenlockian. Unlike the brachiopods, the Silurian echinoderm radiation has one of its major focal points in North America, from ancestral stocks already present in North American Upper Ordovician faunas (Witzke et al., 1979). However, something indistinguishable from Anartiocystis is known from the Russian Ordovician (figured as Scoliocystis Jaekel, 1899, by Hecker, 1964: pl. 3, figs 10, 11a-b; see Paul & Donovan, 2011: fig. 7), so this geographic radiation was probably more complex.

Major offlap might have been initiated near the close of the Wenlockian, and echinoderm diversity declined through the close of the Silurian. Relatively few families originated during this period, and the overall picture is of gradual, and cumulatively severe, attrition. The last known paracrinoids and eocrinoids are Wenlockian (Frest & Strimple, 1981a). The rhombiferan family Pleurocystitidae, diverse and abundant nearly worldwide during the Middle and Upper Ordovician, vanished during the Silurian, only to reappear in the Devonian (Paul, 1982). Attrition continued at the class level well into the Devonian, during which three more echinoderm classes became extinct (McIntosh & Macurda, 1979, listed five, but Ressmeyer & Frest, 1983, and Kolata et al., 1991, extended the range of the Cyclocystoidea and mitrate Stylophora into the Carboniferous). Endemism and provinciality are most evident in the lowermost and uppermost series (Gedinnian and Famennian), and the prolific North American Middle Devonian faunas are largely derived from extraprovincial lineages (McIntosh & Macurda, 1979; Witzke et al., 1979). The presumed oxygen-level crisis of the Ordovician was apparently short-lived. Thecal respiratory structures in the Echinodermata become less widespread, and less diverse morphologically, in the Silurian. Most classes with elaborate structures perished by the close of the Devonian; the highly efficient blastoids are an exception.

WENLOCKIAN ECHINODERM BIOGEOGRAPHY

Diverse and abundant Wenlockian echinoderm faunas are currently known mostly from within the limits of the North Silurian brachiopod Realm (Text-figs 2-3). Major faunas have been described from eastern North America and western Europe, but small numbers are also reported from the former USSR, China, Australia, and western North America. The most diverse assemblages occur within 30°N and S of the Silurian equator (Text-fig. 3), especially in the extensive carbonate platform environments, believed to represent warm, shallow tropical seas, which are developed over much of the North Silurian Realm.

In the contrast to the relatively ubiquitous brachiopods (but see Boucot, 1999), Wenlockian echinoderm faunas show strong endemism. Witzke *et al.* (1979) distinguished two major regions within the confines of the North Silurian Realm, *i.e.*, eastern North America and Europe. We have updated the tabulations contained in that paper (Witzke *et al.*, 1979: text-fig. 1) to reflect new data (Text-fig. 4; Table 1). A high degree of endemism is evident on the familial level within both crinoid and non-crinoid groups – so much so that we consider them to represent true Silurian echinoderm provinces. Boucot (1999) reached parallel conclusions as regards contemporaneous brachiopod provinces.



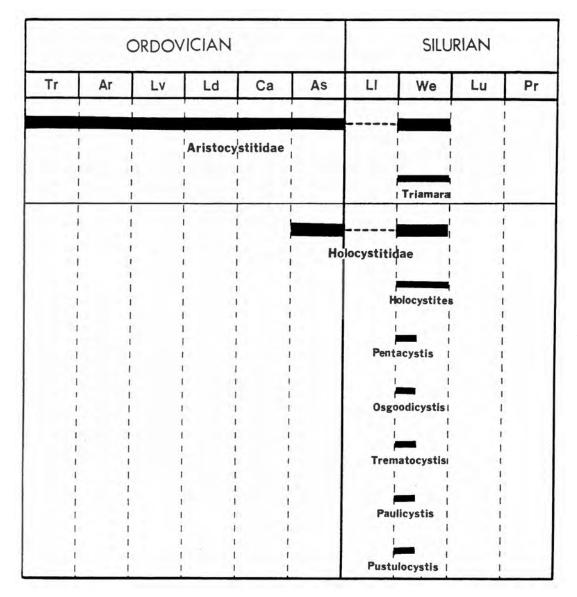
Text-fig. 3. Biogeography of Wenlockian echinoderm faunas. (1) Eastern North American Province; (2) European Province. Letters designate brachiopod realms: C, Cosmopolitan Realm; K, Clarkeia Realm; T, Tuvaella Realm; Boucot (1975) included the Cosmopolitan and Tuvaella realms in his North Silurian Realm. The Clarkeia Realm corresponds roughly with the Malvinokaffric Realm. Shaded portions represent inferred land areas. All echinoderm occurrences are within 30°S latitude of the presumed Silurian equator (tropical seas) and within the boundaries of the Cosmopolitan brachiopod Realm (North Silurian Realm). Base map after Ziegler et al. (1977); brachiopod realms are those of Boucot & Johnson (1973).

Two blastozoan classes (Paracrinoidea and Eocrinoidea), which were common to both areas through much of the

Ordovician (Paul, 1976), are endemic to the eastern North American Wenlockian. The Blastoidea, which originated in

Table 1. Endemic echinoderm groups in the two Wenlockian echinoderm provinces recognized currently.

EASTERN NORTH AMERICAN PROVINCE	EUROPEAN PROVINCE
Crinoidea	Crinoidea
Gazacrinidae	Abacocrinidae
Lampterocrinidae	Polypeltidae
Emperocrinidae	Dactylocrinidae
Prokopicrinidae	Taxocrinidae
Hirneacrinidae	Thenarocrinidae
Homocrinidae	Metabolocrinidae
Zophocrinidae	Mastigocrinidae
Dendrocrinidae	Sphaerocrinidae
Rhombifera	Rhombifera
Caryocrinitidae	Scoliocystinae
Callocystitinae	
Diploporita	
Aristocystitidae	
Holocystitidae	
Sphaeronitidae	
Blastoidea	
Eocrinoidea	
200.11101404	



Text-fig. 4. Diagram showing known age ranges for Holocystites fauna genera and the families to which they belong. Wide bars are family ranges; narrow bars are genera. Dashes indicate time spans from which no taxa are yet known, but must occur if family concepts are correct. The Osgood (latest Llandoverian-early Wenlockian) endemics dominate the picture, but two genera (Holocystites and Triamara) have more extensive Wenlockian ranges. Note the absence of definite Llandoverian taxa.

North America by the Middle Ordovician (Broadhead, 1980a, 1984) remain exclusively North American. The Coronoidea, in contrast, are European in origin (Paul, 1976, 1985; Donovan & Paul, 1985) and occur widely there in the Ordovician, but are abundant and diverse in the eastern North American Province during the Silurian and rare in Europe (Brett et al., 1983). The only described post-Ordovician European coronoids are rare forms from the Pridoli, former USSR (Arendt & Rozhnov, 1984), from the Wenlockian of Great Britain (Donovan & Paul, 1985) and from the Wenlockian and Ludlovian of former Czechoslovakia (Paul, 1985). In the better-known Crinoidea, considerable endemism is evident in both the Camerata and Inadunata (Table 1), even though many genera are cosmopolitian (Witzke et al., 1979). Western North American Wenlockian faunas are poorly known, but an undescribed Nevada fauna shows clear European affinities.

Although the record is of course not as complete as desirable, the major European and eastern North American faunas have been studied extensively for nearly a century. We think it unlikely that future finds in these areas will eliminate the apparent provinciality. Even though modem marine faunal provinces are often defined at the species level, provinciality is clearly reflected at higher taxonomic levels (Campbell & Valentine, 1977), and paleoprovinces can validly be compared to modem provinces. An interesting feature of Wenlockian echinoderm evolution is that vigorous speciation appears to have taken place largely within the confines of the widespread epicontinental seas (Witzke & Strimple, 1981). Silurian continental-margin deposits frequently lack the characteristic interior sea elements and generally have much lower diversities. The optimum opportunities for speciation seem to have occurred within the extensive interior warm epicontinental seas during major transgressive episodes, contra Eldredge (1974), whereas major marine regressions represent times of crisis (Sheehan, 1975), perhaps due to compression and restriction of especially favorable environments into geographically limited areas. The Silurian echinoderm record thus appears to support the niche-variation hypothesis (e.g., Bretsky & Lorenz, 1970). It appears that prolonged stability, whether in North American and European epicontinental sea environments or in modern deep-sea environments (Schopf, 1976), encourages high genetic variability, resulting in close niche partitioning and the development of diverse, complex biotas composed of stenotopic species (Sanders, 1968). Such biotas with narrow environmental tolerances can prove unable to cope with rapid environmental changes, and can be particularly prone to replacement by eurytopic taxa during times of crisis. Ludlovian and Pridolian echinoderm faunas, as contrasted with those of the Wenlockian, do appear to conform to this model. This is most easily demonstrable in areas like Gotland, which has Silurian echinoderm-bearing rocks ranging in age from the Llandoverian to the Ludlovian (Franzén, 1983). Comparison of familial and generic affinities of the crinoids in this sequence indicates not only a decrease in diversity from the late Wenlockian upward, but a decrease in apparent provinciality (Franzén, 1983: figs 2-3).

Among the Crinoidea, the lineages that dominate the Wenlockian seem to have their origins in the Late Ordovician North American fauna (Brower, 1973; Eckert, 1988), from survivors of the so-called Caradocian-Ashgillian biotic crisis. Despite recent work (e.g., Witzke & Strimple, 1981; Eckert, 1984; Ausich, 1984a-b, 1985, 1986a-c, 1987a-b), early and middle Llandoverian crinoid faunas remain poorly known. Available data indicate a high degree of local endemism. The earliest occurrences of many of the more cosmopolitan Wenlockian lineages (e.g., crotalocrinitids, eucalyptocrinitids) are in the late Llandoverian-early Wenlockian Welton Member, Scotch Grove Formation, of Iowa (Witzke, 1976, 1985; Witzke & Strimple, 1981). By the late Llandovery, crinoids and rhombiferans were already diverse and abundant in the carbonate platform environments of North America (Witzke et al., 1979; Witzke & Strimple, 1981). Derivatives of these same late Llandoverian lineages were equally well represented in the European Province by the early Wenlockian. The echinoderms reached a Silurian zenith in the transgressive carbonate sequences of Wenlockian epicontinental seas on both continents, with a decline in diversity, abundance, and provinciality evident with the onset of dominantly regressive conditions during the Ludlovian. Each major epicontinental sea shows similar patterns of echinoderm diversification and abundance by the Wenlockian. Ecologically equivalent faunas exhibit many close morphologic and some taxonomic parallels but frequently display clear endemism at high taxonomic levels. Even in those families and genera common to both, species are invariably distinct.

SILURIAN DIPLOPORITES

The occurrence and history of Silurian Diploporita, most particularly the Holocystites fauna, show a pattern of derivation and diversification similar to that of the Crinoidea, even though the record of the former, as a typically uncommon blastozoan class, is not as completely documented. Silurian Diploporita are distributed among four families: the Aristocystitidae (superfamily Aristocystitida), Sphaeronitidae and Holocystitidae (Sphaeronitida), and Gomphocystitidae (Protocrinitida; generally cited as Glyptosphaeritida, but see Paul, 1984: 65). All four families are present in the Osgood, but the last, constituting the most cosmopolitan Silurian diploporite group, is not here considered a part of the Holocystites fauna. The Gomphocystitidae occur widely in the Silurian of North America and of Europe, and single taxa are abundant in many Llandoverian-Ludlow echinoderm faunas, including the Osgood (Gomphocystites indianensis Miller, 1889). Possibly originating in the European Middle Ordovician from a genus like Pyrocystites Barrande, 1887 (although Bockelie, 1979: 157, suggested that this genus might not be a gomphocystitid, and Paul, 1984: 68, regarded the genus' relation to the Gomphocystitidae as uncertain), they are represented by a single taxon in the uppermost Ordovician of Wales (Paul, 1984). The first undoubted Silurian gomphocystitid occurs in the Late Llandoverian Hopkinton Dolomite of Iowa (Witzke, 1976). The family is present in both provinces by the Wenlockian, but represented in each by endemic genera (Bockelie, 1979). The Aristocystitidae achieved wide distribution and were quite diverse during the Middle and Upper Ordovician in all areas with diploporite faunas except North America (Paul, 1971, 1976). The North American Wenlockian genus Triamara remains the sole Silurian representative. The early history and distribution of the Sphaeronitidae is identical to that of the Aristocystitidae (Paul, 1973, 1976), but the family survives into the Devonian and includes the last known diploporites. Devonian representatives are frequent in Eurasia and North Africa, and occur also in Oklahoma and Canada (Frest, unpubl. data), but are totally absent from the prolific Devonian echinoderm faunas of eastern and central North America, and also from the Silurian of Europe. The Holocystitidae are represented by only two taxa (one genus) from the Upper Ordovician of the United Kingdom and Sweden (Paul, 1971, 1973), but are prolifically represented in the Wenlockian of North America (Table 2).

As emphasized by Paul (1971, 1982), part of the peculiarities of Silurian diploporite distribution might be explained by vagaries of preservation, but not all. Lower Silurian diploporites are almost unknown, but the absence of sphaeronitids and aristocystitids might reflect a genuine evolutionary crisis occurring at the end of the Ordovician. Neither family, for example, is a part of the diverse Hopkinton Formation (Witzke, 1976) and lower Scotch Grove Formation (Witzke, 1985) as-

Table 2. Members of the *Holocystites* fauna and their occurrence.

	Formation					
	Osgood Osgood I		т 1	1 7 11 D 1		XV7 1 1
Taxon	Indiana	Tennessee	Laurel	Joliet	Racine	Waukesha
Family Aristocystitidae						
Triamara ventricosa (Miller, 1879)	X	X				
T. tumida (Miller, 1879)	X			X		
T. multiporata Paul, 1971	X					
T. laevis Paul, 1971	X					
Family Holocystitidae						
Holocystites cylindricus (Hall, 1861)	X	X		X		
H. clavus Frest & Strimple, n. sp.	X					
H. alternatus (Hall, 1861)	X	X	X		X	X
H. abnormis (Hall, 1864)	X	X			X	
H. spangleri Miller, 1891	X				X	
H. scutellatus Hall, 1864	X	X	X	X		
H. ovatus Hall, 1864	X			X		
H. greenvillensis Foerste, 1917						
Pentacystis simplex Paul, 1971	X					
P. sphaeroidalis (Miller & Gurley, 1895)	X					
P. gibsoni Frest & Strimple, n. sp.	X					
Osgoodicystis bissetti Frest & Strimple, n. sp.	X					
O. cooperi Frest & Strimple, n. sp.	X					
O. wykoffi (Miller, 1891)	X					
Trematocystis globosus (Miller, 1878)	X					
T. rotundus (Miller, 1879)	X					
T. wetherbyi (Miller, 1878)	X					
T. magniporatus Frest & Strimple, n. sp.	X					
Paulicystis densus Frest & Strimple, n. sp.	X					
P. sparsus Frest & Strimple, n. sp.	X					
Pustulocystis ornatissimus (Miller, 1891)	X					
P. pentax Paul, 1971		X				
<i>P.</i> sp. Paul, 1971	X					
Family Sphaeronitidae						
Finitiporus boardmani Frest & Strimple, n. sp.	X					
Total genera	8	2	2	2	1	1
species	26	6	2	5	3	1

semblages even though rhombiferans, gomphocystitids, and other blastozoan classes (notably the Paracrinoidea, Frest & Witzke 1980), Blastoidea (Witzke, 1976, unpubl. data) and Coronoidea (Witzke, 1976; Brett et al., 1983) are. The camerate-dominated crinoid faunas of the Hopkinton and lower Scotch Grove are strongly reminiscent of many middle to upper Wenlockian assemblages and contain the ancestral members of nearly all of the camerate lineages prominent in younger Silurian rocks (Witzke & Strimple, 1981). Given the great similarity of Wenlockian platform environments worldwide, provinciality, perhaps caused by limits in larval dispersal potential within epicontinental seas (Witzke et al., 1979: 127), is the likeliest explanation. The relative paucity of Ludlovian-Pridolian Diploporita

worldwide is most likely due to a combination of unfavorable environments and preservational vagaries (Paul, 1982).

THE HOLOCYSTITES FAUNA

Among the taxa most characteristic of the eastern North American Province during the Wenlockian are the members of the *Holocystites* fauna (Table 2). Silurian Aristocystitida and Sphaeronitida are exclusively eastern North American. Most of the 8 genera and 27 species are both restricted to one or a few localities and endemic to single horizons. The fauna flourished during the Lower Wenlockian (Text-fig. 4), but a few species in two genera, *Holocystites* and *Triamara*, span the series. Approximately 6 genera and 20 species are endemic to

the Osgood in Indiana and Tennessee (five holocystitid genera and the sphaeronitid *Finitiporus* n. gen.). Representatives of two genera (again, *Holocystites* and *Triamara*), comprising six species, are more widely distributed. Of the subgenera of *Holocystites*, none is an Osgood endemic, but *Sepulticystis* n. sgen. is found only in the Joliet and the Osgood, approximate time and environmental equivalents.

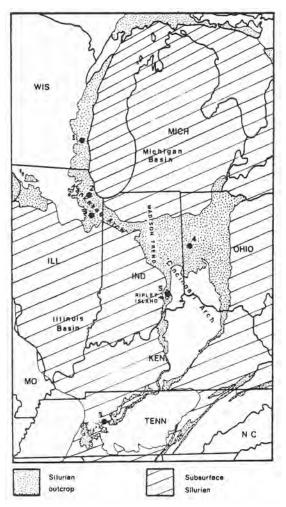
The *Holocystites* fauna is currently reported from six areas (Text-fig. 5); suggested correlations and ages for well-known sites are indicated in Text-fig. 6. Considering the total size of the North American Silurian outcrop area (Berry & Boucot, 1970), *Holocystites* fauna occurrences are rather limited; they are confined essentially to the Continental Interior along the fringes of the Michigan and Illinois Basins (Text-fig. 5). Highest diversities are noted in the terrigenous Osgood Member, Salamonie Dolomite of Indiana and Tennessee, and in the non-clastic Joliet Formation of Illinois; as discussed below, these diploporite occurrences are likely to be of Early Wenlockian age. The Late Wenlockian carbonates of Ohio, Indiana, Illinois, and Wisconsin have a few species of *Holocystites*. Although limited in occurrence to comparatively small areas, the holocystitids are often locally abundant (Frest *et al.*, 1977).

Holocystites fauna occurrences are noted from two very different environments. The largely terrigenous Osgood localities appear to represent soft-bottom, low-energy environments. A diverse invertebrate fauna [including a brachiopod fauna suggestive of BA 4-5 of Boucot (1975) and Frest et al., (1999)] is associated, but no substantial reefs or carbonate build-ups are present. The echinoderm fauna (excluding the diploporites) is moderately diverse, with the crinoid component reduced and the blastozoan component atypically large for a Silurian occurrence. The blastozoans sometimes dominate the fauna in numbers and biomass, but not diversity. Although incompletely known, the Joliet Formation (Illinois) and Manistique Formation (Wisconsin) faunas appear closely similar (Slocom, 1908; Bassler & Moodey, 1943). The low-diversity occurrences are accompanied by a moderately diverse invertebrate fauna, suggestive of BA 3 affinities. The cystoids are often associated with substantial "reefs" (s.l; bioherms or carbonate mud mounds); those of the Racine Dolomite (Illinois and Wisconsin) provide the best example, but the western Ohio occurrences appear to be similar. Detailed paleoecological information is available only for the Osgood (Frest et al., 1999); known data for the Holocystites fauna are summarized below.

AGE OF THE HOLOCYSTITES FAUNA

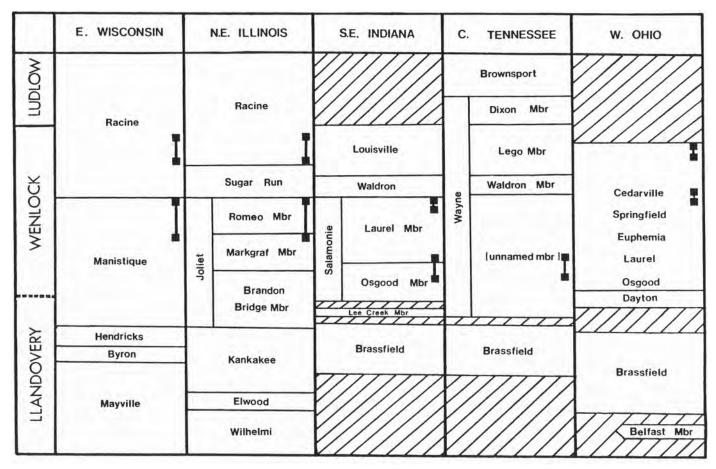
OSGOOD

Our preferred correlations and age interpretations for *Holocystites* fauna occurrences (Text-fig. 6) are based largely on Berry & Boucot (1970). However, much new informa-



Text-fig. 5. Map of a portion of central North America indicating areas with exposed and subsurface Silurian rocks. The *Holocystites* fauna is known from six areas: (1) Racine Dolomite and Manistique formations of eastern Wisconsin; (2) Racine Dolomite and (3) Joliet Dolomite, eastern Illinois; (4) Springfield and Cedarville formations, western Ohio; (5) Laurel and Osgood members, Salamonie Dolomite, southeastern Indiana; (6) Maddox Member, Wayne Group of Barrick (1981, 1983; Wayne Formation of Wilson, 1949), central Tennessee.

tion has accrued during the 1960s and 1970s, necessitating some important deviations from the scheme presented by Paul (1971: fig. 13). Additional information on the precise horizons of diploporite occurrences in Indiana, Wisconsin, and Illinois, was presented by Frest *et al.* (1977). The revision of Illinois Silurian stratigraphy by Willman (1973) is largely accepted here, as is that for Wisconsin by Ostrom (1967) and Mikulic (1977). Although conodonts are rare in some of the critical intervals, we are largely in agreement with the data of Liebe & Rexroad (1977) on the Joliet Formation in Illinois and of Rexroad (1980a) on the Salamonie Dolomite in Indiana. We differ, however, in several minor respects.



Text-fig. 6. Correlation diagram showing the stratigraphie horizons from which the *Holocystites* fauna has been reported. Precise horizons are uncertain in central Tennessee and western Ohio. Based on Paul (1971), Frest *et al.* (1977), Willman (1973), Barrick (1978), and Rexroad (1980b). The "unnamed member" of the Wayne Formation is the Maddox Member of Barrick (1981, 1983).

The age of the Salamonie Dolomite, and especially of the Osgood Member, in southeastern Indiana is problematic. On the basis of agglutinated Foraminifera, several authors (Dunn, 1942; Browne & Schott, 1963; Mound, 1968) placed the Salamonie low in the Midwest Silurian section. Conodonts are sparse in most Salamonie sections, however, Nicoll & Rexroad (1969: 16) found conodonts of their Pterospathodus amorphognathoides-Kockelella ranuliformis assemblage Zone in the lower Salamonie. They regarded this zone as similar to, but not identical with, Walliser's (1964) P. amorphognathoides Zone, and early Wenlockian in age (see also Rexroad, 1967, 1980a; Rexroad & Nicoll, 1972). Refinement in the definition and scope of the Zone 1ed Rexroad (in Shaver et al., 1978: 24) to term the Osgood as early late Llandoverian in age. As interpreted by Barrick & Klapper (1976), the P. amorphognathoides Zone is equivalent to late Llandoverian (C6) and early Wenlockian-age strata. The same authors (1976: 66) regarded Nicoll & Rexroad's (1969) and Nicoll & Rexroad's (1972) samples with P. amorphognathoides Walliser, 1964, as "directly correlative with the amorphognathoides Zone of Europe." In the

Welsh Borderland, the *P. amorphognathoides* Zone is interpreted as late Llandoverian-early Wenlockian in age (Aldridge, 1972). Precise applicability of the Oklahoma zonation of Barrick & Klapper (1976) to the Indiana Silurian section was contested by Rexroad (1980a: 8-10).

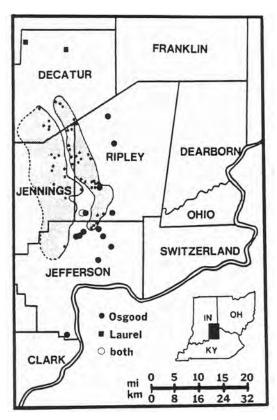
Diploporites are confined to the upper half of the Osgood in Indiana. Because of the stratigraphic occurrence and the general similarity of the crinoid fauna to that of undoubted Wenlockian units such as the Waldron, rather than to late Llandoverian units (such as the Farmers Creek Member, Hopkinton Formation and Welton Member, Scotch Grove Formation), we regard the diploporite-bearing portions of the Osgood as of probable early Wenlockian age. The Osgood equivalents in Tennessee (Osgood Member, Wayne Group of Wilson, 1949; Maddox Member, Wayne Formation, of Barrick, 1981, 1983) are probably very similar in age (Barrick, 1978, 1983).

OTHER UNITS

Diploporites also occur in the lower Wenlockian Joliet Formation in Illinois. Re-evaluations of Joliet stratigraphy by Willman (1973) and of diploporite occurrences by Paul (1971) and Frest et al. (1977) indicate that the diploporites occur in the top of the Markgraf Member and throughout the Romeoville Member. The age of these units is debatable, but we favor an early to middle Wenlockian position, mostly younger than, but in part identical in age to, the Osgood Member in Indiana. Liebe & Rexroad (1977), on the basis of the sparse conodont fauna, regarded the whole of the Romeo and a portion of the Markgraf Member as Wenlockian, and probably above the Pterospathodus amorphognathoides Zone. However, the reported fauna from these units has very low diversity, and very few conodonts were recovered, particularly of critical taxa (for discussion, see Frest & Strimple, 1982a). The lowermost Wisconsin occurrences (Manistique Formation sensu Ostrom, 1967), also termed the Waukesha Dolomite and Cordell Formation in southeastern Wisconsin; Mikulic, 1977), could be of the same age. Middle Wenlockian diploporites (Holocystites spp.) also occur in the top few meters of the Laurel Member, Salamonie Dolomite, in Indiana (Frest, 1975). The age of the Holocystites fauna sites associated with reef-flank facies in eastern Wisconsin and western Illinois is especially difficult to determine precisely. Reexamination of all major Racine Dolomite bioherms indicates that the diploporites occur only sporadically in the Wenlockian portions of the unit and not in the definitely Ludlovian reefs (Frest et al., 1977). A late Wenlockian age is favored for these sites (Holocystites is absent from the Sugar Run and equivalents; Text-fig. 6). The exact age of the Racine, and particularly of the basal portion, is uncertain (compare, for example, comments by Droste & Shaver, 1977, with those of Shaver et al., 1978). Assignment of ages and stratigraphic position to the two Ohio occurrences is highly questionable, because the Ohio Silurian section has not received sufficient recent attention. Holocystites greenvillensis Foerste, 1917, occurs in the so-called Cedarville and Huntington Groups (Foerste, 1917; Busch, 1943); the former is most likely middle Wenlockian, but the latter might be in part equivalent to the Louisville Limestone and hence is likely late Wenlockian (Pinsak & Shaver, 1964; Shaver, 1974a).

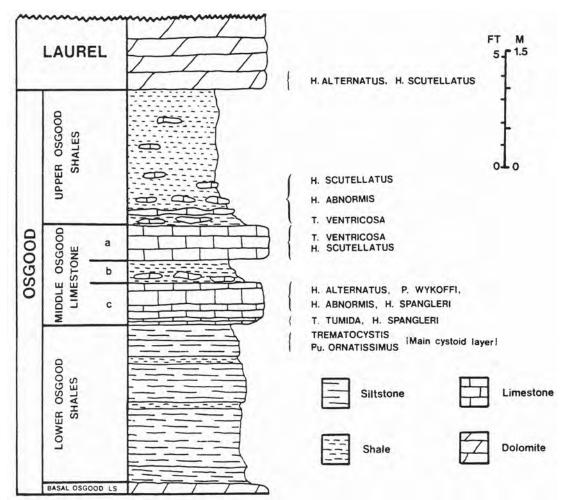
DIPLOPORITE STRATIGRAPHY AND BIOSTRATIGRAPHY

Detailed recent stratigraphic and biostratigraphic information on *Holocystites* fauna occurrences is available only for southeastern Indiana as yet. Diploporites have been collected from *ca.* 16 localities in this area (Text-fig. 7; for details, see Paul, 1971; Frest, 1975; Frest *et al.*, 1977; and Appendix herein). Thirteen sites have Osgood Member specimens only: one (Napoleon) has diploporites in the Osgood and basal Laurel, and two have upper Laurel *Holocystites*. Occurrence information has been compiled from Paul (1971), Frest *et al.* (1977), and the senior author's fieldwork. The diploporite-containing units are pres-



Text-fig. 7. Map of a portion of southeastern Indiana and adjacent areas showing the distribution of diploporite localities in relation to the Ripley Island (probable boundaries indicated by shading). Small dots indicate sections or cores in which the Brassfield Formation is absent; larger symbols are diploporite localities (see Appendix for details). Scattered localities in which the Brassfield is absent also occur in Scott, Clark, and southern Jefferson counties (Rexroad, 1980a). Modified from Paul (1971: fig. 11); data from Foerste (1897), Paul (1971), Frest *et al.* (1977), Rexroad (1980a), and the senior author's fieldwork.

ent over a wide area in southeastern Indiana (Becker, 1974), but diploporite localities are clustered in a much smaller region (Text-fig. 7), closely associated with the so-called Ripley Island (Foerste, 1904) positive feature. This area often shows a prominent disconformity between the top of the Whitewater Formation (Upper Ordovician) and the Brassfield Formation (Lower Silurian). At many localities, the Brassfield is absent (Text-fig. 7). These small-scale local unconformities have been used to mark the approximate position of the "island." Features such as Whitewater pebbles in the Brassfield, Brassfield-filled borings in the Whitewater, and an unnamed remnant basal Silurian unit (Laferriere et al., 1982) immediately above it, cherts and phosphate nodules, and laminated phosphorite crusts at the Ordovician-Silurian contact have been interpreted as indicating an emergent or very shallow-water-covered shoal-like feature, at least on the northern and eastern flanks of the "island" (Paul,



Text-fig. 8. Columnar section and diploporite occurrences characteristic of most Osgood diploporite localities. Based largely on measured sections of Paul (1971: fig. 12) and Frest et al. (1977: fig. 3), but thicknesses and lithologies generally vary little within the area shown in Text-fig. 7. Diploporite occurrences from Foerste (1897), Paul (1971), Frest et al. (1977), and the senior author's fieldwork. H, Holocystites; P, Pentacystis; Pu, Pustulocystis; T, Triamara.

1971; Laferriere *et al.*, 1982). The feature seems to have influenced fossil distribution in southeastern Indiana, minimally through the Wenlockian. All major Osgood fossil localities are on the eastern flank, and Indiana Laurel and Waldron localities with abundant fossils also occur only in close proximity to Ripley Island (Kindle & Barnett, 1909; Frest, 1975, 1977).

The average thickness of the Osgood in southeastern Indiana is *ca.* 4.5 m (15 ft) and the observed range is 3-9 m (10-30 ft; Rexroad, 1980b). Lithologies are varied, ranging from calcareous to dolomitic shales and siltstones to argillaceous dolomites. The upper and lower contacts are commonly unconformable, but in some areas the Osgood grades into the Laurel with gradual diminution of clay content. Over much of the eastern flank of the Ripley Island, the Osgood has four subdivisions. These were informally termed the Basal Osgood Limestone, the Lower Osgood Shales, the Middle Osgood Limestone, and the Upper Osgood Shales by Foerste (1897) and others (Textfig. 8). This terminology is most readily utilizable for the fossil localities in Clark, Jefferson, and Ripley Counties, Indiana, because the named units lose their distinctiveness to the north

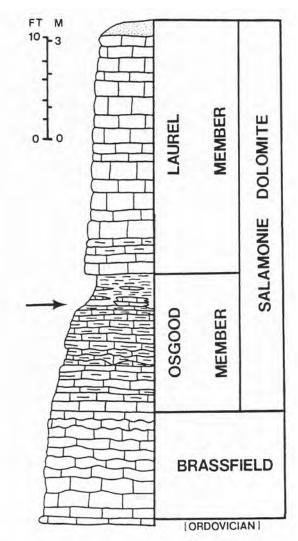
and south. Even within the above-mentioned counties, there is considerable, often very local, rapid facies variation in the Osgood, especially in the immediate vicinity of the Ripley Island. Here the Osgood sometimes rests either directly on the Ordovician, or a remnant unnamed Silurian facies is developed locally beneath the Brassfield (Laferriere *et al.*, 1982).

Foerste's terminology is nevertheless applicable without modification to all of the Osgood diploporite localities, with the exception of Napoleon (Text-fig. 9). At this site, an unusually thick Brassfield section is present (Rexroad, 1980b: 74) and the Upper Shales are only a meter or so in thickness. There is no clear indication of a disconformity between the Brassfield and either the Osgood or the underlying Ordovician unit. Localities with a similar section are more common in Kentucky (Rexroad, 1980b: 72) and in Decatur County, Indiana: but these have no reported diploporites. At occasional localities in the Ripley Island area, the whole Osgood Member is dolomitic. The atypical section at Napoleon (Text-fig. 9) can be interpreted in at least two ways. Rexroad (1980b: 75) suspected that some of the beds above the only shale in the sequence, also placed by him

in the Laurel, "included lateral equivalents of Foerste's Osgood Limestone and Upper Osgood Shale" because the Upper Shales of Indiana are replaced in Kentucky by a limestone. The shale at Napoleon would thus be equivalent to part of the Lower Shales at other localities. We believe that the Napoleon shale unit is more likely equivalent to a part of the Upper Shales. Hence, the Laurel-upper Osgood contact is properly placed at the upper shale-limestone contact at this site. This interpretation is based largely on the diploporite biostratigraphy.

Using diploporites alone, the typical Osgood-basal Laurel sequence can be zoned as indicated in Text-fig. 10. Strata equivalent to the Middle Osgood Limestone and Upper Osgood Shales contain a fauna dominated by Holocystites and related taxa, whereas the "main cystoid layer" (a 15-cm bed near the top of the Lower Osgood Shales) is dominated by the Osgood endemics Trematocystis and Pustulocystis Paul, 1971 (Table 3). These main subdivisions are here designated the Holocystites Zone and Trematocystis Zone, respectively; there are no overlapping taxa at the specific level, and only one genus (Trematocystis) in common. Within the Holocystites Zone, there are several typically consistent subdivisions, here termed subzones. The basal Laurel contains a sparse fauna of three wide-ranging holocystitinid species, none of which is an Osgood endemic (Table 3). The underlying Pentacystinid subzone has a very large echinoderm fauna in which the trematocystinid Paulicystis n. gen. and the pentacystinids Pentacystis and Osgoodicystis n. gen. are conspicuous members. Such comparatively widespread taxa as H. cylindricus (Hall, 1861) and Triamara ventricosa (Miller, 1879) are confined (in the Osgood) to this subzone (lb). The upper limestone band and middle shale of the Middle Osgood Limestone and equivalents (units a and b; Text-fig. 8: subZone 1c, Text-fig. 10) have a small fauna of similarly wide-ranging diploporites (Table 3). The lower limestone unit (unit c; Textfig. 8: subzone Id, Text-fig. 10) and its equivalents also have a distinctive diploporite fauna, notably including common Triamara tumida Miller, 1879, and H. spangleri Miller, 1891. The type species of Sepulticystis n. sgen. is also found only at this level.

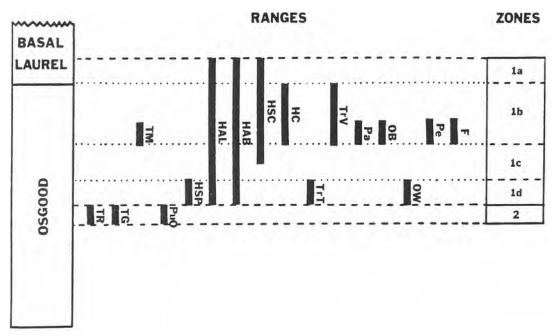
Because of the unusual amount of exposure, the Upper Shales fauna at Napoleon is much larger than that found at other localities (Table 4). Nevertheless, the fauna at Napoleon more closely resembles that of the Upper Shales (*i.e.*, subZone 1b) than that of any other Osgood unit. Shared by both are such non-endemics as *Holocystites cylindricus* and *Triamara ventricosa*, as well as the Osgood endemic species *H. clavus* n. sp. and *Trematocystis magniporatus* n. sp., the paratype of which was found at the base of the Upper Shales on Big Creek (see Appendix). Because the Upper Shales usually cannot be as intensively collected elsewhere as they can at Napoleon, it is presently unclear how much of the typical Osgood Upper Shales are represented at Napoleon. We suspect that the shale



Text-fig. 9. Columnar section of rocks exposed at Napoleon Quarrry. Arrow indicates horizon from which most of the diploporites were collected. Modified from Rexroad (1980b: fig. 4), based on remeasuring in 1981. The quadripartite division of the Osgood common at most fossil localities (Text-fig. 8) is not recognizable here. Diploporites occur throughout the shaly uppermost 1 m of the Osgood and in the lowermost 1 m of the Laurel, but are especially abundant in the shale immediately above the uppermost continuous Osgood limestone band.

at Napoleon might only correspond to the lower part of the normal sequence because none of the new taxa has been collected elsewhere above the basal portion of the Upper Shales. Possibly, the taxa found only at Napoleon could prove eventually to characterize a separate subzone.

Although it might be preferable in principle to define both zones and subzones on the basis of first occurrences only, this is impractical here because of the general rarity of complete and identifiable diploporites. Accordingly, some subzones are defined on the total ranges of member taxa. The *Trematocystis*



Text-fig. 10. Diploporite biostratigraphy of the Osgood and basal Laurel members Salamonie Dolomite; data from all localities. Zones and subzones are: 1, *Holocystites* Zone; (a) *H. alternatus* subzone; (b) Pentacystitinid subzone; (c) Holocystitinid subzone; (d) *Sepulticystis* Zone; 2, *Trematocystis* Zone. F, *Finitiporus* n. gen.; HAB, *Holocystites abnormis*; HAL, *H. alternatus* and *H. clavus* n. sp.; HC, *H. cylindricus*; HSC, *H. scutellatus* and *H. ovatus*; HSP, *H. spangleri*; OB, *Osgoodicytis bissetti* n. sp.; OW, *O. wykoffi*; Pa, *Paulicystis* n. gen.; Pe, *Pentacystis*; PuO, *Pustulocystis ornatissimus*; TG, *Trematocystis globosus*; TM, *T. magniporatus* n. sp.; TR, *T. rotundus*; TrT, *Triamara tumida*; TrV, *T. ventricosa*.

Zone ranges from the first appearances of *T. globosus* (Miller, 1878), T. rotundus (Miller, 1879), and Pustulocystis ornatissimus (Miller, 1891) to the first occurrences of Holocystites spangleri and Triamara tumida, the ranges of which also coincide with the Sepulticystis subzone (Id) of the Holocystites Zone. The base of the Holocystites Zone (1) is marked by the first occurrence of H. spangleri, Triamara tumida, and of the Holocystites species H. alternatus (Hall, 1861), H. clavus n. sp., and H. abnormis (Hall, 1864). The last holocystitinid occurrence in the lower Laurel, also of these last three species, marks the Zone's upper limit. The H. alternatus subzone (lc) occupies a narrow interval between two sets of endemics, i.e., T. tumida and H. spangleri below and a variety of taxa, notably Paulicystis n. gen., Finitiporus n. gen., Pentacystis, and the more common H. cylindricus and T. ventricosa, above. The last occurrences of these abundant Osgood taxa delimit the upper boundary of the Pentacystinid subzone (lb). The Holocystitinid subzone (la) has a diploporite fauna identical to that of lc, except that H. clavus n. sp. is absent.

Because the contact between the Laurel and the Osgood at Napoleon (Text-fig. 9) appears to be disconformable (the contact is irregular and there is a concentration of iron sulphide mineralization along it), it is possible that only a part of the Upper Shales (*i.e.*, Zone 1b) is present. Accepting Rexroad's boundaries, an average thickness of Osgood (4.5 m) is repre-

sented, despite the unusually thick Brassfield (*ca.* 2.5 m). We have terminated the ranges of the Napoleon endemics well within the lower part of the subzone, but the actual ranges are not yet well known. Possibly only the uppermost part of Zone 1b is represented by shale at Napoleon. The limestone immediately beneath has not yet yielded diagnostic species.

PALEOECOLOGY OF THE HOLOCYSTITES FAUNA

ORDOVICIAN DIPLOPORITES

Alteration of original lithologies to dolomite hampers investigation of the paleoecology of many *Holocystites* fauna sites (Frest *et al.*, 1977), so that much of the following discussion will necessarily focus on the Osgood occurrences, with available information on other localities incorporated where possible.

Ordovician diploporites thrived in both polar and tropical seas (Paul, 1976) and could survive on a variety of substrata, although highest diversity assemblages seem to be associated with carbonates. A striking feature of the Diploporita in general (Paul, 1979, 1988; *Eumorphocystis* Branson & Peck, 1940, is an interesting exception, see Parsley, 1982), and of all *Holocystites* fauna members in particular, is the absence of a stem. Most Ordovician diploporites were permanently fixed, needed some sort of solid substratum for initial attachment,

Table 3. Distribution and ranges of the Osgood-lower Laurel diploporites by zone.

Zone 1 (Holocystites zone) (a) Holocystitinid subzone

Holocystites (Holocystites) alternatus

H. (H.) clavus

H. (H.) scutellatus

H. (H.) ovatus

(b) Pentacystinid subzone

H. (H.) alternatus

H. (Megacystites) abnormis

H. (H.) clavus

H. (H.) cylindricus

H. (H.) ovatus

H. (H.) scutellatus

Triamara ventricosa

Pentacystis gibsoni

Osgoodicystis bissetti

O. cooperi

Paulicystis sparsus

P. densus

Finitiporus boardmani

(c) H. (H.) alternatus subzone

H. (H.) alternatus

H. (M.) abnormis

H. (H.) ovatus

H. (H.) scutellatus

(d) Sepulticystis subzone

H. (H.) alternatus

H. (M.) abnormis

H. (Sepulticystis) spangleri

Trimara tumida

Osgoodicystis wykoffi

Zone 2 (*Trematocystis* Zone)

Trematocystis globosus

T. rotundus

Pustulocystis ornatissimus

Ranges unknown

Triamara laevis

T. multiporata

T. sp. Paul, 1971

Pentacystis sphaeroidalis

P. simplex

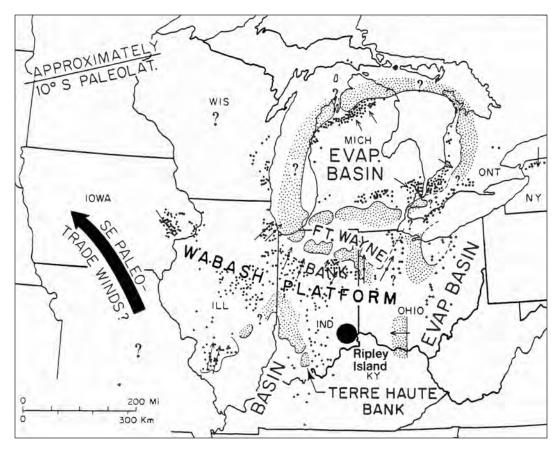
Pustulocystis pentax

P. sp. Paul, 1971

Table 4. Diploporita of the Upper Osgood Shales.

Taxon	Occurrence		
	Napoleon	"normal"	
Triamara ventricosa	X	X	
T. tumida	;		
Holocystites alternatus	X	X	
H. clavus	X	X	
H. abnormis	X	X	
H. scutellatus	X	X	
H. ovatus	X	X	
Pentacystis gibsoni	X		
Osgoodicystis bissetti	X		
O. cooperi	X		
Trematocystis magniporatus	X	X	
Paulicystis densus	X		
P. sparsus	X		
Finitiporus boardmani	X		
Total Genera	7	3	
Species	14	7	

and could not readily adjust their position. Most of the British Ordovician species investigated by Paul (1973) had large bases of attachment and presumably could not tolerate high rates of sediment influx. Even though the Ordovician species were fixed throughout life, Paul (1988) suspected that attachment might have been primarily epidermal: specimens preserved either still attached to a hard substratum or retaining the object to which they were attached are very rare, unless the attachment was to another cystoid. Abundances were sometimes extraordinary, with individual thin horizons in Sweden literally packed with millions of individuals (see, e.g., Regnéll, 1945). British Ordovician diploporites lived in relatively shallow water and are associated with shelly rather than graptolitic facies, both in areas with strong currents and in relatively quiet water. They are often found immediately above local unconformities and were among the first organisms to recolonize such areas when sedimentation recommenced (Paul, 1973: 17-18). Although sometimes found in relatively "pure" stands, they equally often occur with large faunas including numerous echinoderms and other invertebrate groups (e.g., the Boda Limestone of Sweden; Paul, 1979). Diploporites and other pored echinoderm groups flourished especially in the Ordovician, perhaps because their respiratory capacities gave them a compensatory advantage in comparison with the generally poreless but subvectively more efficient Crinozoa (Paul, 1976, 1977, 1979).



Text-fig. 11. Map of a portion of central North America in the late Silurian showing paleogeography and locations of major physiographic and biologic structures. "reefs" indicate single (carbonate mud mounds); dot shading designates major "reef tracts." Note position of Ripley Island (large dot) on Wabash Platform and flanked by reef tracts except on side facing the open sea. Slightly modified from Shaver et al. (1978: fig.

SILURIAN DIPLOPORITES

Later diploporites are comparatively scarce and less diverse, with the sole exception of the Osgood. Expansion of "reef" environments (carbonate mud mounds, here regarded as early equivalents of the classic Walsortian mounds) seems to have led to a proliferation of the camerate crinoids (Lane, 1971), at the expense of the inadunate crinoids and blastozoan groups. Possibly, stemless and largely sessile Diploporita were unable to tolerate the agitation and shifting substratum believed to typify Silurian carbonate environments with mound development (Lane, 1971). Among Holocystites fauna occurrences, the most diverse faunas are in the Joliet Formation in Illinois and Salamonie Dolomite in the lower part of the southeastern Indiana Silurian section. This part of the Silurian notably lacks reefs in the areas in which holocystitids occur (Willman, 1973; Shaver, 1974a). The most persistent occurrences are in the southeastern Indiana Silurian in which large mud mounds are absent (Shaver, 1974a; Shaver et al., 1978: fig. 1; Text-fig. 11). Very small-scale mud mounds or so-called bioherms are present both in the Osgood and in the Waldron (Halleck, 1973; Frest, 1975; Archer & Feldman, 1986). Holocystitinids are associated with the Osgood occurrences, but not present in the Waldron. Later Wisconsin, Illinois, and Ohio Holocystites fauna occurrences are often mound-associated. However, the

holocystitids are few in number and appear to be associated with the more inadunate-rich, quieter- (or deeper-) water, initial phase of mound development, rather than with the later roughwater, very strongly camerate-dominated phase (Lowenstam, 1957; Nicol, 1962).

The echinoderm faunas associated with so-called Racine "reefs" exhibit considerable variation in composition and abundance. Intact echinoderms generally are confined to flanking beds, which they often dominate. Echinoderms are either absent or very scarce except locally near or in the mound "core" that, however, often has common echinoderm debris as the only recognizable macrofossil. The fauna of the echinodermdominated flanking facies, if it occurs, is mostly crinoids, although small numbers and low diversities of blastozoan groups (blastoids, coronoids, rhombiferans, and diploporites) are often present. Crinoids are generally strongly dominant in terms of both abundance and diversity, but some rhombiferans (especially Caryocrinites Say, 1825) can also be numerous. In high-diversity, high-abundance, mound-associated Racine echinoderm occurrences, diploporites are rare. Often only one or two species of *Holocystites* are found (especially *H*. alternatus, but also H. cylindricus and H. abnormis), whereas Gomphocystites Hall, 1864, is the most common diploporite. In such faunas, diploporites are subordinate in number and diversity to rhombiferans. This is precisely the opposite of the Osgood blastozoan fauna, in which callocystitids and Gomphocystites are rare, whereas Caryocrinites is subordinate in numbers (but not diversity) to diploporites. A single species of Caryocrinites is typically very common in Racine mound flank echinoderm-dominated faunas, but species belonging to several callocystitid genera (Hallicystis Jaekel, 1899, Coelocystis Schuchert, 1903, and *Callocystites* Hall, 1852) are often present in small to sizeable numbers. Very occasionally, other blastozoans are associated in negligible numbers, notably single species of the coronoid Lysocystites Miller, 1889, and (very rarely) the spiraculate blastoid Troosticrinus Shumard, 1865. Echinozoa, Homalozoa, and Asterozoa have not been reported from the Racine. Among the crinoids, camerates are preeminent, with the rock frequently packed with thousands of calices belonging to the genera Eucalyptocrinites Goldfuss, 1831, Dimerocrinites Phillips, 1839, Lampterocrinus Roemer, 1860, or Siphonocrinus Miller, 1888. Good examples of this type of occurrence are found in the Horlick reef complex and the Bridgeport reef (see Appendix for localities).

More commonly, echinoderms are abundant in flank facies, but the fauna consists largely of camerate and inadunate crinoids and Caryocrinites, i.e., other blastozoans are rare or absent. Examples are the Whitnall Park and Wind Point reefs (see Appendix). Still more often, echinoderms do not constitute a distinct facies (they do not dominate the fauna or form distinct thickets or "gardens"), but are instead rare in or even absent from a mound complex (Moody reef, Soldier's Home reef, among others; locations given in the Appendix). It would thus appear that Racine mud mound environments (generally BA 3 in Boucot's 1975 scheme) were not necessarily optimal locations for echinoderm growth. Shaver (1974a) suggested that high species diversity within certain Silurian invertebrate genera was due to "species packing" in newly evolved reef habitats. This could apply to some camerate genera (e.g., Periechocrinus Morris, 1843, Siphonocrinus) but is not true of most blastozoans, with the possible exception of the rhombiferan family Callocystitidae. Highest diversities and abundance for diploporites and coronoids are in the nonreefal, argillaceous Osgood (BA 4-5). For the rhombiferan Caryocrinites, highest diversity is in the Laurel Member (Frest, 1975: BA 3) and in the Osgood Member, Salamonie Dolomite; specimens of a single taxon are much more numerous, however, in the Racine. Blastoids (Troosticrinus only) are exceedingly rare in the Racine carbonate mounds and much more common in argillaceous, more offshore BA 3-5 units such as the Waldron (Decaschisma Fay, 1961), Henryhouse (Polydeltoideus Reimann & Fay, 1961) and Brownsport (Troosticrinus and an undescribed Decaschisma), and Bainbridge (Troosticrinus and an undescribed fissiculate).

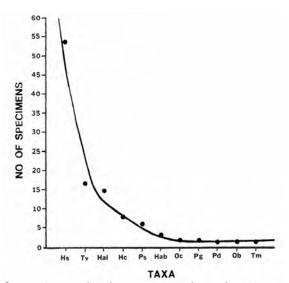
As mentioned above, callocystitids are uncommon but persistent members of Silurian carbonate mound faunas, especially

in the Racine. Some endemic genera (*Hallicystis*, *Coelocystis*) occur in the Racine. Generally, as noted by Paul (1971), callocystitids are common where *Caryocrinites* and diploporites are rare, and *vice versa*. Not all North American Silurian callocystitids are associated with mounds or biostromes, however; occurrences (*e.g.*, of *Brockocystis*) in shallow-water terrigenous and lime mud environments, *i.e.*, BA 2-3 of Boucot (1975), are equally common.

It is worth noting that the two American Silurian units with the most diverse reported echinoderm faunas [Laurel (Wenlockian) of Indiana, Brownsport (Ludlovian) of Tennessee] do not have the abundant echinoderms associated with reefs or biostromes (for the Laurel, see Frest, 1975; old lists for both are by Bassler & Moodey, 1943; see also discussion by Frest et al., 1999). Because echinoderms are faunal dominants in many central North American Silurian units, and many such units contain prominent organic buildups, it is often wrongly assumed that highest echinoderm diversities occur in or near "reef" environments. In fact, mound facies of some units have lower diversities than do corresponding intermound or nonmound facies. In Indiana, for example, the mound facies of such units as the Waldron and Salamonie in northern Indiana have far fewer reported echinoderm taxa than do the southern Indiana nonmound or minor mound facies (compare Shaver, 1974a, b, with Bassler & Moodey, 1943, for the same units). Relative abundance is more difficult to evaluate, but it must be noted that echinoderm-dominated facies seem equally as common in nonmound environments (e.g., parts of the Bainbridge Group in Missouri; parts of the Hopkinton and Scotch Grove in Iowa; Laurel and Osgood Members, Salamonie Dolomite in southern Indiana) as in areas with extensive lime mud buildups. Skeletal limestones with bioclasts overwhelmingly derived from echinoderms can occur from BA 2-4.

Whatever role Silurian "reefs" might have played in accelerating or stimulating echinoderm diversification, the effect would seem secondary to the expansion of widespread carbonate platform environments early in the Silurian; extensive mound development is one consequence of this. Perhaps the major effect of Silurian carbonate mud mounds upon echinoderms generally was not to enhance diversity but to stimulate the development of new forms specialized for mound environments. That such specialization did occur is evident from both quantitative and qualitative approaches (Manten, 1971; Franzén, 1983; Brett, 1984). However, for many units, the point requires more detailed investigation. At least one investigator (Manten, 1971) found no difference in taxonomic composition between mound and intermound faunas in Gotland; on the other hand, Franzén (1983: 4) argued that population densities, size, and diversity of Gotland crinoids "increased with increasing proximity to the reefs."

Shaver (1974a) found marked differences between reef and



Text-fig. 12. Species abundance in a typical Napoleon Quarry collection of 103 whole specimens. Actual abundance of first few taxa is probably greater, based on likely identifications of incomplete thecae and isolated plates. Hal, *Holocystites alternatus*; Hc, *H. cylindricus*; Hs, *H. scutellatus*; Ob, *Osgoodicystis bissetti* n. gen., n. sp.; Oc, *O. cooperi* n. gen., n. sp.; Pg, *Pentacystis gibsoni* n. sp.; Pd, *Paulicystis densus* n. gen., n. sp.; Ps, *P. sparsus* n. gen., n. sp.; Tm, *Trematocystis magniporatus* n. sp.; Tv, *Triamara ventricosa*.

interreef invertebrate faunas in the northern Indiana Silurian, as well as a progressive increase in species diversity of reef dwellers through time. The suggested trend seems valid if unrevised taxonomic lists for reefal portions of whole formations are used (Shaver, 1974a: fig. 6), but evaporates if lists from individual reefs of varying age are used (Shaver, 1974a: fig. 7). The latter is perhaps a better measure, given the widely varying sizes of outcrops and exposure areas of the northern Indiana units. Again, if total (unrevised) diversities are compared, Shaver's most strongly reefal unit (the upper Liston Creek) at 137 taxa (ca. 250 if the whole Liston Creek is considered) does not seem particularly species-rich in comparison with an earlier, nonreefal unit (e.g., the Waldron, with 200-300 taxa; Bassler, 1915).

Whatever the trends in invertebrates generally, the mud mound echinoderm faunas do not seem to show a progressive increase in diversity through time. In the Gotland sequence, apparent echinoderm diversity peaks in the lower Wenlockian and declines drastically thereafter (Franzén, 1983), even though echinoderms are an important element of the fauna throughout. There are few identified echinoderm taxa at all in the northern Indiana Late Silurian reefs (Shaver, 1974b), in contrast to both the Racine mounds and age-equivalent non-mound environments (e.g., lists by Bassler & Moodey, 1943). Franzén's (1983: 14) suggestion of a "specialized crinoid fauna rich in individuals but poor in genera and species" for such units deserves consideration. It is perhaps also noteworthy that

holocystitids have not been reported from any of the northern Indiana Silurian units (Shaver, 1974b).

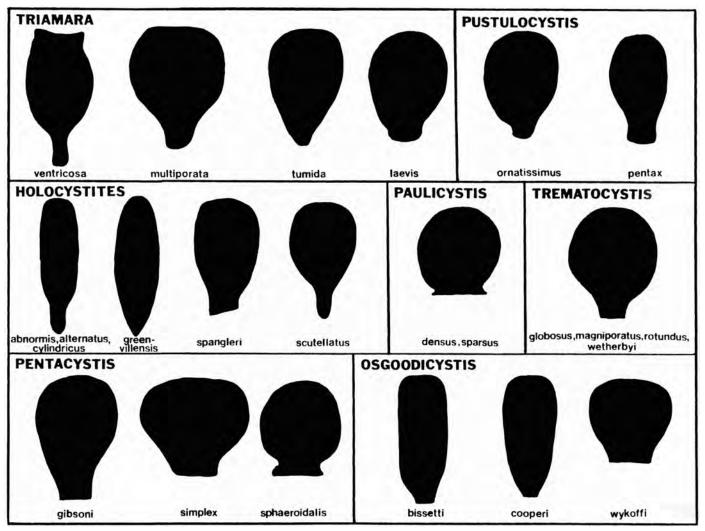
Holocystitid occurrences in the Cedarville and Huntington in Ohio appear to be much like the diverse-fauna, moundassociated Racine assemblages. A variety of camerates is present, as are abundant Caryocrinites, uncommon Gomphocystites, and Holocystites (represented by H. greenvillensis), and rare Lysocystites, blastoids, and callocystitids. As with the Racine, diverse holocystitids and Triamara are not present. Joliet Dolomite (Illinois) and Manistique Formation (Wisconsin) localities sometimes contain a comparatively diverse diploporite assemblage (three or more Holocystites and Triamara species). Holocystites fauna taxa in these nonmound settings are apparently more abundant proportionately than in the Racine. Crinoids generally are less common, whereas inadunates constitute a more significant portion of the total echinoderm fauna (Slocom, 1908). Camerates, however, are still the most numerous and diverse echinoderm group. Callocystitids and blastoids have not been reported from either unit, but coronoids [including "Stephanocrinus" Conrad, 1842 (= Cupulocorona Donovan & Paul, 1985) and Lysocystites] do occur. Overall, the Joliet and Manistique echinoderm faunas most closely resemble that of the Osgood.

Waukesha Dolomite localities (such as Sussex and Genessee; see Appendix) present a different picture altogether. Here, all echinoderms are rare: besides a few *Holocystites* (*H. alternatus* and *H. cylindricus*), only one other echinoderm (also a blastozoan; *Caryocrinites*) has been noted. The common fossils are orthoconic and cyrtoconic nautiloids and trilobites. Most likely, the rare Waukesha holocystitid specimens represent thecae living elsewhere but detached and killed, then drifted in and stranded on shallow-water lime mud flats (Frest *et al.*, 1977). Other *Holocystites* fauna occurrences, with the exception of the *Trematocystis* Zone fauna of the Osgood (discussed below), appear to represent autochthonous assemblages.

In general, echinoderm diversity parallels that of co-occurring invertebrate groups, *i.e.*, increases offshore through BA 4-5. Relative abundance can, however, be greater in certain more nearshore, BA 2-3 settings. For more extended discussion of the summary data presented here, consult Frest *et al.* (1977); for community context, see Frest *et al.* (1999).

Diploporite Adaptive Strategies in the Silurian

Low diversity and high diversity *Holocystites* fauna occurrences differ considerably in taxonomic composition, especially at the species level, and in the range of morphologies present, but some patterns are evident. Of the eight constituent genera, only two, *Triamara* and *Holocystites*, are not Osgood endemics. These two genera are generally dominant in terms of abundance at any *Holocystites* fauna site. Only the Upper Osgood Shales localities have great enough abundance that one can



Text-fig. 13. Thecal shape (lateral views) in well-known members of the *Holocystites* fauna. Shape of the theca and basal attachment size are characteristic of some genera (*e.g., Trematocystis*, *Paulicystis* n. gen.), but vary widely in others (*Triamara*, *Holocystites*), and most likely represent adaptations at the specific level to relatively few microenvironments.

expect relatively complete representation of original diversity. Even so, the pattern exhibited by the Napoleon locality (Text-fig. 12) is characteristic of all, as far as present data allow. One or two species, generally combinations of *H. scutellatus* Hall, 1864, *H. alternatus*, and *T. ventricosa* commonly constitute 60-80% of total diploporites collected. Other species of the same genera are sometimes present but in relatively small numbers. The remaining genera are found only locally and are generally quite rare, but in specialized environments (*e.g.*, Zones 2 and Id of the Osgood, discussed below) can be quite prolific.

Holocystites fauna members are quite variable in morphology (e.g., Text-fig. 13, which compares thecal shape of well-known species), but invocation of relatively few factors is needed to explain the observed patterns of abundance and distribution. In particular, we wish to emphasize thecal shape (Text-fig. 13)

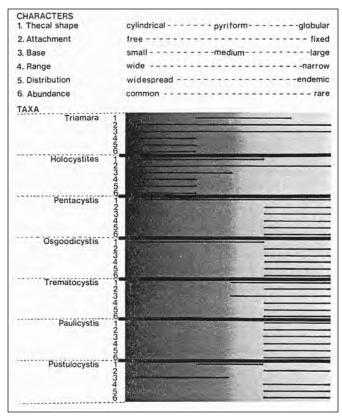
and attachment (Table 5). Some *Holocystites* fauna genera show little variation in either factor. For example, *Paulicystis* n. gen. and *Trematocystis* are globular forms with comparatively large attachment bases, that are believed to have been attached (sessile) throughout life. Other genera (*e.g.*, the pentacystinids *Pentacystis* and *Osgoodicystis* n. gen.) are quite variable in shape, but consistently have large attachment bases. Still others (*Holocystites* and *Triamara*) exhibit a wide range of variation in both. Looking at the fauna as a whole, two basic adaptive strategies are evident (Text-fig. 14). Those genera that have comparatively wide stratigraphic and geographic ranges (Group 1; some species of *Holocystites* and *Triamara*) tend to have cylindrical thecae, small attachment bases, and might have been free (unattached) as adults. Strongly endemic genera (Group 2; most or all species of *Osgoodicystis* n. gen., *Pentacystis, Trematocystis, Paulicystis* n.

Table 5. Mode of adult attachment in some *Holocystites* Fauna members. Asterisk denotes most common condition.

Taxon	Adult	Substratum
Triamara ventricosa	free	*dendroid bryozoans massive bryozoans
Holocystites scutellatus	free	*flat surfaces bryozoans
H. alternatus	free	flat surfaces
Trematocystis	attached	flat surfaces
Paulicystis	attached	*flat surfaces brachiopods nautiloids corals
Pentacystis	attached	*flat surfaces nautiloids
Osgoodicystis	attached	flat surfaces
Pustulocystis	attached	*flat surfaces trilobites bryozoans

gen., and *Pustulocystis*) frequently have globular or low pyriform thecae, large attachment bases, and were apparently sessile throughout ontogeny.

Those genera with all Group 2 species are Osgood endemics. Genera with both Group 1 and Group 2 species are most successful [i.e., abundant, widespread in space and time, and (frequently) most diverse]; only Zone 2 of the Osgood is not dominated (in both absolute abundance and diversity) by Holocystites or Triamara. Functional interpretation of both adaptations is straightforward. Group 2 species are stenotopic, i.e., substratum-limited and probably comparatively intolerant of rapid rates of sediment accumulation. The low globular form and large attachment base probably originally represented adaptations for relatively rough or agitated water, as is likely the case for many Ordovician forms (Paul, 1973; but see also Paul, 1988). Group 1 species are comparatively eurytopic, i.e., less substratum-limited and more tolerant of variable or high rates of sediment influx. Large-based, low forms required large areas of solid substratum (either hardground or comparatively stable debris mounds). These were available on a large scale in shallow Ordovician seas, but in the Silurian, increased competition from crinoids, especially camerates, might have limited these forms to what were now relatively marginal environments for most echinoderms, i.e., areas with terrigenous influx but some solid substratum, from which they would be rapidly excluded by crinoids. Certainly they were unable to exploit the newly widespread mud-mound environments very successfully. One



Text-fig. 14. Ranges of variation of six features of the better-known *Holocystites* fauna genera. Two basic adaptive strategies are apparent. The wide-ranging taxa that are common, have broad time ranges, and are geographically widely distributed (Group 1: *Triamara, Holocystites*) tend to have cylindrical thecae, small bases, and are free as adults, whereas taxa that are endemic, rare, and have narrow time ranges (Group 2: *Osgoodicystis* n. gen., *Pentacystis*, *Trematocystis*, *Paulicystis* n. gen., and *Pustulocystis*) are frequently globular, are always attached as adults, and generally have large bases.

implication of this is that typical large-scale Silurian carbonate mud mounds very likely had little hardground or cemented substratum areas available for echinoderm colonization. Echinoderms generally requiring extensive hard substratum are mostly absent from such environments in the Silurian. Group 2 diploporites are one example and edrioasteroids are another.

Group 1 species, like most known diploporites, required hard substrata initially [see Table 5, which contrasts the most common Group 1 species (*Triamara ventricosa*, *Holocystites scutellatus*, and *H. alternatus*) with some Group 2 taxa]. However, the well-preserved Osgood material indicates that these species were free as adults. Most diploporites, whether preserved as either autochthonous or allochthonous faunal elements, retain evidence of the substratum to which they attached, usually either flat hardground surfaces or large skeletal debris pieces. Group 2 taxa always retain distinct impressions

of their host substratum, but Group 1 taxa retain impressions only on young specimens. Adults usually have rounded bases (compare Pl. 1, Figs 1-3, with Pl. 2, Fig. 6) or, in some cases, are never found with the base intact. Unattached adults might have been able to adjust the position of the theca somewhat, either by means of the subjective appendages or, in one case, by employing soft-tissue podia covering diplopores (e.g., Paul, 1971: 49-52, for *Triamara*), but in any case would have been more tolerant of soft substrata or sites with limited available stable skeletal debris. Group 1 taxa also have in common the presence of an aboral projection, i.e., a modified, stem-like extension of the theca, always situated aborally. Presumably, this served one major function, namely to elevate the theca off the bottom — a distinct advantage in areas with sustained sediment accumulation. The cylindrical thecal shape of most Group 1 species might have served a similar function. Neither of these last two thecal modifications is confined entirely to Group 1 species, and the combination of them with a free-living habit in adulthood (often indicated by a small attachment base) was most effective. Indirect evidence indicates that many Group 1 species living on soft substrata were unattached adults. Frequently, specimens are found with offset peristomes facing directly upward and adorally curved thecae (e.g., Pl. 3, Figs 3 and 5; see Paul, 1971: 41, for detailed discussion), indicating the theca was initially upright, but fell over and continued growing. When collected in place, these specimens characteristically have the peristome uppermost. Both globular and cylindrical species of largely Group 2 genera never have offset peristomes. These taxa also presumably grew with the peristome uppermost, but arrived at this position by offsetting the large aboral attachment base if necessary. Thus, the theca of each of these taxa remains largely symmetrical around the main thecal axis and is never adorally curved.

The general rarity of diploporites (including Group 1 taxa) in the diverse echinoderm faunas of the Silurian stands in marked contrast to their relative ubiquity in the European Ordovician. A shift in the balance between feeding versus respiratory requirements is the most likely explanation. Although the specialized respiratory systems of the Diploporita and other blastozoan classes must have been of considerable survival value during the Ordovician (Paul, 1976, 1979), they were of less significance during the Silurian. Several blastozoan classes with specialized pore systems either became extinct or greatly restricted in distribution at the close of the Ordovician (e.g., Parablastoidea, Edrioblastoidea, Eocrinoidea, Paracrinoidea) or tend to lose the thecal pore system (e.g., Eocrinoidea). Even some crinoids had thecal pore systems, presumably respiratory in function during the Ordovician (prominent examples are the Porocrinidae, Sphaerocrinidae, Carabocrinidae, and Acolocrinus Kesling & Paul, 1971). These groups either do not survive into the Wenlockian (Porocrinidae, Carabocrinidae) or are represented by poreless taxa (Sphaerocrinidae, *Paracolocrinus* Brett, 1980; for a discussion of the latter, see Brett, 1980). This is despite increasing efficiency of pore systems, in those groups that retained them, during the Silurian (Paul, 1977, 1979). The crinoid arm, however, is a typically more efficient feeding organ (Paul, 1977). Blastozoans are thought to lack tube feet on their appendages (Sprinkle, 1973), so that even with a convergent arrangement in which large arm-like free trunks bear much smaller appendages (brachioles), these latter might not be as efficient at food capture as are crinoid pinnules. Thus, pinnate Blastozoa might never be exact homeomorphs of pinnulate crinoids.

Additionally, increasingly more complex organization of echinoderm communities during the Silurian might have enhanced crinoid survivability. By the Wenlockian, Silurian levelbottom communities might have subdivided available food resources among filter-feeding groups according to their relative height above the substratum (Lane, 1963; Walker & Bambach, 1974; Watkins & Hurst, 1977; Frest & Strimple, 1978; Brett, 1981; Meyer, 1982). The diverse echinoderm (mostly crinoid) communities of the Lower Carboniferous (Mississippian) probably were trileveled (Ausich, 1980; Ausich & Bottjer, 1982, 1990). In Silurian echinoderm communities, two levels could have been present (Frest & Strimple, 1978; Brett, 1981). Long-stemmed crinoids and convergent blastozoan groups (Rhombifera, Eocrinoidea) constituted an upper story, whereas short-stemmed or stemless crinoids and blastozoans, including diploporites, as well as numerous other invertebrates (especially bryozoans, brachiopods, and various epifaunal filter-feeding molluscan groups) might have constituted one or more lower stories. Low-level echinoderm groups, although facing more competition from nonechinoderm filter feeders and more risk of displacement by vagrant grazers and deposit feeders, probably could better exploit the rich food resources available at the sediment-water interface and were likely protected as well from strong currents. Brett (1981: 150) believed that most shortstemmed echinoderms occupied an intermediate level, whereas only a few (e.g., calceocrinids) were directly competitive with such groups as bryozoans and brachiopods. Because they are stemless, Silurian diploporites would be confined to this level. It seems plausible to us that a combination of increasing competition from more efficient high-level and intermediate-level Crinozoa and increasingly efficient low-level nonechinoderm invertebrates might have drastically limited niches available for stemless, more or less sessile Blastozoa such as diploporites. At the very least, lack of a stem or other means for rapid adjustment of the orientation of the subjective system to changing current regimes, and hence food supplies, would have placed them at a disadvantage in comparison to competing stemmed, low-level echinoderms (such as calceocrinids) that had such an option.

OSGOOD ECHINODERM PALEOECOLOGY

Introduction

The recorded diploporite subzones and zones in the Osgood can reasonably be related to differences in depositional environment. Even though Silurian diploporites are on the whole stenotopic, at least two major microhabitats are distinguishable, allowing three possible combinations. Although the Silurian sequence in both the eastern United States (Shaver et al., 1978) and in the southeastern continental margin, including southeastern Indiana (Barrick, 1978, 1983), is readily interpretable as a dominantly transgressive sequence, minor local or even continent-wide fluctuations analogous to those of the Iowa Llandoverian sequence (Johnson, 1975; Witzke, 1985) can be expected. The southeastern Indiana Silurian consists largely of carbonate sediments, deposited steadily with few interruptions; carbonates become less common through the Wenlockian. Occasional pulses of terrigenous sediments from an eastern source (Rexroad, 1980b) are noted, particularly in the Osgood and Waldron. No truly deep-water sediments (BA 5-6) are preserved, but the Ripley Island area seems to have progressed from near emergence in the Llandoverian to comparatively deep submergence in the Wenlockian.

DESCRIPTION

Diploporites first appear in the calcareous siltstones near the top of the Lower Shales. The fauna is small (Table 3), and all are Group 2 taxa. Both Trematocystis and Pustulocystis are common, and have been collected at numerous localities (Paul, 1971). None is preserved in life position, and most occur in scattered groups with no preferred orientation. All specimens show definite attachment scars, but the objects to which they attached (commonly large flat surfaces, but also smaller, curved or irregular ones such as nautiloids, trilobites and bryozoans; Table 5) are not associated. Many specimens are ruptured along whichever surface is uppermost as preserved, however, the attachment areas are not damaged. The associated fauna is extremely sparse; only occasional orthoconic nautiloids, brachiopods (Whitfieldella Hall & Clarke, 1893), and bryozoans were noted (Paul, 1971: 117). Many specimens supported a varied epifauna including bryozoans, worm tubes, inarticulate brachiopods, echinoderm holdfasts, and colonial corals (Paul, 1971: 117). The diploporites clearly are not preserved in situ, and Paul (1980: 86) suggested that they were attached to seaweed in life, with each cluster attached to a single plant. Because both genera have been found attached to a variety of hard substrata much like that noted for the Upper Shale species found in place (Table 5), we think it more likely that the Zone 2 species inhabited a similar environment. Probably they were detached and killed during an episodic event (e.g., a storm), drifted to their present locations while buoyed by gases produced by decay, and

sank when further decay caused rupture or loss of gas through thecal orifices. The diploporites might have been stranded in comparatively shallow (nearer shoreline), but quiet situations, after having drifted in from the more faunally and lithologically diverse, deeper offshore or more agitated nearshore sites in which they lived. This interpretation assumes that the small and globular thecae of *Trematocystis* and *Pustulocystis* were capable of floating for longer distances (further in or offshore) than associated large cylindrical or elongate pyriform taxa (*Holocystites* and *Triamara*). Floatation and stranding of *Holocystites* thecae on lime mud flats did occur at some Wisconsin localities (Frest et al., 1977).

The basal 7 cm of unit c of the Middle Osgood Limestone (Zone Id, Text-fig. 10; Table 3) also contains a Group 2 fauna, in this case large-based pyriform species of *Triamara*, *Holocystites*, and *Osgoodicystis* n. gen. Occasional specimens of *H. alternatus* and *H. abnormis* (Group 1 taxa) are also found; these become more abundant near the top of the unit. The associated fauna is sparse, but includes coronoids, *Eucalyptocrinites*, a few brachiopods, and bryozoans. None of the diploporites appears to be in place, but unruptured whole specimens are frequent, implying little transport. This unit is a rubbly limestone with some terrigenous material locally surrounding nearly pure carbonate lenses. Diploporites are uncommon but persistent, and usually preserved whole; isolated plates are rare.

Clastics are more abundant and evenly distributed in Zone 1c, which typically is developed as a paired thin shale overlain by argillaceous limestone. An abundant macrofauna is present, including diverse brachiopods and common bryozoans, solitary and colonial corals, gastropods, and trilobites. The Holocystites alternatus subzone has only Group 1 species (Table 3); two are tall cylindrical species and two have pyriform to ovate thecae; all are believed to have been unattached as adults. Diploporites and brachiopods here commonly lack epizoa, in contrast to the preceeding assemblages, and no Group 2 species are present. Presumably sediment was deposited either semicontinuously but too rapidly or incrementally and too erratically to maintain them, even though abundant skeletal debris for attachment was available. The associated echinoderm fauna is large, and includes a variety of crinoids in addition to common coronoids. Diploporites are abundant, but difficult to extract from this unit; isolated plates are also common. Brachiopods are commonly disarticulated, and a higher energy environment than any preceding is indicated.

A recurrence of the same species, plus *Holocystites clavus* n. sp., is found in Zone 1a (*H. alternatus* subzone) in the lower 1 m of the Laurel. Lithologies are similar except that a higher proportion of calcareous and clastic mud is present, and skeletal debris is generally more common. Much of the diverse invertebrate fauna is absent, and this subzone is strongly echinoderm-dominated. Whole diploporites are rare, and most camerates

Table 6. Echinoderm fauna (genera) of the Osgood Member, Salamonie Dolomite, in southeastern Indiana.

Occurrence			Occurrence		
Taxon	Napoleon	Other Osgood	Taxon	Napoleon	Other Osgood
Class Diploporita			Class Crinoidea		
Gomphocystites		X	Botryocrinus	X	
Triamara	X	X	Eohalysiocrinus	X	X
Holocystites	X	X	new calceocrinid	X	X
Pentacystis	X	X	new zophocrinid	X	
Osgoodicystis	X		Pisocrinus	X	X
Trematocystis	X	X	Paracolocrinus	X	
Paulicystis	X		Myelodactylus	X	X
Pustulocystis		X	Thalamocrinus	X	X
Finitiporus	X		Macrostylocrinus	X	
Class Rhombifera			Lyriocrinus	X	X
Callocystites	X	X	Eucalyptocrinites	X	X
Caryocrinites	X	X	Periechocrinus	X	
Class Paracrinoidea			Melocrinites	X	
Allocystites		X	Hirneacrinus	X	
Class Eocrinoidea			Lecanocrinus	X	X
Ampheristocystis	X		Class Coronoidea*		
Class Blastoidea			Stephanocrinus	X	X
Decaschisma	X		Cupulocorona	X	X
Class Cyclocystoidea			Lysocystites	X	
Sievertsia	X		new coronoid	X	
Class Echinoidea					
echinoid plates	X				

^{*} It is now generally accepted that coronoids are a sister group of the Blastoidea, not crinozoans (see Paul & Smith, 1984).

are replaced by inadunates (e.g., Pisocrinus De Koninck, 1858, Zophocrinus Miller, 1891); coronoids are also common. Most echinoderms are disarticulated, but there is little evidence of current activity. The rare brachiopods are often whole and trilobite debris is common, but whole specimens are very rare, and burrowing activity was intense. The subzone was probably deposited fairly rapidly, in relatively quiet water; a very similar horizon occurs at the top of the Laurel, where it also has Holocystites (alternatus) and hirneacrinid crinoids (unit 1 of Frest, 1975; Frest & Strimple, 1977). The large, camerate-dominated, Laurel crinoid fauna described by Springer (1926) is confined to units 2 and 3 (of Frest, 1975) of the Laurel, which units lack holocystitids.

The Upper Shales and equivalents (Zone 1c, Pentacystinid subzone; upper 2 m in typical sections) have a diverse diploporite fauna, comprising 7 genera and at least 14 species (Table 4). There is also a rich invertebrate fauna that includes a moderately diverse, and taxonomically unusual, echinoderm fauna. At

most localities, approximately a half-dozen diploporite species are present, mostly of Group 1 (Table 4). In such localities, diploporite abundance, and fossil abundance generally, decrease upward, whereas the proportion of clay and silt to carbonate increases concomitantly. Near the base of the unit, a fauna of ca. 50 species was listed by Bassler (1915) and Boyce (1956), including bryozoans, brachiopods, colonial and solitary corals, gastropods, nautiloids, trilobites, and worm tubes. Besides diploporites, the echinoderm fauna typically includes rare Caryocrinites, two coronoids (Cupulocorona), Eucalyptocrinites, and Pisocrinus.

At Napoleon, the fauna is more diverse. Equal numbers of Group 1 and 2 diploporites are present (Table 4). A moderately sized crinoid fauna of approximately 13 genera has been recovered, as well as representative of several echinoderm classes rare in the Silurian, including eocrinoids, echinoids, cyclocystoids, a probable paracrinoid, and a blastoid (Table 6). A half-dozen coronoid taxa are found and an equal number of rhombifer-

ans (*Caryocrinites*, plus very rare *Callocystites*). Among other groups, bivalves, rostroconchs, and sponges are added to the normal Upper Shales faunas. Total diversity equals or surpasses that of the Waldron Shale, from which over 200 species have been described (Hall, 1882). Many taxa have very close Waldron counterparts, so much so that earlier workers (*e.g.*, Boyce, 1956) used the same species names, but in many cases the Osgood species appear to be distinct.

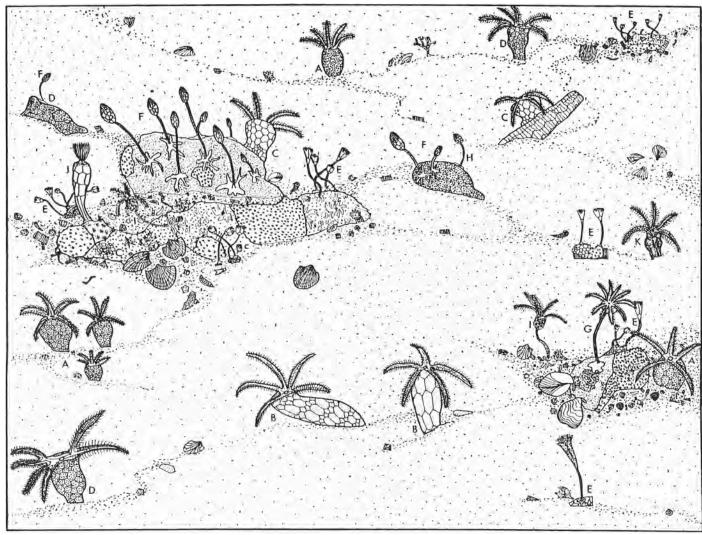
The general environment and distribution of fossil localities in the Upper Shales is much like that in the Waldron. Except for the area around the Ripley Island, the unit has few or no macrofossils. Around the "island," fossil localities uncommonly have small massive algal-stromatolitic masses or incipient carbonate mud mounds (Halleck, 1973; Frest, 1975; the "small scale bioherms" of Archer & Feldman, 1986). The top of the underlying limestone unit is a minor discontinuity or omission surface. It is bored and has encrusting bryozoans and attached crinoid roots. Algal masses and debris piles in the Waldron can reach 1.0-1.5 m (3-5 ft) in height and diameter; those of the Upper Shales are generally much smaller. In both cases, fossils occur also in the surrounding rock, but are much more abundant and diverse approaching debris mounds and masses. At Napoleon, echinoderm and bryozoan debris mounds provided important areas of hard substratum, and the stromatolitic masses are commonly densely covered with echinoderm holdfasts (in order of decreasing abundance those of Eucalyptocrinites, Cupulocorona, and Caryocrinites) and diploporite bases. Massive encrusting dendroid bifoliate arthrostylid and twig-like rhomboporid bryozoans and solitary corals are also well represented. Group 2 taxa have been found in place on debris mounds and attached to the discontinuity surface in dense colonies, but are nearly or completely absent in the surrounding (overlying) shales. Coronoid and caryocrinitid diversity and abundance are also greatest in the vicinity of the mounds, and many crinoid genera are similarly restricted. Group 1 taxa are found throughout the Upper Shales, but are most abundant on or near debris piles and mounds. Like coronoids and caryocrinitids, Group 1 taxa do occur in the overlying shales, but only at localities in which debris mounds or encrusted hard substrata are present at the base of the unit (not necessarily extending through it). This circumstance suggests that fossil distribution in general is controlled by depth-related factors.

There are thus two distinct subenvironments at Napoleon. Greatest abundance and diversity in all groups coincides with the distribution of available hard substrata, but some taxa could tolerate soft substrata more readily. We interpret the Upper Shales environment at Napoleon more or less as in Text-fig. 15.

Given the similarities between the Waldron and the Osgood Upper Shales, the absence of diploporites from the former is puzzling, but faunal and sedimentologic considerations suggest a tentative explanation. Even if the rare Racine occurrences are also included, the gross faunas are very similar (Table 7). Most groups show closely similar abundance (and diversities) with slight differences perhaps attributable to preservation. However, some differences are apparent on detailed examination. Corals, stromatoporoids, and green algae (Receptaculitida) are more common and diverse in the Racine; low diversity of these groups can be attributed either to turbidity or to depth differences (the Osgood representing a muddier and more offshore environment). Brachiopod diversity is greater in the Osgood, however, Watkins (1979) and Mikulic & Watkins (1981) ascribed similar changes in brachiopod and trilobite diversity in an onshore-offshore sequence in the Ludlow of the Welsh Borderland to increasing depth. In that situation, lithologies throughout the sequence were closely similar, and sedimentary structures and faunal compositions support the hypothesis that the diversity gradient correlates with a depth gradient. The relationship between depth and diversity in Paleozoic epicontinental seas is thought to be the same as that in modern marginal seas (Sanders, 1968; Huston, 1979), regardless of questions about the exact nature of the evolutionary mechanism responsible. Racine reef brachiopods are usually regarded as belonging to the rough-water phase of Boucot's (1975) BA

Table 7. Comparison of abundances of some invertebrate groups in three North American Silurian faunas. A, absent; C, common; R, rare; U, uncommon.

Taxon	Racine	Waldron	Osgood
Diploporita	U	A	С
RHOMBIFERA			
Callocystitidae	U	A	R
Caryocrinites	С	U	С
Crinoidea	С	С	С
"Stephanocrinus"	R	U	С
Brachiopoda	С	С	С
CORALS			
Colonial	С	U	R
Solitary	U	С	С
Stromatoporoidea	С	U	U
Receptaculitida	U	R	A
MOLLUSCA			
Bivalvia	R	U	R
Gastropoda	U	С	С
Rostroconchia	R	A	R
Cephalopoda	С	U	С
Trilobita	С	U	R
Porifera	R	U	R
Bryozoa	R	U	С



Text-fig. 15. Reconstruction of Upper Osgood Shale echinoderm communities. Group 1 diploporite taxa, plus "Stephanocrinus" and an unnamed eocrinoid genus, are not completely restricted to hard substrata, whereas Group 2 taxa, most crinoids, Finitiporus n. gen., and Caryocrinites occur only on or near small bioherms or accumulations of skeletal debris. Letters denote echinoderm taxa as follows: A, Holocystites scutellatus; B, H. alternatus; C, Paulicystis n. gen.; D, Triamara ventricosa; E, "Stephanocrinus" s. l. (several species); F, Eucalyptocrinites; G, Lyriocrinus Hall, 1852; H, Lecanocrinus Hall, 1852; I, Caryocrinites; J, Finitiporus n. gen.; K, unnamed eocrinoid genus.

3. The Waldron brachiopods represent a similar but less agitated depth assemblage (BA 3-4), whereas the Osgood brachiopods occupy a position within BA 4 or near the BA 4-5 boundary (A. J. Boucot, pers. comm., 1990). The echinoderm faunas show the greatest contrast. Racine faunas contain abundant crinoids, mostly camerates, with a moderate proportion of endemics. Diploporites are rare, as are coronoids, and among the Rhombifera callocystitids and a single species of *Caryocrinites* are abundant. The Waldron echinoderm fauna is less diverse than that of the Racine, and consists almost wholly of camerates, with only one endemic genus. Rhombifera are uncommon to rare (Tennessee) or absent (Indiana), and one coronoid

is common. The Osgood, however, has more numerous blastozoans. Ignoring the rare classes, diploporites, coronoids and Caryocrinitidae are abundant and diverse, but callocystitids are very rare, and crinoids less diverse. Among the latter, there are no endemic camerates, but the Inadunata are disproportionately represented (Table 6).

Interpretation

The differences probably result from a combination of factors. On average, depth is apparently greatest in the Osgood and least in the Racine. The Osgood probably also represents the least agitated environment of the three, and is certainly the most

clay-rich. The role of the Ripley Island in controlling fossil distribution is the consequence of an unusual physiographic situation. Situated atop the Cincinnati Arch (Text-fig. 5), it seems to have functioned through most of the Silurian as an isolated bathymetric island, an area of comparatively shallower water surrounded by relatively deep water for some distance in all directions. During much of the Wenlock and Ludlow, it occupied a central position on the Wabash Platform and was flanked on three sides by carbonate or reef banks which themselves fringed restricted basins (Text-fig. 11). Two of these (the Michigan and Ohio Basins) accumulated evaporites by the Ludlovian, but all had normal marine faunas and sediments during the time of Osgood deposition. The Ripley Island might have provided patches of hard substratum on an overwhelmingly soft bottom, which were only available for colonization by Group 2 taxa when water depth or other factors permitted, e.g., when rare major storms denuded high spots sufficiently to allow successful larval settling. Composition of such communities would be controlled by dispersal potentials and by rate of sediment influx, but generally represented geologically short-lived events. T. Guensburg (in litt., 1983) pointed out that the relative thinness of Osgood units could also suggest short duration episodes. The sharp contacts between thin, lithologically distinct units that characterize fossiliferous Osgood localities (i.e., those showing Foerste's quadripartite scheme, plus Napoleon) support such an interpretation. Where the upper surfaces of the carbonate units are well exposed, as at Napoleon, they are clearly minor omission surfaces.

Diploporites were apparently pioneer colonizers. They were successful only if relatively small areas with hard substrata were available in quiet environments at certain shallow subtidal depths but sufficiently deep as to preclude colonization by taxa adapted for agitated, shallow-water environments, such as many camerate crinoids. Observed contrasts between the Waldron and Osgood (Upper Shales) faunas could result from comparatively minor differences between areas in such an environment. Some of these can be used to decipher the causes of the minor environmental variation. In the Waldron, skeletal debris is more abundant and except in one bed with abundant Eucalyptocrinites in the Tennessee Waldron (Liddell & Brett, 1982); epizoa are on average less common. In the Osgood, any available hard substratum, notably including most diploporite tests, quickly became colonized by a variety of organisms (Table 8). Most diploporite genera were both pitted [presumably by the same organisms as described by Franzén (1974) and Brett (1978) for a number of Silurian crinoid horizons] and encrusted by epizoa, but more host specificity is noted for the diploporite pits. Except for Triamara, the rough surface of which might have made it less suitable for larval settling (Paul, 1980), all genera have epifauna, generally in proportion to smoothness of thecal surface and abundance in the fauna, and

Table 8. Epifauna and borings of *Tremichnus cystoidiphilus* n. sp. on *Holocystites* Fauna members. Organisms, listed in order of decreasing abundance, include the colonial coral *Favosites* Lamarck, 1816, the solitary coral *Duncanella* Nicholson, 1874, and the inarticulate brachiopod *Petrocrania* Raymond, 1911.

Taxon	Tremichnus	Epifauna		
	Abundance	Abundance	Organisms	
	none		bryozoans	
Triamara			worm tubes	
		rare	crinoid bases	
			Duncanella	
			bryozoans	
Holocystites	common	uncommon	crinoid bases	
			worm tubes	
	common	common	bryozoans	
Pentacystis			worm tubes	
			Favosites	
0 1: .:	common	uncommon	crinoid bases	
Osgoodicystis			bryozoans	
	uncommon	abundant	crinoid bases	
			bryozoans	
Trematocystis			Favosites	
			Petrocrania	
			Duncanella	
Paulicystis	none	uncommon	bryozoans	
	common	common	bryozoans	
Pustulocystis			crinoid bases	
•			worm tubes	

most are pitted. Only a few species of crinoids (calceocrinids and *Eucalyptocrinites*; Paul, 1971; Brett, 1978; pers. obs.) are pitted in the Waldron.

In the Osgood, circular-parabolic pits belonging to Brett's (1978) types 1 and 2 are found on occasional crinoid specimens. As in the Rochester Shale, type 1 pits (Tremichnus paraboloides Brett, 1985) are restricted to Ichthyocrinus Conrad, 1842, and type 2 pits (also *T. paraboloides*, according to Brett, 1985: 627) occur on an undescribed calceocrinid. In both cases, little deformation of stereom occurs. Rarely, similar pits accompanied by extensive deformation affect segments of crinoid stem of uncertain taxonomic affinity. These are probably attributable to T. cysticus Brett, 1985. In general, only a small proportion of the available Osgood crinoids are affected. Large circular-parabolic pits (formerly termed T. sp. aff. puteolus Brett, 1985; described below as T. cystoidiphilus n. sp.) however, affect sizeable numbers of Osgood diploporites. Only two genera (Triamara and Paulicystis n. gen.) lack pits, which vary in abundance on the other holocystitid genera (Table 8). Because most diploporites are rare, precise figures on proportion of pitted specimens are difficult to come by. Pits are uncommon on *Trematocystis* (perhaps less than 5% pitted), but more common on *Pustulocystis*. A high proportion of the few known specimens of *Pentacystis* and *Osgoodicystis* n. gen. are pitted. Pits are common on *Holocystites* spp.; an average sample of *H. scutellatus* has *ca.* 8% bored, whereas in *H. alternatus*, the proportion approaches 20%. Pits have been noted (Paul, 1971; pers. obs.) on specimens of *H. clavus* n. sp., *H. cylindricus*, and *H. abnormis*.

As noted by Paul (1971), diploporite pits differ somewhat in morphology from those on thecae of other echinoderms. They vary in size, but most are uniform and ca. 3.5-4.0 mm in diameter and 2 mm in depth, larger than those reported for crinoids (Franzén, 1974; Brett, 1978, 1985). Additionally, strong deformation (secretion of large amounts of excess stereom) is the rule, as with crinoid stems but not cups. There is no evidence of differing pit morphology among affected holocystitid taxa, but some sign of preferred location. As observed by Paul (1971: 41) and in our specimens, there is a tendency to concentrate pits around the ambitus and oral surface - presumably the exposed portion in life. Several cylindrical holocystitid specimens have pits along the whole of one side only; in a few cases, these also have deflected peristomes and the pits are located along the deflected (presumably uppermost) side. Paul (1971) developed several lines of evidence, much like those employed by Rodriguez & Gutschick (1975), to demonstrate that pit formation took place only while the diploporite was alive.

Paul (1971) and Frest *et al.* (1977) considered the possibility that diploporite pits were caused by parasitic snails, but noted that penetration to the interior, a characteristic of the borings of modern stiliferid gastropods, did not occur. Franzén (1974) and Brett (1978, 1985) concluded that the pits represent embedment structures, and that the organism, of unknown affinities, was not parasitic. Brett proposed the ichnogenus *Tremichnus* Brett, 1985, for circular-parabolic pits in crinoids. The same genus, albeit a different species, is applicable to those of Osgood diploporites. As far as we are aware this is the only published instance of such pits on blastozoans. None has yet been noted on such common and abundant Silurian blastozoan taxa as the rhombiferan *Caryocrinites* or the coronoids *Stephanocrinus*, and *Cupulocorona*.

Sedimentation rate might also have been greater in the Waldron, as delicate or fragile fossils such as whole trilobites are more often preserved whole. Crinoid crowns are rare in both units, but more common in the Waldron. In both, crinoid cups, calices, and crowns are proportionately rare compared to isolated plates. However, in the Waldron the proportion of intact examples is greater. Few thecae or cups are filled with crystalline calcite (suggesting live burial or very rapid burial following dislodgement), but in the Upper Osgood Shales > 1% are not mud-filled, whereas < 10% of Waldron *Eucalyptocrinites*

are. More robust forms do not reflect this. Brachiopods are usually found whole in both, indicating that the rate of sedimentation was not slow, and that disturbance typically was minor or episodic. On the other hand, sedimentation rate could not have been very rapid. Supporting this is the small proportion of intact delicate organisms. Also, Osgood diploporites almost never retain the oral and anal covering plates, whereas even some buried, exhumed, and reburied Ordovician diploporites can retain theirs (Paul, 1973). Moreover, epizoa are often restricted to the upper surfaces of specimens collected in place at Napoleon, suggesting that these were only partly buried during life and not completely buried for some time following death. The thick-plated, tightly sutured diploporite thecae might have been more resistant to disaggregation than those of most echinoderms. Additional information on the preservation, epifauna, and borings on Holocystites fauna members was presented by Paul (1971, 1980) and Frest et al. (1977).

Conclusions

Silurian diploporites thrived only in specialized environments when an unusual combination of paleobiogeographic, substratum, depth, and sedimentation conditions was met (Frest & Strimple, 1981b). Compared to their Ordovician relatives, they are more stenotopic and usually occupied only marginal positions as low-level feeders in tiered Silurian echinoderm communities. Hard substrata for suitable attachment sites in comparatively quiet, offshore, dominantly soft-bottomed environments were a necessity for successful colonization. Acceptable habitat could have been provided by episodic, rare events such as severe storms that locally stripped the sea bottom of mud. Not all hard substrata were successfully colonized by Silurian diploporites. On most Silurian nearshore hard substrata, camerate crinoids (among high-level filter feeders), plus other lowlevel filter-feeding invertebrate groups, could frequently outcompete diploporites.

Osgood diploporite assemblages comprise two major groupings, representing at least three microenvironments. Group 1 species were free as adults, had narrow bases, aboral projections, and (frequently) elongate thecae. Group 2 species remained attached permanently while alive, had wide attachment areas, lacked aboral projections, and were usually globular in shape. In the Osgood, some pioneering assemblages on hard substrata comprise only Group 2 species. More commonly, sedimentation was rapid enough that only Group 1 species could maintain themselves. In rare instances, an unusual balance was struck between the amount of available hard substratum and the rate of incoming terrigenous sediment, such that both groups thrived in contiguous subenvironments that also supported a diverse invertebrate assemblage and a unique associated echinoderm fauna with moderate crinoid diversity and high blastozoan representation.

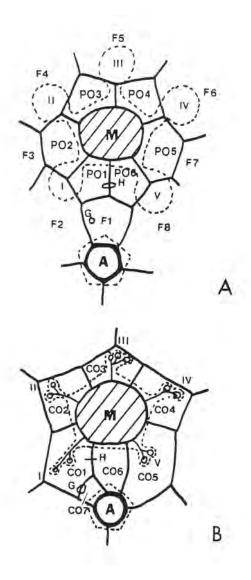
MORPHOLOGY AND TERMINOLOGY

Diploporita are extinct blastozoan echinoderms in which the bulk of the soft tissue (excluding most of the subvective system) is enclosed within a primitively globular theca. The theca is composed of numerous randomly to precisely arranged calcitic thecal plates, some or all of which are pierced by pore structures, the distribution and specialized morphology of which suggests that they were respiratory in function (Paul, 1968, 1972).

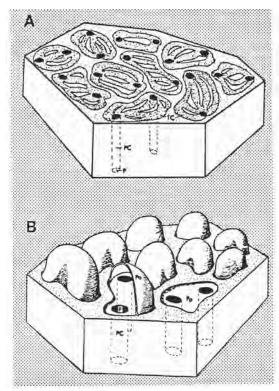
Commonly the theca has distinct oral and aboral poles, with thecal plating at each terminus showing more or less specialization. The Osgood diploporites described herein belong to two families, Sphaeronitidae and Holocystitidae, both currently included within the superfamily Sphaeronitida. The aboral theca in sphaeronitids is comparatively unspecialized, but as in most diploporites was modified for attachment to a (usually) solid substratum. No known sphaeronitid has a true stem (Paul, 1973), but many have the aboral thecal plates tapering into a distinct, narrow cylindrical aboral projection (Pl. 1, Figs 6-17). A flat, terminal attachment base or disk is usually present.

The adoral pole invariably has a definite oro-anal area, which bears four principal orifices, two large and two quite small. A sizable peristome is usually located at the adoral terminus at the center of the ambulacral (food gathering) system. The other large opening, generally offset from the main thecal axis, contains the anal opening and is a periproct. Between the major orifices are commonly two smaller orifices, one of which is often a small (ca. 0.5-1.0 mm diameter) circular pore (gonopore), whereas the other is a small, narrow, slit-like or sieve-like opening, presumably connected to the water vascular system and thus a hydropore. All four orifices are set within a small number of relatively fixed plates, the configuration of which is often constant at a high taxonomic level. Radiating from the peristome are five or fewer ambulacra, terminally bearing free ambulacral appendages, which gathered food and passed it to the mouth via single or multiple short epithecal food grooves in each ray, which terminate distally in ambulacral facets.

Major variations in the morphology of the pore system and the plates of the oro-anal area are infrequent and therefore usually accorded high importance in classification. The two Osgood sphaeronitid families differ considerably from each other on both points (Text-figs 16-17), but share many common features. In both, the mouth is a relatively large orifice, presumably set within soft tissue somewhere in the area of the peristomial opening. The peristomial opening is commonly oval or circular and set within the quadrangular or pentagonal peristome. The peristomial border is situated between the peristomial opening and the peristomial margin and bears the hypothecal portions of the ambulacral system (food grooves). In the Holocystitidae, the peristomial border is pierced by a variable number of circular oral pores, which presumably gave rise to oral podia (possibly sensory in function; Paul, 1971) in



Text-fig. 16. Oro-anal areas of the thecae of the two sphaeronitid families occurring in the Osgood Member. A, Holocystites cylindricus; B, Eucystis angelini (both redrawn from Paul, 1973: text-fig. 8). A, anus; CO2-CO7, circumoral plates of Sphaeronitidae; F1-F8, facetal plates of Holocystitidae; G, gonopore; H, hydropore; M, mouth; PO1-PO6, perioral plates of Holocystitidae. Roman numerals indicate ambulacra. Ambulacral facets, peristomial border (around mouth), and periproctal border (around anal opening) outlined by dashed lines. In both families, the peristome is covered by 6 palatal plates and the periproct by a small pyramid of 5 or more anals, which are seldom preserved. In the Holocystitidae, the short food grooves end in single large ambulacral facets; the peristomial frame is composed of 6 (usually) or fewer interradial periorals and then a circlet of 6, 8, or 10 radial and interradial facetals. In the Sphaeronitidae, the narrow food grooves are of variable length and end in one to several small ambulacral facets; the peristomial frame is made up of 6 circumorals; a seventh small plate (CO7) occurs regularly in the posterior interradius; note that most circumorals are radial in position.



Text-fig. 17. Diagrammatic representations of the structure of humatipores (A), characteristic of the Holocystitidae, and diplopores (B), characteristic of the Sphaeronitidae and many other Diploporita. Common to both are a pair of perpendicular canals (PC) opening internally as pores (P). Externally the perpendicular canals are connected by several fully calcified tangential canals (TC) in the Holocystitidae, but are connected by a soft tissue papula (Pa) in the Sphaeronitidae. Diplopore perpendicular canals open externally in pores (P) set within a slight depression, termed the peripore (Pp). Internal plate surface is toward the base of each figure. After Paul (1971: fig. 6), slightly modified.

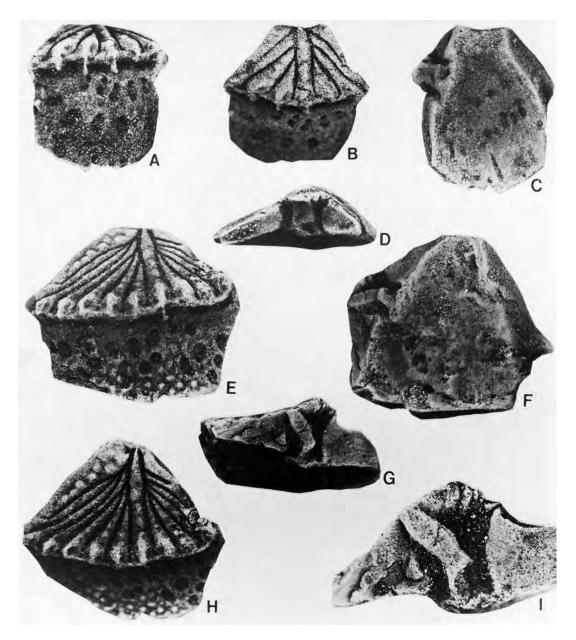
life. The peristome is commonly central on the evenly rounded adoral terminus of the theca. In some holocystitids, it is slightly protrusive (Pentacystinae), and in some sphaeronitids, the surrounding plates are protruded into a raised, flat-surfaced ambulacral platform (Paul, 1973: 15). The peristomial frame is composed of a small number of variously modified thecal plates. The Holocystitidae have the peristomial opening surrounded by one or two definite plate circlets (Text-fig. 16A). The smaller and more adoral perioral circlet (PO, plural POO) is composed of 6 plates typically, but 10 in the Ordovician Brightonicystis Paul, 1971. In advanced holocystitids (e.g., the Pentacystinae), this circlet is much reduced, incomplete (Osgoodicystis n. gen.; Pl. 4, Fig. 5), or even absent in one genus (Pentacystis; Pl. 4, Fig. 7). Peripheral to the POO is a circlet of 8 (usually) or 10 (Brightonicystis) facetals (F or FA, plural FF or FAA). In the Sphaeronitidae, the peristomial frame is made up of seven plates

(Text-fig. 16B), called the circumorals (CO, plural COO). Six of these are contiguous around the peristomial opening, whereas the small CO7 is displaced aborally. Although the Sphaeronitidae are likely ancestral to the Holocystitidae (Paul, 1971, 1973), it is not clear if the circumorals and periorals are homologous. According to Paul (pers. comm., 1983), they are not. Sphaeronitid circumorals are mostly radial in position, whereas holocystitid periorals are dominantly interradial (Textfig. 16). Facet location determines the symmetry; in sphaeronitids, the facets and ambulacra are located on the circumorals, but those of holocystitids are on the facetals generally, not on the periorals. Possible circumoral-perioral homology is based largely on position (each is the circlet that forms the peristomial border in their respective families). If periorals are regarded as an "extra" circlet, lost or never developed by sphaeronitids, then holocystitid facetals and sphaeronitid circumorals could be homologs. If so, the symmetry patterns would be identical. The comparative instability of periorals, as compared to facetals and circumorals, could corroborate this suggestion (but admittedly highly conjectural). Loss of one or two facetals (?FA3 and FA7) and shift of the hydropore onto a bipartite FA1 (= CO6 and CO7) would also be required. The sphaeronitid arrangement is ubiquitous to the whole family; an analogous arrangement occurs in the rather distantly related protocrinitid family Gomphocystitidae (Bockelie, 1979). Both the gomphocystitids and holocystitids show some variation in peristomial plate arrangement at the generic or subfamilial level, but well-known sphaeronitids are completely consistent. The peristome was covered in life in all Sphaeronitida by a flattened pyramid of six thin, triangular plates called the palatals (Paul, 1973: text-fig. 8). These are seldom preserved.

The food grooves are short, narrow, incised, and radiate from the edge of the peristomial opening onto the perioral or circumoral plates, terminating in one or more ambulacral facets in each ray. Grooves can be single (holocystitids, some sphaeronitids) or multiple and branching in various ways (many sphaeronitids). In either case, the facets are grouped in each ray. Rays are designated clockwise by Roman numerals, beginning to the left of the periproct (Text-fig. 16). Where the peristome is four-sided, the anterior ray (III) is missing.

The four- to seven-sided periproct normally is located near the peristome. The anal opening, which contained the anus proper, is invariably circular and inset into the surrounding plates. The often-pentagonal periproctal border is a shelf-like structure on which the (usually five) plates of the anal pyramid articulated (Paul, 1973; Text-fig. 8). In the Diploporita, these are often triangular, arranged in a single circlet and largely non-overlapping (C. Paul, pers. obs.).

The gonopore is situated between the two larger orifices, most often displaced to the left. It is a small circular pore, frequently 0.5-1.0 mm in diameter and often terminal on a short,



Isolated Text-fig. 18. specimens of circumoral 6 of Finitiporus boardmani n. gen., n. sp. A-D, SUI 48173, maximum dimension = ca. 5 mm (A-C), 5.4 mm (D); note paired groups of ambulacral facets, simple diplopores, and hydropore and gonopore openings with associated ducts. A, external lateral view; B, top (oral) view; C, internal lateral view; D, sutural view. E-H, SUI 48174, a larger specimen with more facets and tubercular ornament, maximum dimension = ca. 7 mm (E-F, H). E, external lateral view; F, internal lateral view; G, sutural view, maximum dimension = 6.1 mm; H, top (oral) view. I, enlargement of portion of sutural view (G), to show details of hydropore and associated duct, maximum dimension = 3.5mm. specimens coated with ammonium chloride sublimate.

frustrum-shaped tubercle (Pl. 4, Figs 3, 7). Like the larger orifices, it was covered by a pyramid of thin, triangular plates in the Protocrinitida (Paul, 1967, 1973) in life, but these are rarely found in place. Although likely present, these plates are as yet unknown in any other diploporite superfamily. In the Sphaeronitidae, the gonopore is commonly on CO7 or across the CO1:CO7 suture; holocystitids have it usually in FA1 (Pl. 4, Fig. 6) or FA2 (Pl. 4, Fig. 4). One holocystitid genus, *Trematocystis*, infrequently lacks an obvious gonopore.

The hydropore is most often a narrow (1-2 mm length), slit-like structure (Pl. 4, Fig. 6), often slightly elevated on a low tubercle and covered in life by a very thin, highly po-

rous continuous calcite sheet (Pl. 4, Figs 3-4), rather than a pyramid of small plates. In some genera, *e.g.*, *Finitiporus* n. gen., the hydropore is instead represented by an area of very porous calcite stereom with multiple tiny openings, much like the madreporite of starfish or the hydropore of some crinoids (Breimer, 1978; Text-fig. 18). In other genera, notably those of the Pentacystinae, the hydropore is cryptic, *i.e.*, either not readily recognizable or developed within the soft tissue of the peristomial opening. Where present, the hydropore is frequently located along a line connecting the peristome and periproct, nearer the former. Sphaeronitids have it central on the CO1:CO6 junction, whereas most holocystitids place it

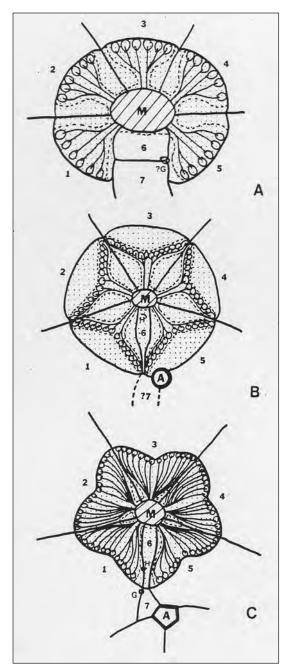
on the corresponding PO1:PO8 suture (Text-fig. 16). In some pentacystinids, it appears to be located on the FA1:FA8 suture instead.

Interpretation of thecal orifices in an extinct class is necessarily speculative, but a consensus of opinion about those of diploporites and closely related groups now exists. Jaekel (1899) first presented this interpretation, although the reasoning behind it has only been stated explicitly comparatively recently (Paul 1967, 1971). Briefly, the orifice covered by flat-lying plates at the center of the ambulacral system clearly functioned for ingestion of food and contains the mouth. The large offset orifice with a covering pyramid (in effect a one-way valve opening outward and functioning as an exit) is by analogy with echinoids an anal opening. The small round orifice has a similar covering pyramid and also functioned to allow egress of body products and thus is most likely a gonopore. The remaining small orifice lacks a pyramid of covering plates and is often sieve-like. Probably, such a sieve served to filter out particles to prevent them from entering the theca. By analogy with living Asterozoa, Echinozoa, and Crinozoa, it is the entrance to the water vascular system and hence probably the hydropore.

The subvective appendages of the Diploporita are seldom preserved and their precise morphology is a matter of dispute. Despite the passage of time, Jaekel's understated summary (1899: 355) remains pertinent: "die Finger der Diploporiten sind noch wenig bekannt." According to Paul (1979: 431), at least three genera had uniserial terminal structures. However, Chauvel (1966, 1978) insisted that some genera are biserial. Parsley (1982) interpreted the free major appendages of Eumorphocystis to be triserial with biserial brachioles. Sprinkle (1987) regarded the major thecal appendages in this genus to be free ambulacra bearing brachioles; we concur with this interpretation. This point has been regarded as of more than passing significance because uniserial appendages are generally thought to be characteristic of the Crinozoa not the Blastozoa. The importance of biseriality versus uniseriality, especially in primitive echinoderms, is currently de-emphasized (e.g., Paul, 1979: 431; Bockelie, 1981), in our opinion guite justifiably, and most authors now concur in assigning the Diploporita to the Blastozoa (Sprinkle, 1976, 1980, 1987; Paul, 1977, 1979, 1988; Broadhead, 1980b). In the Sphaeronitida, the appendages were very likely poorly calcified and formerly (e.g., Paul, 1973) were completely unknown. However, two Osgood holocystitid genera are known from specimens that retain one to several proximal ambulacral plates. In the genera Osgoodicystis n. gen. (Pl. 4, Fig. 5) and Pentacystis (Pl. 4, Fig. 7), at least the proximalmost ambulacral plates are uniserial. Whether this is true or not of all genera or of the distal parts of the main ambulacral appendages, is unknown. Uniseriality is somewhat surprising, because most Blastozoa do have biserial appendages, and Osgood diploporites generally have divided ambu-

lacral facets (Pl. 4, Figs 2, 7). In Paulicystis n. gen., the huge elongate facets are divided both transversely and longitudinally into an alternating series of small fields (Pl. 4, Fig. 2). Possibly, these represent alternating muscle- and ligament-bearing areas; on exceptionally preserved material, the stereomic architecture of the facet is complex, rather like that of a crinoid (Pl. 4, Fig. 1). This is consistent with the premise that the large ambulacral appendages of the holocystitids require relatively advanced facet morphology to be at all flexible. Alternatively, the appendages of Paulicystis n. gen. might have been biserial. Quite likely, the major, facet-articulating appendages of these diploporites were ambulacral structures, bearing numerous small brachioles, as in Lepadocystis, Eumorphocystis, and several other blastozoan genera. The less likely possibility, that the large appendages were modified brachioles as in the Pleurocystitidae, cannot be rejected completely on present evidence.

The neutral terms "ambulacral facet" and "ambulacral appendage" are used here because of considerable doubt as to the homology of these structures with blastozoan (e.g., rhombiferan) brachioles. In most Blastozoa, these appendages are small, biserial, unbranched, and originate from very small facets (Sprinkle, 1973). The facets of the Diploporita most often resemble those of other Blastozoa, but are most divergent in the Sphaeronitida, especially notably in the forms dealt with here. Sphaeronitidae usually have small facets (often 0.5-1.0 mm in diameter) and in taxa with ambulacral platforms they might be even smaller. One genus (Diplosphaeronis Paul, 1973) has comparatively large facets approaching 3 mm in diameter (Paul, 1973). Holocystitids have much larger facets, often 5 mm or more in diameter and reaching 20 mm lengths in Paulicystis n. gen. Large facets are also common in the Aristocystitidae. Paul (1973: 15) believed that such large facets most probably supported arms (i.e., ambulacral appendages, which can range from completely recumbent to completely free among various blastozoans) rather than brachioles or pinnules. In most crinozoans and blastozoans, the terminal appendages are thin, often less than 0.5 mm in diameter. The large thecae of diploporites very likely could not have been adequately nourished by a small number of even very large brachioles. Thus, the main appendages of holocystitids and perhaps even some sphaeronitids were most likely pinnate arms, that is, ambulacral trunks bearing numerous small brachioles. This is not without precedent among Blastozoa. The "eocrinoids" Trachelocrinus Ulrich, 1929, and *Bockia* Hecker, 1938, have biserial main arms (?brachiolar trunks), which bear smaller biserial terminal appendages (Sprinkle, 1973; Bockelie, 1981). These somewhat resemble the arms and pinnules of paracrinoids (Parsley & Mintz, 1975) and are either similar in origin or represent convergent structures. The rhombiferan Caryocrinites has large free arm-like structures (actually composed of ambulacral flooring plates; Sprinkle, 1975), which bear biserial brachioles. The un-



Text-fig. 19. Diagrammatic representations of peristomial morphology of advanced sphaeronitid genera with epipanniculate ambulacra. A, *Codiacystis bohemica* (Barrande, 1887), reinterpreted from Prokop (1964); B, *Tholocystis kolihai*, reinterpreted from Chauvel (1941) and Kesling (1968); C, *Finitiporus boardmani* n. gen., n. sp. Circumorals numbered; peristomial border indicated by dashed line; areas with secondary calcite dotted; periproctal border indicated by heavy black line. A, anus; G, gonopore; H, hydropore; M, mouth. Not to scale.

usual diploporite *Eumorphocystis* has been interpreted as having triserial main arms bearing biserial brachioles (Parsley, 1982); it is also possible that the brachiole-bearing trunks are actually

uniserial, and that the remaining two plate series are modified ambulacral flooring plates. The appendages of the coronoids are biserial brachiolar trunks ("arms") bearing very small biserial brachioles (Brett et al., 1983; Donovan & Paul, 1985). Very probably, holocystitids and other diploporites with large facets also had similar appendages, either large, unbranched "arms" [perhaps in the style of the eocrinoid family Rhipidocystidae (Hecker, 1940; Bockelie, 1981) or the rhomibiferan Hillocystis Jell, 1983] or, more likely in our opinion, free brachiole-bearing (pinnate) trunks, analogous to those of Eumorphocystis. The latter would be relatively efficient feeding organs, perhaps rivalling, but not exceeding, in efficiency those of some crinoids. The crinoid subvective system also consists of two major sizes of calcified appendages, at least in pinnulate forms like camerates: uniserial to biserial main arms and uniserial pinnules. The latter, however, bear triads of soft-tissue tube feet, presumably absent in Blastozoa, and also serve a genital function in modern forms.

The acquisition of pinnate arms by diploporites would be in line with a general tendency toward increased surface area (and efficiency) of feeding organs in primitive echinoderms (Paul, 1979). Certainly, most Silurian diploporites had large facets or large numbers of small ones, whereas most Ordovican forms possessed fewer and smaller ones. The rather large thecae of holocystitids and aristocystitids might have required relatively large and complex feeding organs to support them. Paul (1973: 15) noted that *Diplosphaeronis*, the largest British Ordovician diploporite, is the only one with large facets.

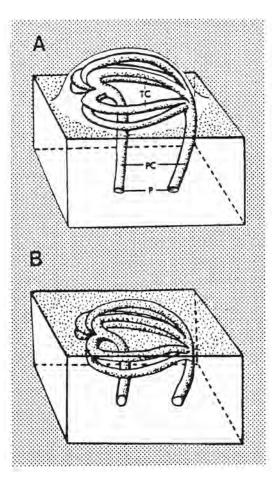
Enlargement of facets was one of two strategies pursued by diploporites to increase the area of the subvective system relative to thecal volume. Some sphaeronitids increased the number of small facets in each ray, either spreading them over the theca or concentrating them on the circumorals, ultimately forming a closed circle of facets (Text-fig. 19). Genera showing this type of ambulacral structure are here termed epipanniculate.

Most primitive Blastozoa had extensive thecal pore systems. Various morphologies were more or less successful (Paul, 1968; Broadhead, 1980b). Diploporites experimented with two main types. Both are exothecal systems sensu Paul (1968, 1977), that is, systems which circulated body fluids to the exterior of the theca, with oxygen exchange between internal fluids and seawater taking place outside of the theca. Diplopores (Textfig. 17B) are characteristic of Sphaeronitidae and many other diploporite groups. Pore system morphology is a conservative feature in Diploporita, and the otherwise divergent members of Sphaeronitidae show little change from the basic morphology (Paul, 1973). Humatipores (Text-fig. 17A) are found only in the Holocystitidae. Humatipores and diplopores are similar in some respects. All diploporite pore structures consist of numerous small units (frequently < 1 mm in diameter), usually not crossing plate sutures and randomly arranged (not preferentially oriented). Often, large numbers are present and they are distributed evenly over the whole theca and over each thecal plate (with the exception of those affected by an ambulacral groove system). Both diplopores and humatipores consist essentially of two elements: a pair of perpendicular canals that pierce the body of the plate and open internally, and some form of tangential connecting system on the outside of the theca.

The two types of pores differ as follows. In diplopores, the perpendicular canals terminate externally in paired pores set within an often bordered shallow depression, the peripore, which was presumably covered by a soft tissue papula in life (Text-fig. 17B). In most, this was not rigidly, or alternatively was not at all, calcified. The humatipores of the Holocystitidae have the external opening of the perpendicular canals connected by several fully calcified (externally covered) tangential canals. In most diploporites, pore system morphology is consistent within a family and changes little from genus to genus. Humatipores are more variable (Text-figs 20-21). Flat tangential canals deployed in a single plane parallel to the plate surface are the rule (Table 9), but two other morphologies are known. In one subgenus of Holocystites (i.e., Sepulticystis n. sgen.), the tangential canals are arrayed three-dimensionally, i.e., as if each were tangent to the surface of a hemisphere or semiellipsoid. The whole structure is buried beneath the outer plate surface, which is flat (Text-fig. 17B). In others, the tangential canals are also nonplanar, but the whole system is raised into tubercles. The tangential canals can be either radially arranged (Pustulocystis) or not (Holocystites s. s.). This last category (raised tangential canals) is here termed sursumate. As mentioned above, pore system variations from the established morphology are infrequent within a family. Such an occurrence within a genus is very

Table 9. Humatipore types in the Holocystitidae.

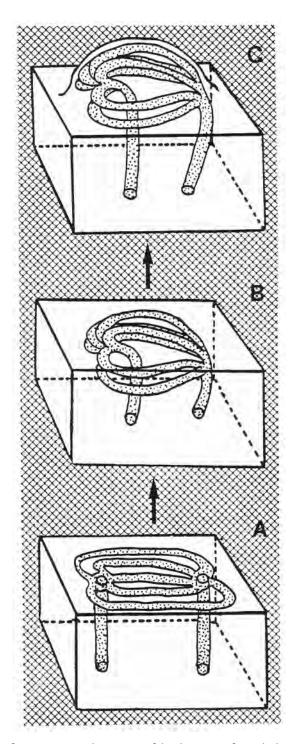
		Humatij	pore
Taxon	Flat 2D	Flat 3D	Raised 3D
Subfamily Holocystitinae			
Holocystites (Holocystites)			X
Holocystites (Sepulticystis)		X	
Holocystites (Megacystites)	X		
Brightonicystis	X		
Subfamily Pentacystinae			
Pentacystis	X		
Osgoodicystis	X		
Subfamily Trematocystinae			
Trematocystis	X		
Paulicystis	X		
Pustulocystis			X



Text-fig. 20. Diagrammatic representations of the structure of three-dimensional humatipores characteristic of *Holocystites s. l.* (A) Raised three-dimensional humatipores of *Holocystites* (*Holocystites*). Based on Paul (1971: fig. 7). (B) Buried three-dimensional humatipores of *Holocystites* (*Sepulticystis*). In each, paired perpendicular canals (PC) end internally in a single pair of pores (P), but branch externally into a series of tangential canals not deployed in a single plane.

unusual. Paul (1973: 20-27) accorded major variants separate subgeneric status in *Sphaeronites* Hisinger, 1828, a practice that we here apply to *Holocystites*.

Diplopores are very efficient respiratory structures, but the presumed soft-tissue external bulb (papula) could have been subject to attack by predators. Osgood (Silurian) diploporites have calcified exothecal pore structures (Paul, 1977: 145) and could have better resisted attacks of this sort. In most diploporites, the pores are scattered evenly over the thecal or individual plate surface. This condition is here termed omniporate. There is a trend in the Ordovician, however, toward fewer, more efficient diplopores (Paul, 1973, 1977). Some genera (e.g., Finitiporus n. gen.) eliminated pores over a part of the theca or individual plate surface, a trend perhaps comparable with the diminution and loss of epispires in later eocrinoids (Sprinkle,



Text-fig. 21. Presumed sequence of development of raised, three-dimensional (sursummate) humatipores of *Holocystites* (*Holocystites*) (C) from forms with tangential canals on a single plane (essentially two-dimensional), as in *H.* (*Megacystites*) and most Holocystitidae (A), via an intermediate step with buried but essentially three-dimensional deployment of tangential canals, as in *H.* (*Sepulticystis*) (B). In each, internal surface toward bottom; plate material white; canals dotted.

1973, 1980). Such echinoderms are here termed partiporate. No aporate (*i.e.*, without pores in a group characteristically possessing them) diploporites have yet been described, and the last known taxa (Lower Devonian *Eucystis*-like forms) are rather typical omniporate forms.

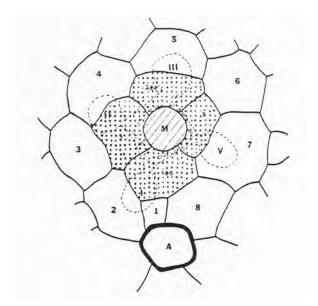
PHYLOGENY

APPROACH

The presence in the *Holocystites* fauna of a large number of nearly or exactly contemporary, commonly co-occurring species and genera allows construction a detailed generic and specific level phylogeny for the abundant and diverse family Holocystitidae. With the infusion of much new material of both old and new taxa, many species are now fairly well known. The availability of large samples of several different species from what could have been true populations, *i.e.*, possibly isochronous samples, has enabled us to re-evaluate low-level taxobases and to distinguish evolutionary trends in some cases.

Careful watch for "abnormal" (i.e., variant or damaged) specimens has given some grasp of what constitutes a pathologic abnormality and what a true mutation in the family. For example, four or five ambulacral (arm) facets are standard. By far the most common variation is for five-armed taxa to develop four only. Almost always, facet III (anterior ray) is dropped. The only exception, a specimen of Holocystites ovatus Hall, 1864 (SUI 48188; Text-fig. 22) is clearly abnormal in several respects and represents the results of teratology or injury. Next most frequently, the four-armed taxa add another - facet III. The best example of this occurs in Pustulocystis. The type species (P. ornatissimus) always has four facets, and is known from a number of specimens. Pustulocystis pentax Paul, 1971 (known from a single specimen) has five. No instances of fourfaceted forms losing any or gaining more than one facet were noted, either in the Osgood or in the literature. Similarly, there are no known cases of normally five-faceted taxa gaining or losing more than one facet. Only one holocystitid specimen yet found has an extra facet in any one ray (Brightonicystis gregarius Paul, 1973: 56). One can reasonably conclude that facet number change in this group involves a mutation associated with the anterior ray, and that a directional evolutionary trend is involved — reduction from five to four by loss of facet III. Enough material was available in several cases to determine, or distinguish from teratology, such trends.

In formulating a holocystitid phylogeny, both traditional taxonomic and quantitative phenetic (sensu Sneath & Sokal, 1973) approaches were used. Because numerous closely sampled, long stratigraphic intervals were not available, a stratophenetic classification (sensu Gingerich, 1979) could not be attempted, and all taxa were treated as if contemporary. Phenetic rather than cladistic (e.g., Eldredge & Cracraft, 1980) methods



Text-fig. 22. Interpreted camera lucida drawing of oro-anal area of abnormal specimen of *Holocysties* (*H.*) *ovatus* (SUI 48188). Large numbers on facetals (white), small numbers on periorals (dotted), ambulacral facets with Roman numerals, periproctal border with heavy line. Symbols as outlined under Abbreviations, p. 52. Ambulacral facet IV is missing, there are only four periorals, and neither a gonopore nor hydropore is apparent.

were preferred for several reasons. Available data on diploporites were more readily coded as multistate characters. As yet, transformation series could not be resolved into synapomorphies and plesiomorphies, or alternative pathways producing superficial rather than real homeomorphy be demonstrated, without invocation of numerous ad hoc explanations. In part, this situation is due to the fact that very few diploporite phylogenies of any sort have been suggested. It was therefore thought desirable to use at least one method (i.e., Wagner trees or networks) that did not assume irreversible evolution and readily allowed for independent evolution of the "same" characters as judged by preserved hard part morphology, in otherwise rather distantly related lineages. The argument over presumed superiority of either cladistic or quantitative phyletics has been acrimonious. Claims generally revolve around two points: (1) best congruence of the model-generated phylogeny with the "true" phylogeny (generally evaluated by comparing relative ambiguity of proposed solutions and by contrasting robustness in the face of new information), and (2) supposed methodological superiority. As regards the former (contra Wiley, 1981), existing information seems to indicate that both approaches are equally robust (see Schuh & Polhemus, 1980, and Rohlf & Sokal, 1981, for vigorously argued summaries of the literature). On methodology, we are in general agreement with Cartmill (1981) in regard to cladistic approaches (Farris, 1983, notwithstanding; see also Cain, 1982; Dunn & Everitt, 1982; Kluge, 1983; and Abbott et al., 1985, for further discussion on some of the same points). There is a certain circularity of reasoning involved in both cladistic and phenetic approaches to interpretation of paleontological phylogenies (Cracraft, 1979; Eldredge, 1979; Forey, 1982; see also the papers cited by Felsenstein, 1983, and Duncan & Steuessy, 1984). Only a completely historical approach, almost never practical because of limited data and perhaps impossible in principle, could avoid such problems entirely. Given real databases, the cladistic approach probably best approximates the real phytogeny unless there is a severe dearth of information. Thus, for first attempts in groups with both no surviving near relatives and no phylogenetically wellknown closely related fossil group (like diploporites), we advocate the phenetic approach. Nevertheless, in the future we intend to adapt our database to allow for direct comparison at both the generic and specific levels using both phenetic and cladistic methods (T. Frest, unpublished).

Numerical taxonomic studies on fossil echinoderms are as yet uncommon. Kesling & Sigler (1969) and Rowell (1969) analyzed the inadunate family Calceocrinidae, using both the Wagner tree approach and forms of cluster analysis. Webster (1981) conducted UWPGA and PCA analyses on the same input matrix, which involved the inadunate family Cromyocrinidae. Brower (1977, 1982) used all four techniques in his studies of early calceocrinid phylogeny. For higher echinoderm taxonomy, cladistic approaches (s. l.) have been employed by Paul & Smith (1984), Smith (1984, 1986, 1988) and Paul (1988). For details of usage as regards echinoderms, see the cited references. For general discussion of each method, see Sneath & Sokal (1973), Neff & Marcus (1980), Wiley (1981), Gauch (1982), Dunn & Everitt (1982), and Abbott et al. (1985). We compare all of the above approaches, first on a generic-level dataset (also classified intuitively) and then on the specific level.

PHYLOGENETIC TRENDS

Selecting and coding of characters was done on the basis of both long-established and newly formulated evolutionary trends. Where practical and where the direction of trends was uncertain from Wenlockian forms alone, the better-known Ordovician sphaeronitids were used for comparison (e.g., Paul, 1973). Only one non-Wenlockian holocystitid is known, the Upper Ordovician genus *Brightonicystis* (Paul, 1971, 1973), and on grounds of its early appearance, many of its characters were regarded as primitive. The use of stratigraphy-based lineages has been vigorously criticized by some cladists (e.g., Cracraft, 1979; Eldredge, 1979) and just as vigorously defended by other workers (Gingerich, 1976; Bretsky, 1979). For our purposes, we have adopted the compromise procedure advocated by Fortey & Jefferies (1982); their points against both

extremes are largely convincing. Because all other holocystitids are Wenlockian contemporaries and some features have no exact parallels in other diploporite groups, it was not always possible to establish the direction of some apparent trends. For this reason as well as those listed earlier, a cladistic analysis was not attempted. Most cladistic procedures and most quantitative phenetic methods require specification of the direction of trends, *e.g.*, explicit or implicit designation of apomorphies, plesiomorphies, and synapomorphies. The Wagner tree procedure is more accommodating and additionally readily allows the inclusion of hypothetical taxa in the phylogeny (Farris, 1970). In practice, however, "primitive" and "advanced" (shared derived) characters could be detected fairly readily in many cases.

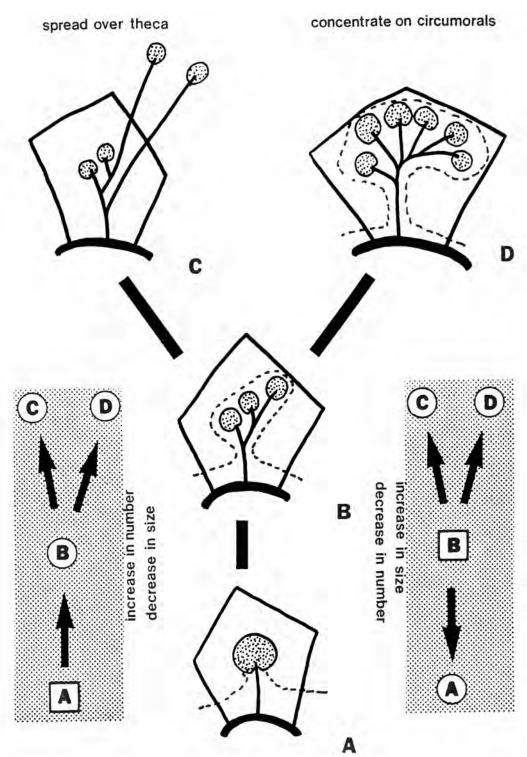
In regard to diplopores, the trend toward reduction in number per plate is well accepted (e.g., Paul, 1976, 1977, 1979; Bockelie, 1984). Additionally, we believe that the functional importance of diplopores is less in the Silurian than in the Ordovician, as argued previously. In Finitiporus n. gen., for example, diplopores are confined to the adoral portion of the theca. Holocystitids tend to maintain widely distributed humatipores (all known taxa are omniporate rather than partiporate or aporate), but variation in size (diameter), number of tangential canals, and packing are obvious. We regard densely packed pores that are large-sized and have numerous tangential canals as "primitive" and sparse, small humatipores with few tangential canals as "advanced." The functional significance of sursumate versus flat humatipores is unclear, but existing morphologies can be arrayed in a presumed evolutionary sequence (Text-fig. 21). Only Silurian forms are sursumate, so we presume a progression from planar tangential canals (flat-surfaced plates) to raised structures (pustules on plates) via an intermediate stage with flat plates but nonplanar tangential canals; among the subgenera of Holocystites, Sepulticystis n. sgen. is an example of such a form, whereas Holocystites and Megacystites n. sgen. represent the two extremes.

Evolution of ambulacral facet morphology in the Sphaeronitida can be interpreted in two ways (Text-fig. 23). Forms with single moderately large facets, a few facets on circumorals only, many facets on circumorals only, and many facets spread over the theca have been described, and are essentially contemporaneous, in the Ordovician. Two sequences are possible. (1) The single large facet (Text-fig. 23A) is primitive, and the trend is to increase facet number and decrease size; location of the numerous small facets tends to two functionally equivalent extremes, either to spread them over the theca (C) or concentrate them around the peristome (D). (2) One or a few small facets is the ancestral state (B), and end members A, C, and D are all strategies to increase the size of the subvective system relative to thecal volume. As mentioned above, there is some reason to prefer alternative 2. The new Osgood taxa, because they are younger stratigraphically and presumably more advanced, provide some new evidence in favor of the second alternative; all have single large facets in each ray.

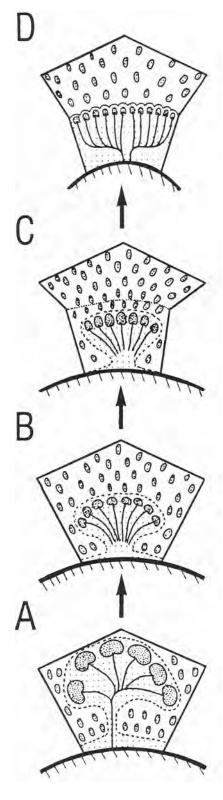
In the sphaeronitid subfamily Herpetocystinae, the sequence B-D is carried to the ultimate extreme, although other sphaeronitid genera show the same trend (see, e.g., Bockelie, 1984, on Haplosphaeronis Jaekel, 1926). Genera with ambulacral platforms tend to increase the number of small facets until these constitute an essentially continuous ring of facets at the edge of the platform, which is also the peristomial periphery. Ordovician genera can be arranged in a sequence, linking increasing protrusion of the ambulacral platform, increased number and decreased size of ambulacral facets, and gradual exclusion of pore structures from the immediate ambulacral area, ultimately leading to development of an epipanniculate peristome (Text-figs 24A-C). Secondary calcite is secreted on that portion of the circumorals that bears ambulacral grooves, and these plates are typically much thicker in their adoral portions. The most extreme development of an epipanniculate peristome, however, significantly is not encountered until the Silurian. Finitiporus n. gen. (Text-figs 19C, 24D) has facets adjoining except in a narrow band in the posterior interray, has no diplopores on the ambulacral platform proper, and has the raised adoral halves of the circumorals much thicker than the aboral (Text-fig. 18). The presumed evolution within the more diverse and better-known Herpetocystinae is shown in Text-fig. 19 and will be discussed in detail in a later section.

The Holocystitidae possess only large facets. In contrast, large-faceted forms are rare in Ordovician Sphaeronitidae (*Diplosphaeronis* is the best example). Holocystitid facets are conspicuously larger than those of any sphaeronitid, with *Paulicystis* n. gen. the most extreme yet known. It seems reasonable to regard both the holocystitids and *Finitiporus* n. gen. as representing equally specialized responses to a need for increased subvective efficiency, as suggested by alternative 2.

Trends in thecal plating are relatively clear. Many authors (e.g., Sprinkle, 1973; Paul, 1977, 1988; Frest & Strimple, 1978) have regarded unorganized, irregularly polygonal, and numerous thecal plates as primitive features in the Blastozoa. Trends toward reduction in number of elements, increasing symmetry, and regular organization have been noted in all large classes. In the Diploporita, such trends have been established in the Aristocystitida (Chauvel, 1941) and in the Sphaeronitida (Regnéll, 1960; Paul, 1971, 1973; Bockelie, 1984). In both orders, the same sequence of development is assumed (Textfig. 25). Early members have no clear organization, and plates are added as needed all over the theca (Text-fig. 25A). More advanced taxa show some signs of regular plate organization (grouping into crude size classes) and tendencies to add more than one plate simultaneously (Text-fig. 25B). Accentuation of these trends leads to development of multiple regular plate generations (circlets). How easily these can be recognized is often



Text-fig. 23. Possible evolution of ambulacral facet morphologies in the Sphaeronitidae. (A) Single large facet, as in *Eucystis pentax* Paul, 1973, or *Diplosphaeronis*. (B) One or a few small facets on circumorals, as in *E. angelini*. (C) Few to many small facets developed on the plates besides circumorals (e.g., E. raripunctata). (D) Small facets concentrated on circumorals, as in *Archegocystis desiderata* (Barrande, 1887). Assuming that an increase in the subvective area relative to the cal volume is a major evolutionary "goal" in Diploporita, evolutionary trends in known diploporites can be interpreted in two ways: (1) (left of figure) possession of one large facet could be primitive and the overall trend is to increase the total number of ambulacral facets (B, C, and D are advanced); (2) (right of figure) the same overall trend is assumed, but the primitive state is possession of one or a few small facets, and single large facets (such as those of the Holocystitidae) represent either a very large "arm" or brachiole, or a trunk bearing true brachioles (A, C, and D are advanced states).



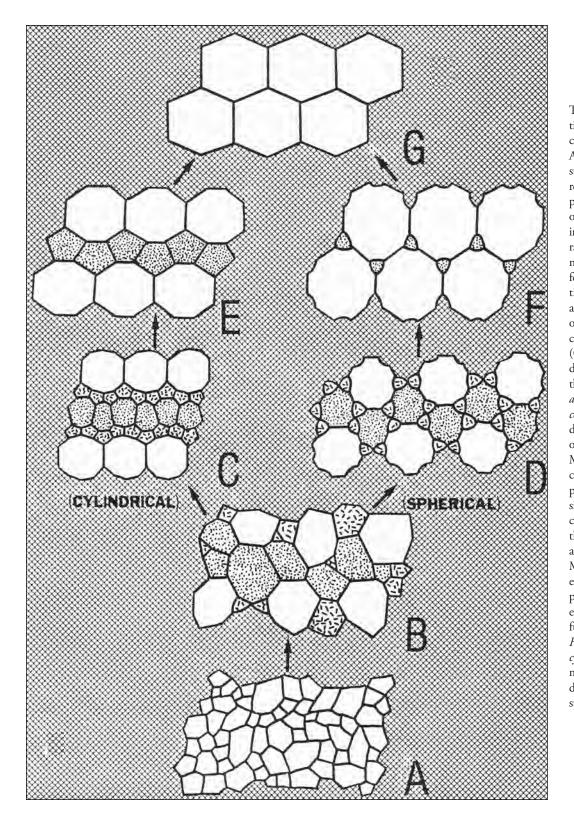
Text-fig. 24. Presumed evolution of epipanniculate ambulacra in the Sphaeronitidae. Peristomial opening marked by heavy line and partial scoring; peristomial border by dashed line; areas with secondary calcite secretion dotted. (A) Few comparatively large facets on aboral part of circumoral, no platform, ambulacral diplopores numerous on entire circumorals, as in Archegocystis stellulifera (Salter, 1866). (B) Concentration of smaller, more numerous facets on adoral portion of circumoral; no ambulacral platform; diplopores still on whole of circumoral, but fewer adorally. (C). As in B, but ambulacral platform developed, still fewer diplopores adorally on circumoral, as in Haplosphaeronis multifida Paul, 1973. (D) Well-developed ambulacral platform with many small facets occupying whole adoral portion of circumoral; diplopores only on aboral part of circumorals, as in Finitiporus boardmani n. gen., n. sp.

dependent on thecal shape. In the Holocystitidae, species with cylindrical thecae (*H. alternatus*, *H. abnormis*) show more distinct plate generations, with secondaries and later generations

frequently much smaller than primaries (Text-figs 25C, E; see also Pl. 2, Fig. 3). More spherical species (H. scutellatus, H. spangleri) tend to have less obvious circlets (plates of a single generation are not always adjoining), and later plate generations might reach the size of the primaries (Text-figs 25D, F; see also Pl. 2, Figs 1-2, 4). Eventually, a stage with only a single generation of large adjoining, dominantly hexagonal plates in the adult is reached (H. cylindricus; Text-fig. 25G). At the same time, there is also a tendency to reduce the number of plate circlets. If each generation is counted as a separate circlet, H. cylindricus has only one-third the number of H. alternatus. Among subspherical taxa, the ultimate in simplicity is reached with Haplosphaeronis, which has a theca of only two plate circlets (Paul, 1973). Reduction in number of plates per circlet also occurs; in the Sphaeronitidae, the small number of plates in Eucystis Angelin, 1878, as against Diplosphaeronis, provides a good example (Paul, 1973). In the Holocystitidae, forms with eight primaries per circlet are known (Holocystites), whereas genera like Pentacystis and Paulicystis n. gen. retain > 20 plates per circlet. A detailed discussion of the advantages of the different modes of thecal and plate growth was included by Paul (1971: 14-18).

Trends toward plate circlet loss or reduction in numbers of components are also evident in the peristomials, although these show less drastic changes. In the Holocystitidae, the Upper Ordovician *Brightonicystis* can be regarded as primitive; it has 10 periorals and (probably) 10 facetals. Both circlets are prominent. Most Silurian holocystitids have eight facetals (*e.g.*, *Holocystites*), but one has six (*Pustulocystis*). The perioral circlet is diminished in size or lost completely in some pentacystinids.

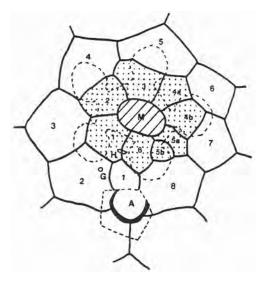
We regard species that as adults have large numbers of plates (whether this feature is defined as total number of plates, circlets, periorals, facetals, or plate generations) as primitive or ancestral forms, and those with reduced plate numbers as advanced. Our reasoning is as follows. (1) It is generally agreed that primitive echinoderms had large numbers of plates, whereas reduction is characteristic of advanced taxa; this is especially the case with blastozoans, as argued previously. (2) The only known Ordovician holocystitid, Brightonicystis, has numerous thecal plates, i.e., 10 periorals and facetals, and multiple plate generations and circlets, but later (Silurian) forms often have fewer in each category, and always do if facetals and periorals are compared. (3) Most variant specimens (whatever the cause of variation) show reduction, not augmentation, in the characters mentioned. Only four exceptions come to mind. We illustrate (Text-fig. 26) a specimen of Holocystites (Sepulticystis) spangleri with extra periorals. In addition, Paul (1971: 129, fig. 54) mentioned three examples of Trematocystis rotundus with FA1 represented by two plates. Also, the holotype of T. wetherbyi (Miller, 1878) has nine facetals (Paul, 1971: 118, 130, fig. 55b).



Text-fig. 25. Presumed evolution of regular thecal plate circlets in the Sphaeronitida and Aristocystitida. (A) Primitive state, with numerous small, irregularly arranged and shaped plates with variable numbers of sides; new plates intercalated individually, more or less at random, as in Sphaeronites and many aristocystitids. (B) Plates fewer, larger, arranged in indistinct generations, i.e., new plates added in multiples simultaneously, as in many Eucystis species and Brightonicystis gregarius. (C, D) Several (three illustrated) distinct, regular generations of thecal plates, as in Holocystites alternatus and Triamara ventricosa; configurations as typically developed in cylindrical (C) or spherical (D) thecae. (E, F) More advanced two-generation configurations of large, regular plates with comparatively few sides, as displayed in taxa with cylindrical (E) or spherical (F) thecae, such as H. abnormis and Osgoodicystis wykoffi. (G) Most advanced state; single generation of relatively few, large plates in a few circlets persisting essentially throughout almost full ontogeny; examples are Haplosphaeronis and Holocystites cylindricus. Primaries or indeterminate plates white; secondaries dot stippled, tertiaries with line stipple.

C. Paul (pers. obs.) suggested that plate reduction is plausibly interpreted as pedomorphosis. He noted that all Sphaeronitidae have seven plates in the basal and circumoral

circlets. Variation in plate number normally occurs only in the intervening plate circlets. In this view, addition to the basic two circlets (e.g., in *Sphaeronites*) could be an advanced feature,

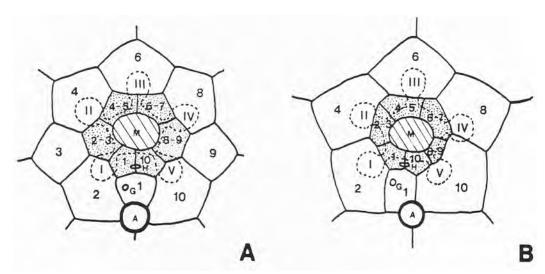


Text-fig. 26. Interpreted camera lucida drawing of oro-anal area of an abnormal specimen (SUI 48197) of *Holocystites* (*Sepulticystis*) *spangleri*. The gonopore is on FA2 and the peristomial opening is surrounded by 8 periorals. Symbols as outlined under Abbreviations, p. 52.

whereas possession of two circlets only, as in *Haplosphaeronis*, could indicate a primitive taxon (if a general trend to additional circlets occurs) or either a surviving primitive taxon or an advanced (pedomorphic) one, if this trend is followed by a later tendency to reduce plate number secondarily. Present evidence in our opinion does not conclusively favor either possibility for sphaeronitids, due mostly to the lack of convincing immediate ancestors for Middle and Upper Ordovician sphaeronitid lineages. However, we think a case can be made that reduction, regardless of origin, is an advanced feature for holocystitids.

In the Sphaeronitidae, there is no clear family-wide trend demonstrating pedomorphosis in plate morphology. Neither the oldest nor youngest known sphaeronitids are those with the greatest number of plates. The abundant and diverse Middle and Upper Ordovician forms (e.g., the British faunas described by Paul, 1973, 1984) show a particularly wide range of variation. There appears to be no single clear unidirectional trend in Eucystis, the most diverse and long-ranging genus (Regnéll, 1945, 1951; Prokop, 1964; Paul, 1973; Bockelie, 1984). Circumoral and basal plate configuration and number are indeed mostly invariant throughout the family. In contrast, the peristomial plating, although more conservative (smaller range of variation, slower rate of change) than other thecal plate circlets, does vary in the Holocystitidae. One circlet (perioral) is lost completely in some, and reduced numbers of both facetals and periorals characterize many taxa. Overall, there is mosaic evolution in plate characters. Even though most known holocystitids are Wenlockian contemporaries, the stratigraphically precedent *Brightonicystis* is a logical ancestor to the later forms. The mentioned plate features of all holocystitids can be arranged in a parallel transformation series. If this is done, the morphology of *Brightonicystis* can consistently be considered ancestral, thus fixing the direction of plate trends. Moreover, as will be discussed below, holocystitid phylogenies constructed using four different numerical taxonomic techniques are essentially identical. Three require that the direction of presumed evolutionary trends be specified, but the Wagner tree procedure does not. Because its results are congruent with those of the other methods, it seems likely that the hypothesized trends are correctly coded.

It is not yet clear which diploporite group is ancestral to Sphaeronitidae. Hence, it is also not certain whether the invariant and comparatively small number of circumoral and basals is a primitive or advanced feature in this family. No complete ontogenetic series are known, but many diploporites do appear to add plates during ontogeny. In the Holocystitidae, this must occur very early in ontogeny, as the smallest observed specimens of Holocystites alternatus, H. ovatus, and H. scutellatus have the full complement. Most sphaeronitids add plates throughout the known ontogeny. It is thus quite possible that Haplosphaeronis, which is unique in the family in that its plating is constant in number and regular (Paul, 1973: 27), is pedomorphic, rather than derived from an ancestor which never added plates. On the whole, holocystitid plate configurations, regardless of number per circlet, are more stable, and plate stability itself is likely to be an advanced, but not pedomorphic, feature in this family. Based on known taxa, no particular configuration is as evidently basic to the Holocystitidae as is that of Haplosphaeronis to the Sphaeronitidae. This lessens the likelihood of pedomorphosis as an explanation for reduction in plate numbers in this family. It seems likely that many holocystitid taxa were derived from ancestors with more adult plates. There is no evidence that *all* plates in taxa belonging to either family are added either one at a time or in groups. However, it is clear that at least some circlets or generations are added simultaneously in both families. This applies particularly to circlets below the peristome. The concept of plate generations (Paul, 1971, 1973) in the Sphaeronitidae might apply to peristomials in either or both families as well; alternatively these plates might be added discontinuously early in ontogeny. As both mechanisms are likely used by both families, and as early ontogeny of some plate types (peristomials especially) is unknown, demonstration of pedomorphosis is difficult. In those taxa with reduced peristomial plating, identification of the remaining plates and specification of the mechanism of their loss [e.g., by fusion of adjacent elements, "loss" (failure to develop), or combinations of these two mechanisms] are often difficult. Examination of deviant specimens could help indicate the actual sequence of events. Among cylindrical species, occasional specimens show



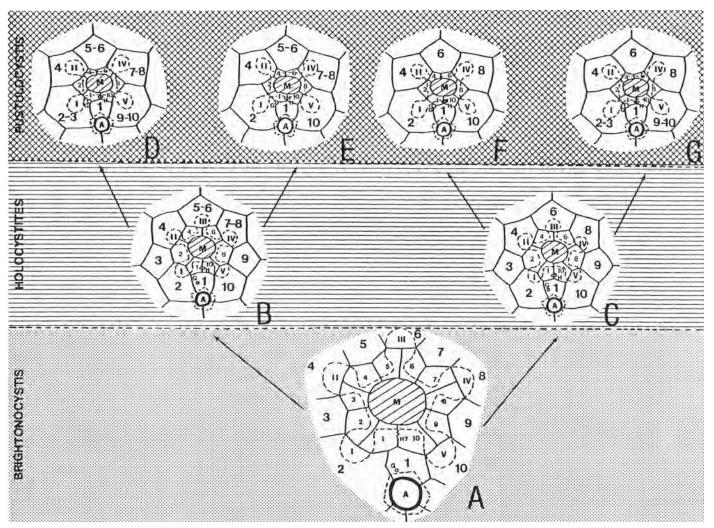
Text-fig. 27. Diagrammatic representations of the oro-anal areas of normal (A, USNM S3070) and abnormal (B, SUI 48172) Holocystites cylindricus. Both assume the plate configuration of Brightonicystis gregarius represents the full (primitive) complement (see text). Facetals (white) and periorals (dotted) numbered; peristome lined. Symbols as outlined under Abbreviations, p. 52. Periproctal border indicated by heavy line. Not to scale. Note reduction (loss) of non-facet-bearing facetals and of some thecal plates (unnumbered, white).

reduced numbers of regular or irregular facetals (Text-fig. 27), but more have been found with the normal numbers, but with widely varying facetal sizes, as might be expected if gradual loss occurred. Specimens with more than the typical facetal or perioral complement are exceedingly rare, and none has been seen with regularized "extra" facetals or periorals. Individuals with extra peristomial plates are also abnormal in other ways, and hence probably damaged or pathologic. A good example is the specimen (SUI 48197) of *H. spangleri*, illustrated in Text-fig. 26, which has irregular facetals and periorals, and displaced facets and gonopore. Even with a large sample for both members of a presumed ancestor-descendant sequence exhibiting a range of variation in peristomial morphology, it is still often difficult to choose between lateral fusion or abrupt loss of critical elements.

Major alternatives for one sequence (evolution of Pustulocystis from Brightonicystis via Holocystites) are illustrated in Text-figs 28-29. In each, plates are numbered consecutively from the left of the periproct in a clockwise direction. Brightonicystis is used as the standard to facilitate plate identification in later taxa. The positions of the ambulacral facets remain generally fixed, and provide another standard of reference. Only two of our specimens have facets displaced onto usually non-facet-bearing facetals (Text-figs 22, 26). In the case of the facetals, the most likely course of evolution is reduction in Holocystites by gradual loss of FAA5 and 7 of Brightonicystis. Examples of H. scutellatus with small FAA5 and 7 have been seen, so that the sequence A-C is more probable than A-B (both figures). The large size of the posterior FAA in *Pustulocystis* could indicate origination via fusion of paired FAA2 and 3 and 9 and 10 of Holocystites (sequence A-C-G of both figures) or by loss of two additional plates, FAA3 and 9 of Holocystites (sequence A-C-F). Again, specimens of *H. scutellatus* with unusually small plates in these areas have been collected. Curiously, no specimen with very

small or strongly unequal facet-bearing FAA has yet turned up, so that fusion of other plates with these relatively stable elements is unlikely. In specimens we have examined there is little evidence to indicate whether reduction in number of periorals was achieved by loss (abrupt or gradual) or by fusion. In Brightonicystis, the periorals are paired, but the first reductions disrupt the pattern (Text-figs 28B-C, 29B-C). Periorals 1 and 10, which have the hydropore, are likely to have persisted unchanged; in Osgoodicystis cooperi n. gen., n. sp., only these two periorals survive. Fusion of adjacent PO pairs 2-3, 4-5, 6-7, and 8-9 is most likely because no Holocystites specimens have been found that have a full complement of POO, and aside from POO1 and 10, the entire circlet is lost by equal and gradual diminution, not complete plate loss, in all known taxa. Accordingly, the sequence A-C-F in Text-fig. 29 is probably the correct one. Additionally, loss of a peristomial plate circlet is probably a phylogenetically significant event, judging by the general stability of these elements in many Diploporita, especially in the related family Sphaeronitidae.

Accompanying loss of the periorals, a shift in the position of the hydropore occurs, as would be expected because this orifice normally is situated on the PO1:PO6 suture. Displacement to FA1 or into soft tissue is a probable consequence, with relocation to FA1 or the FA1:FA8 border less drastic and more readily demonstrable. Gonopore location varies; most taxa have it on FA1, but in a few, it is displaced to FA2, and in *Pustulocystis*, it is variable in position and sometimes located on the common border of FA1, FA2, and PO1. Functional or phylogenetic significance of these locations is unclear; the character was coded by frequency of occurrence. Similarly, possession of five ambulacral facets is thought to be primitive (pentameral symmetry is basic to most echinoderms for functional reasons; Stephenson, 1976, 1980), and the four-facet condition is thought to be advanced. In the Sphaeronitidae, the

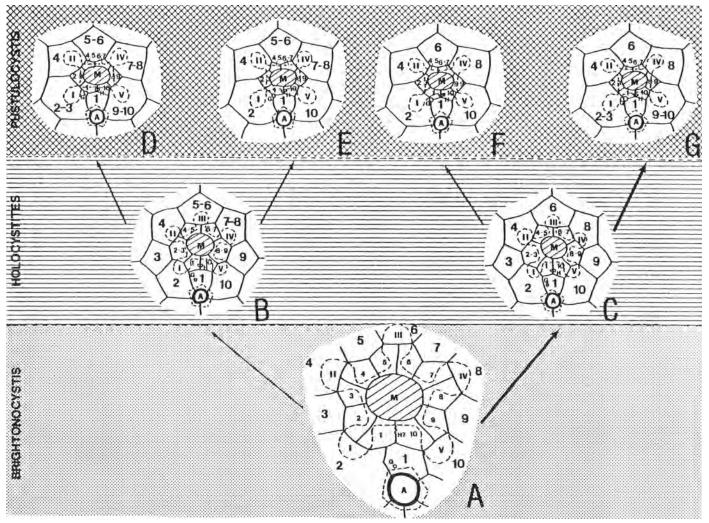


Text-fig. 28. Possible evolution of advanced holocystitid (*Pustulocystis*) from primitive taxon (*Brightonicystis*). One intermediate stage (*Holocystites*) also shown. This figure assumes that reduction in plate number is the basic trend, here achieved by loss of POO3, 5, 7, and 9, and by a combination of lateral fusion and loss of facetals. (A) Basic (primitive) holocystitid peristomial plate configuration of 10 periorals and 10 facetals (*Brightonicystis*). (B, C) More advanced configurations of *Holocystites*, with 6 periorals and 8 facetals; reduction to 6 facetals achieved either by (B) fusion of PO5 with 6 and PO7 with 8, or (C) loss of PO5 and PO7. (D-G) Highly advanced configuration of *Pustulocystis*, composed of 6 periorals and 6 facetals. Presupposing (B), further reduction could result from (D) fusion of PO2 with PO3 and PO9 with PO10, or (E) loss of PO3 and PO9. Alternatively, presupposing (C), simple loss of PO3 and PO9 (F) or fusion of PO2 with PO3 and PO9 with PO10 (G) would produce identical results. Symbols as outlined under Abbreviations, p. 52.

number of facets is less taxonomically diagnostic. It is generally insignificant on the generic level, however, Bockelie (1984) has recently revised the species of *Eucystis*. The major criterion used to erect *Tetreucystis* Bockelie, 1984, was the quadrilateral peristome (no facets in Ambulacrum III) versus the pentagonal peristome of *Eucystis (s. s.)*. Still, facet number in sphaeronitids generally is more variable than in the Holocystitidae, and uncorrelated with other morphologic features; it is usually used as a species taxobasis (e.g., Paul, 1973). In the Holocystitidae, this character is generally consistent at the generic or subfamilial level (*Pustulocystis pentax* is the only exception), and correlates

well with other major differentiating features. For example, among the hundreds of specimens of *Holocystites scutellatus* and *H. ovatus* examined, only one had four facets, and it was clearly pathologic (Text-fig. 26); the periorals and facetals are irregular in size and shape, there are only four periorals, the facet size varies, and the remaining facets are displaced from their usual positions.

In addition to features showing definite or readily inferred evolutionary trends, several characters preliminarily regarded as ecologically influenced or determined were included. Major differences between Group 1 and Group 2 species relate to thecal



Text-fig. 29. Possible evolution of *Pustulocystis* from *Brightonicystis* via *Holocystites*, assuming lateral fusion of some pairs of periorals (2 and 3, 4 and 5, 6 and 7, 8 and 9). Facetal evolution in B-G as in Text-fig. 28. Heaviest arrows (A-C-G) indicate most likely alternative; another, less likely possibility is the sequence A-C-F. Symbols as outlined under Abbreviations, p. 52.

shape, size of the base for attachment, presence or absence of an aboral projection, and fixed or free status of adults. These characters were previously cited as species taxobases only. As discussed above, most can be interpreted as adaptations to soft or shifting substrata or to high rates of sediment accumulation.

Most diploporites are globular or sac-shaped, but many holocystitids are cylindrical or pyriform. The presumed sequence of development is from globular to pyriform to cylindrical thecae; the unusual spindle-shaped theca of *Holocystites greenvillensis* is treated as most advanced. Large-based forms are most frequent among all Sphaeronitida, as is the life habit of permanent attachment to hardgrounds or other stable substrata. Hence, small bases are considered advanced, as are abilities to detach from a hard substratum, adjust thecal position, or otherwise adapt to a soft-bottom habitat. Fixed (primitive) versus free (advanced) adults represent a related trend. Elevation

of the theca above the substratum is also affected by growth gradients, with cylindrical thecae clearly being advantageous, as these become taller relatively faster than globular forms if equal volume increments are compared. Even more effective is the development of an aboral projection, which performed some of the functions of a stem, especially in elevating the peristome and subvective system above competitive low-level feeders. Absence of an aboral projection is considered a primitive feature (sphaeronitids lack them), whereas development of a long one (relative to other *Holocystites* fauna species) is considered a derived character. Generally, most cylindrical forms have aboral projections, as do some pyriform species; globular forms do not develop them.

PHYLOGENY

Prior to application of numerical methods, an attempt was

made to establish genera intuitively on the basis of peristomial morphology. Using a minimum of characters and the previously-existing generic-level taxonomic framework (Paul, 1971), seven genera could be distinguished, as follows:

Brightonicystis: ?10 FAA, 10 large POO, 5 ambulacral facets (F, plural FF) on POO and FAA, hydropore on POO.

Holocystites: 8 FAA, 6 large POO, 5 FF on both POO and FAA, hydropore on POO.

Pentacystis: 8 FAA, POO absent, 5 FF on FAA only, hydropore on FAA.

Osgoodicystis n. gen.: 8 FAA, 2-6 very reduced POO, 5 FF on FAA only, hydropore on FAA or cryptic.

Trematocystis: 8 FAA, 6 small POO, 4 FF on FAA only, hydropore on POO.

Pustulocystis: 6 FAA, 6 small POO, 4 FF on FAA only, hydropore on POO.

Paulicystis n. gen.: 8 FA A, 6 small POO, 4 FF on FA A and lower thecal plates, hydropore on POO.

Using these features only, three major groupings are apparent, and here defined as subfamilies (Text-fig. 30):

Holocystitinae: 5 round FF on both POO and FAA, large POO, hydropore on POO (*Brightonicystis* and *Holocystites*).

Pentacystinae: 5 round FF on FAA only, POO vestigial or absent, hydropore on FAA or cryptic POO (*Pentacystis, Osgoodicystis* n. gen.).

Trematocystinae: 4 elliptical FF on FAA only or also overrunning lower thecal plates, small POO, hydropore on POO (*Trematocystis, Paulicystis* n. gen., and *Pustulocystis*).

Suggested relations among these genera are indicated in Text-fig. 30. Extremes of trends with large observed ranges (i.e., POO size, number of FAA and POO, position of facets) are made termini (Pentacystis, Pustulocystis, and Brightonicystis), whereas averages are located near the center of the figure. The unique elongate facets of Paulicystis n. gen. also seem to warrant addition of a special branch to accommodate the genus. Trematocystis and Pustulocystis are the only other holocystitids with elliptical facets, and derivation of Paulicystis n. gen. from the former seems more likely because Pustulocystis has only 6 FAA.

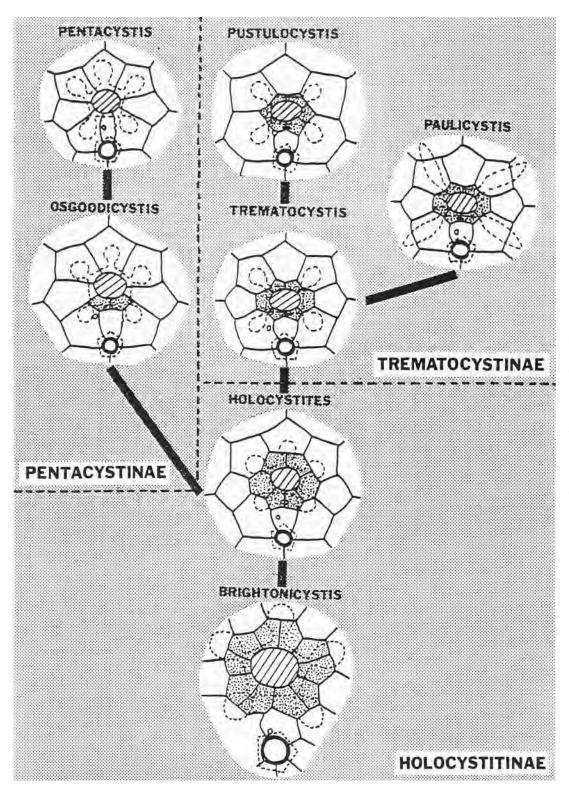
Following the preliminary intuitive grouping (Text-fig. 30), the same characters were coded in presumed evolutionary sequence, and one additional character with high taxonomic value (humatipore morphology) was added (Table 9); this last feature required subdivision of *Holocystites* into subgenera, but otherwise made no changes. Thus at the generic level, nine taxonomic units and seven characters were used to construct the initial generic-level datamatrix (Tables 10-11). For the species-level matrix, all well-known taxa (23; see Systematic

Paleontology for details) were included. All of the characters outlined above were coded and treated equally (not weighted); 20 were used (Tables 12-13).

Three techniques were tried for both the generic and specific matrices. Unrooted and rooted Wagner tree analyses were attempted using the WAG78 program of J. S. Farris. Essentially identical results were obtained (Brightonicystis gregarius was selected by the program as root taxon, and also plots as distinct in the unrooted analysis); only the unrooted results are figured (Text-figs 31-32). This technique also generates the minimum necessary hypothetical taxa required to link the real ones; the character matrices for the hypothetical genera and species are listed in Tables 14 and 15. An unweighted cluster analysis was also performed, using Sokal's average distance (Sneath & Sokal, 1973: 124) as the metric and the UWPGA option in NTSYS (Rohlf et al., 1974; Text-figs 33-34). Using the same program package, a principal components analysis was also run on the same input matrices. Plots of all factors with Eigen vector values > 1 (Tables 16-17) were generated; some of these are

Table 10. Characters and states used for generic-level phylogeny of the Holocystitidae.

Character	States	Coding
1. Number of facetals:	Indistinct	0
	(probably 10)	
	8	1
	6	2
2. Number of periorals:	10	0
	6	1
	2 or 0	2
3. Size of periorals:	Large	0
	Small or partial	1
	Absent	2
4. Position of ambulacral	On periorals	
facets:	and facetals	0
	On facetals only	1
	Overrunning	
	facetals	2
5. Number of ambulacral	5	0
facets:	4	2
6. Hydropore location:	On periorals	0
	On facetals	2
7. Humatipore type:	Flat, essentially	
	two dimensional	0
	Flat, three	
	dimensional	1
	Raised, three	
	dimensional	2



Text-fig. 30. Possible relationships of the genera of the Holocystitidae. Intuitive approach based on peristomial morphology, but ignoring stratigraphy and presumed evolutionary trends. Three subfamilies are distinguished: Holocystitinae, with large periorals, ambulacral facets on both periorals and facetals, and 5 ambulacral facets; Trematocystinae, with medium-sized periorals, ambulacral facets on facetals only, and 4 ambulacral facets; and Pentacystinae, with very small or absent periorals, ambulacral facets on facetals only, and 5 facets.

illustrated here (Text-figs 35-36).

Very similar results were obtained from all techniques. In particular, all produced identical generic groupings (subfamilies). Three major groups are evident, with *Brightonicystis* pos-

sibly representing a fourth. This genus probably will eventually be placed in a separate subfamily or family, but because of its isolated stratigraphic position and incompletely known morphology, that step is not taken here, and we construe holo-

Table 11. Initial data matrix for generic-level phylogeny of the Holocystitidae.

			Cł	ıarac	ter		
Taxon	1	2	3	4	5	6	7
Subfamily Holocystitinae							
Brightonicystis	0	0	0	0	0	0	0
Holocystites (Holocystites)	1	1	0	0	0	0	2
Holocystites (Megacystites)	1	1	0	0	0	0	0
Holocystites (Sepulticystis)	1	1	0	0	0	0	1
Subfamily Pentacystinae							
Osgoodicystis	1	2	1	1	0	2	0
Pentacystis	1	2	2	1	0	2	0
Subfamily Trematocystinae							
Trematocystis	1	1	1	1	2	0	0
Paulicystis	1	1	1	2	2	0	0
Pustulocystis	2	1	1	1	2	0	2

cystitid subfamilies broadly. In the Wagner tree plot (Text-fig. 31), each subfamily appears comparatively widely separated from the others. Megacystites n. sgen. is the central (ancestral) holocystitinid taxon, whereas Trematocystis occupies a similar position in the Trematocystinae. Brightonicystis, although isolated, bears the same relationship to Megacystites n. sgen. as does Holocystites. Within the genus Holocystites, the sequence of subgenera is Megacystites-Holocystites-Sepulticystis. Pentacystis succeeds Osgoodicystis n. gen. in the Pentacystinae, and is more peripheral in the plot. The genera of the Pentacystinae are distantly related to the other subfamilies and approximately equidistant from Trematocystis and Megacystites n. sgen. Paulicystis n. gen. is decidedly peripheral in position, as against Pustulocystis. The UWPGA cluster analysis phenogram (Textfig. 33) produces the same major groupings (subfamilies), but the arrangement of branches is somewhat different. In the Holocystitinae, Brightonicystis is more isolated, whereas the sequence of Holocystites subgenera here is Sepulticystis-Megacystites-Holocystites. Similarly, in the Trematocystinae Trematocystis and Paulicystis n. gen. are closely related, whereas

Table 12. Characters and states used for species-level phylogeny of the Holocystitidae.

Character	States	Coding
1. Thecal shape	Globular	0
-	Pyriform or ovate	2
	Cylindrical	3
	Spindle-shaped	4
2. Base	Large	0
	Intermediate	2
	Small	4
3. Aboral projection	Absent	0
	Short	2
	Long	4
4. Adult attachment	Fixed	0
	Free	4
5. Thecal plate generations	2 or 3 indistint, irregular	0
	3 distinct	2
	2 distinct	3
	Single	4
6. Thecal plate circlets	Indistinct	0
	Regular	2
	Partial & regular	4
7. Number of thecal plates per circlet	Many (more than 12)	0
	Intermediate (8-12)	2
	Few (less than 8)	4
8. Number of thecal plates per circlet (below facetals)	Numerous (more than 8)	0
	Intermediate (5-8)	2
	Few (4 or less)	4

9. Total number of thecal plates	Numerous (more than 120)	0
•	Intermediate (80-120)	2
	Few (80 or less)	4
10. Number of ambulacral facets	5	0
	4	4
11. Ambulacral facet position	On periorals and facetals	0
-	On facetals only	2
	Overrunning facetals	4
12. Number of facetals	Indistinct (probably 10)	0
	8	2
	6	4
13. Number of periorals	10	0
	6	2
	2 or 0	4
14. Size of perioral circlet	Large	0
	Small	2
	Partial or absent	4
15. Gonopore location	On FAl	0
	On FA2	2
	On FA1, FA2 & P01	4
16. Hydropore location	On PO1-PO6 border	0
	On FA1	2
	Indefinite location	4
17. Humatipore type	Flat, two dimensional	0
	Flat, three dimensional	2
	Raised, three dimensional	4
18. Humatipore packing	Dense	0
	Intermediate	2
	Sparse	4
19. Average number of humatipore canals	6 or more	0
	3 - 6	2
	Less than 3	4
20. Humatipore size	Large	0
	Small	4

the relationship of either to *Pustulocystis* is more distant. The pentacystinid genera plot as closely related, and their branch shows as more closely related to the Trematocystinae than to the Holocystitinae. The PCA plots show similar results: again, three major groupings are evident (Text-fig. 35). *Brightonicystis* is somewhat isolated from the other Holocystitinae. Among the subgenera of *Holocystites*, *Sepulticystis* n. sgen. and *Holocystites* generally plot close together, whereas *Megacystites* n. sgen. is more distant. *Pustulocystis* is generally isolated from the other two trematocystinids, whereas the pentacystinid genera are also near neighbors. Subfamilial relationships are equivocal, with the trematocystinid cluster perhaps nearer to the holocystitinid cluster than to the pentacystinid cluster. Of interest is the strong congruence of the results of the numerical methods with the

intuitive arrangement. The final generic phylogeny (Text-fig. 37) is not strictly identical with either, but is strongly weighted toward the numeric results.

For the species-level matrix, agreement between methods is also strong. Grouping of species into clusters largely identical to the intuitively established genera and subfamilies is evident, with only occasional deviations. In the Wagner network plot (Text-fig. 32), *Brightonicystis gregarius* is strongly isolated from the remaining Holocystitinae. Suggested groupings of *Holocystites* species into subgenera seem supported. The sequence of origination in *Holocystites* is *Sepulticystis-Holocystites-Megacystites*. The pentacystinid branch is equidistant from that of the Holocystitinae and the Trematocystinae. *Osgoodicystis* n. gen. is shown as polyphyletic, with *O. bissetti* n. gen., n. sp.

Table 13. Initial data matrix for species-level phylogeny of the Holocystitidae.

											Char	acter								
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Brightonicystis gregarius	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Holocystites alternatus	3	4	4	4	2	0	4	0	0	0	0	2	2	0	2	0	4	2	0	4
H. clavus n. sp.	3	4	4	4	3	0	4	0	0	0	0	2	2	0	2	0	4	2	0	4
H. cylindricus	3	4	4	4	4	2	4	0	2	0	0	2	2	0	0	0	4	2	0	4
H. scutellatus	2	4	2	4	3	0	4	0	0	0	0	2	2	0	0	0	4	0	0	4
H. ovatus	0	4	2	4	3	0	4	0	0	0	0	2	2	0	0	0	4	0	0	4
H. greenvillensis	4	4	4	4	4	2	4	2	4	0	0	2	2	0	0	0	4	2	0	4
H. spangleri	2	2	0	0	3	0	4	0	0	0	0	2	2	0	0	0	2	2	0	4
H. abnormis	3	4	4	4	4	2	4	2	4	0	0	2	2	0	0	0	4	2	0	4
Pentacystis simplex	2	0	0	0	4	2	0	0	0	0	0	2	2	4	2	4	0	4	4	4
P. sphaeroidalis	0	0	0	0	4	2	0	2	0	0	0	2	2	4	0	4	0	0	2	0
P. gibsoni n. sp.	2	0	0	0	4	2	0	0	0	0	0	2	2	4	0	4	0	0	2	0
Osgoodicystis bissetti	3	0	0	0	4	2	0	0	0	0	0	2	4	4	2	4	0	4	4	4
n. gen., n. sp.)	U	U	U	4		U	U	U	U	U		4	4		4	U	4	4	4
O. cooperi n. gen., n. sp.	3	0	0	0	4	2	2	0	0	0	0	2	4	2	2	4	0	0	4	4
O. wykoffi	2	0	0	0	3	2	0	0	0	0	0	2	4	2	2	4	0	2	4	4
Trematocystis globosus	0	2	0	0	4	2	2	4	4	4	2	2	2	2	2	0	0	2	2	4
T. rotundus	0	2	0	0	4	2	2	4	4	4	2	2	2	0	0	0	0	2	2	4
T. wetherbyi	3	2	0	0	4	2	0	2	2	4	2	2	2	2	0	0	0	2	2	4
T. magniporatus n. sp.	0	0	0	0	4	2	2	2	4	4	2	2	2	2	0	0	0	0	2	0
Paulicystis densus n. gen.,	0	0	0	0	4	4	0	0	0	4	4	2	2	2	0	0	0	0	2	0
n. sp.		U	U	U	4	4	U	U	U	4	4				U	U	U	U		U
P. sparsus n. gen., n. sp.	0	0	0	0	4	4	0	0	0	4	4	2	2	2	0	0	0	4	2	4
Pustulocystis ornatissimus	0	2	0	0	4	2	2	2	4	0	2	4	2	2	4	0	4	4	2	4
P. pentax	2	0	2	0	4	2	2	0	4	4	2	4	2	2	4	0	4	4	2	4

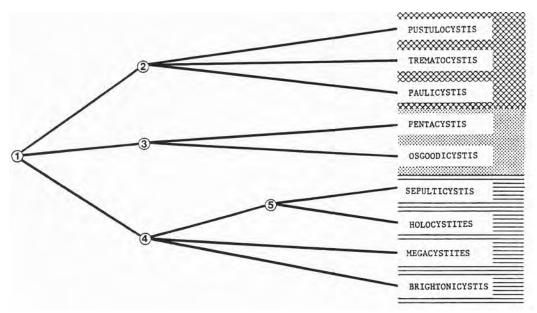
as the problem taxon. Among the Trematocystinae, the species of *Pustulocystis* are terminal taxa; the species of *Paulicystis* n. gen. are comparatively isolated from those of *Trematocystis*, in contrast to the generic version. The species-level UWPGA plot (Text-fig. 34) reflects the familiar three major groupings. As in the Wagner network, the isolated position of *Brightonicystis* is evident. Examining the *Holocystites* subgeneric clusters, the species of *Megacystites* n. sgen. and *Sepulticystis* n. sgen. are again distinct subgroups, but *Holocystites* itself appears poly-

Table 14. Character matrix for hypothetical genera in unrooted Wagner Tree phylogeny of the Holocystitidae.

		Character								
Stem	1	1 2 3 4 5 6 7								
1	1	1	1	1	0	0	0			
2	1	1	0	0	0	0	0			

phyletic. The position of *H. clavus* n. sp. is particularly interesting. The Pentacystinae here appear more closely related to the Trematocystinae. *Osgoodicystis* n. gen. is not polyphyletic, and *Pustulocystis* is somewhat removed from the related species groups of *Trematocystis* and *Paulicystis* n. gen. As with the Wagner network species-level plot, the species of *Osgoodicystis* n. gen. appear after those of *Pentacystis* in a distinct pentacystinid branch. The *Trematocystis* grouping precedes that of *Paulicystis* n. gen. in the Trematocystinae.

In the PCA plots (Text-fig. 36), the separation into three major point clusters (subfamilies) remains obvious. Most variable in position are the species of *Pustulocystis* and *Brightonicystis*, as might be expected from previous results. Generic and subgeneric clusters show considerable coherency, aside from minor problems (terminal branch reversals) in single plots with *Megacystites* n. sgen. and *Paulicystis* n. gen. Separation at both the subfamilial and generic levels is most evident in the least redundant plot (Factor 1 versus Factor 2), which also uses the



Text-fig. 31. Unrooted Wagner tree phylogeny of known holocystitid genera and subgenera based on the characters in Tables 10-11, 14; numbers represent hypothetical taxa (characters given in Table 14). Note that the same grouping results from both intuitive (Text-fig. 30) and quantitative approaches. Trematocystinae cross hatched; Pentacystinae dotted; Holocystitinae lined.

two factors that account for most of the observed variance. Significantly, both the generic and specific PCA plots indicate similar relationships of major clusters (subfamilies) if the corresponding factors are compared (Text-figs 35-36). Apparently, the addition in the species plot of many more characters (20 versus 7 in the generic) has only slightly modified the outcome at higher taxonomic levels. This could indicate that the chosen generic and subfamilial characters are robust relative to other possibilities. General congruence of the results of all three numeric methods on both generic and specific level matrices as regards major groupings can be taken as buttressing this contention. At the specific level, however, parallelism between the results of the numeric techniques is not as strong. The large number of hypothetical species and few direct ancestor-descendant relationships between known species in the Wagner network plot (Text-fig. 32), for example, underscore the incompleteness of the record at this level as yet. In our opinion, a species-level phylogeny would be premature. A consensus phylogeny of the Holocystitidae to the subgeneric level is suggested here, however (Text-fig. 37). In view of the tentative nature of many of the phylogenetic trends and characters used in its construction, no known taxon is shown as directly ancestral to any other. Our reasons for choosing this particular arrangement are discussed at length later under various taxonomic headings, but are stated here in summary form.

Despite large differences in diplopore and peristomial morphology, the Holocystitidae most closely resemble the Sphaeronitidae among described diploporite families. Parallelism in thecal, peristomial, and subvective morphologies suggests relationship, as do some apparent evolutionary trends in the Sphaeronitidae. The Holocystitinae, with a compara-

tively large number of peristomial plates and five ambulacral facets, are most likely ancestral to the other two subfamilies. Within the Holocystitinae, many features of Brightonicystis are judged ancestral, and its stratigraphic occurrence lends support to placement of it somewhere near the ancestral line to the other Holocystitinae. Known species of Holocystites appear to fall into three groups. One lineage has advanced raised (sursumate) humatipores and several advanced thecal features (Holocystites); although diverse and successful, none of its species appears to be ancestral to any other genus in the family. Sepulticystis n. sgen. has a pentacystinid-like thecal shape and base, but the multiple plate generations and buried three-dimensional humatipores place it as an offshoot of the line leading to Holocystites. Megacystites n. sgen. resembles the Pentacystinae in having flat humatipores, and a reduced number of plate generations, but also has advanced thecal shape and retains the holocystitinid peristomial plate arrangement. It could represent an independent lineage that is an offshoot of that (largely unknown) which gave rise to the Pentacystinae. In that subfamily, the general trend toward loss of periorals probably means that Pentacystis was derived from Osgoodicystis n. gen. or a form much like it. As yet, there is a moderate gap between both of these genera and known Holocystitinae, but considerable internal coherency with the exception of O. wykoffi (Miller, 1891) and, possibly, O. bissetti n. sp. Relations of the trematocystinid genera are more problematic. Paulicystis n. gen. is a likely offshoot of Trematocystis, but there is a substantial gap between these fourfaceted genera and Pustulocystis. The latter's sursumate humatipores could indicate closer relationship with the Holocystitinae [particularly Holocystites (Holocystites)], but more likely represent an independent evolution of the sursumate condition.

										C	harac	ter								
Stem	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	0	0	0	0	3	0	0	0	0	0	0	2	2	0	0	0	0	2	0	4
2	0	0	0	0	4	2	0	0	0	0	0	2	2	2	0	0	0	2	2	4
3	0	0	0	0	4	2	0	0	0	4	2	2	2	2	0	0	0	2	2	4
4	2	2	0	0	3	0	4	0	0	0	0	2	2	0	0	0	2	3	0	4
5	2	4	2	4	3	0	4	0	0	0	0	2	2	0	0	0	4	2	0	4
6	0	2	0	0	4	2	2	2	4	4	2	2	2	2	0	0	0	2	2	4
7	3	4	4	4	3	0	4	4	0	0	0	2	2	0	0	0	4	2	0	4
8	2	0	0	0	4	2	0	0	0	0	0	2	2	2	2	4	0	2	4	4
9	3	4	4	4	3	0	4	0	4	0	0	2	2	0	0	0	4	2	0	4
10	2	0	0	0	4	2	0	0	0	0	0	2	2	4	0	4	0	2	4	4
11	3	4	4	4	4	2	4	0	4	0	0	2	2	0	0	0	4	2	0	4
12	0	2	0	0	4	2	2	2	4	4	2	4	2	2	4	0	4	4	2	4
13	0	0	0	0	4	4	0	0	0	4	4	2	2	2	0	0	0	2	2	4
14	2	0	0	0	4	2	0	0	0	0	0	2	2	4	0	4	0	2	4	4
15	2	0	0	0	4	2	0	0	0	0	0	2	2	4	2	4	0	4	4	4
16	2	0	0	0	4	2	0	0	0	0	0	2	4	2	2	4	0	2	4	4
17	3	4	4	4	4	2	4	0	2	0	0	2	2	0	0	0	4	2	0	4

Table 15. Character matrix for hypothetical species in unrooted Wagner Tree phylogeny of the Holocystitidae.

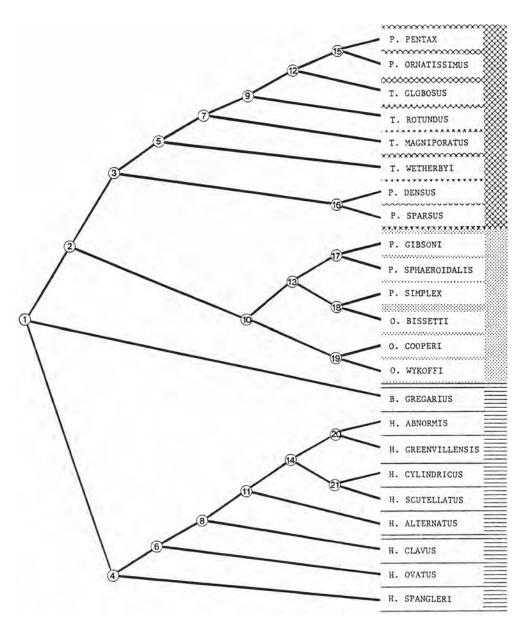
The reduced facetals are unique, and would seem to be a highly advanced feature. At present, peristomial features suggest linkage with *Trematocystis* and *Paulicystis* n. gen., but no close relationship. Both trematocystinid lineages probably share an unknown common ancestor linking the group as a whole with

Table 16. Factors 1 to 3 and their highest correlation (loading) characters for generic-level matrix. Loading values are correlations of each character with the new axes established from the Eigen vectors. For more complete character descriptions refer to Table 10.

Factor	Character	Correlation
1	3. Size of periorals4. Position of ambulacral facets7. Humatipore type	0.605 0.654 -0.691
2	2. Number of periorals5. Number of ambulacral facets6. Hydropore location	0.633 -0.744 0.764
3	Number of facetals Number of periorals	-0.598 -0.417

the Holocystitinae. There is no indication of any tendency to lose or reduce the perioral circlet, and the trend toward four elliptical ambulacral facets has no parallel in the Pentacystinae or Holocystitinae, for that matter. Still, the two subfamilies do share some major features, namely, tendencies to have a single plate generation (here regarded as advanced), numerous plates per circlet (primitive), globose thecae (primitive), and large attachment bases (primitive). Derivation of the Trematocystinae from the Holocystitinae still appears probable, however, perhaps from a large-based form ancestral also to *Sepulticystis* n. sgen.

Returning to the intuitive phylogeny (Text-fig. 30), one notes major differences in two areas. The first concerns the placement of *Pustulocystis*, as discussed previously. The second involves splitting of those species formerly grouped under *Holocystites*. Both modifications in our opinion are substantive advantages of the consensus phylogeny over the intuitive. The type species of *Holocystites*, for example, is a relatively advanced form in the present treatment, which is not evident in the intuitive arrangement. Specification of directional trends, moreover, makes the consensus phylogeny into a testable hypothesis about relationships. Table 18 summarizes the relative values of different morphological features within the Superfamly Sphaeronitida on the basis of the phylogenetic analyses above.



Text-fig. 32. Unrooted Wagner tree phylogeny of the known holocystitid species, based on the characters outlined in Tables 12-13 and 15; data for hypothetical taxa (circled numbers) are listed in Table 15. Subfamilies indicated as in Text-fig. 31. Note strong congruence with generic-level phylogeny, with the possible exception of Osgoodicystis bissetti n. gen., n. sp. Genera (from top): P. Pustulocystis; T, Trematocystis; P, Paulicystis n. gen.; P, Pentacystis; O, Osgoodicystis n. gen.; B, Brightonicystis; H, Holocystites.

SYSTEMATIC PALEONTOLOGY

MORPHOLOGICAL AND TERMINOLOGICAL CONVENTIONS

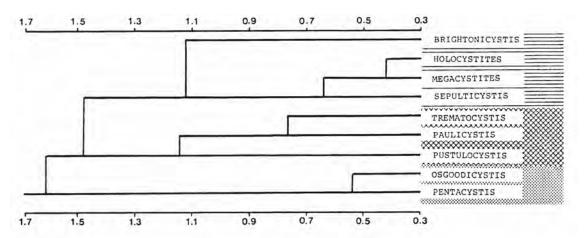
The standard reference for terminology used to describe diploporites is Kesling (1968). This work provides an historical review of past practices and a glossary. Recent work on the Sphaeronitida (e.g., Paul, 1971, 1973) has made necessary the introduction of some new terms. For basic orientation and terminology, plus suggested identification of thecal orifices, we follow Kesling (1968). Detailed plate and ambulacral system terminology is derived from Paul (1971, 1973). Descriptive terms for pore system morphology were systematized by Paul (1968, 1971). In a few cases, we have coined new terms or

modified Paul's definitions. Important instances were discussed at length in the earlier section on morphology and terminology, but all are defined briefly here.

Plates:

circlet—complete ring of nearly same-sized and -shaped thecal plates of one generation.

generation—continuous to discontinuous ring of more or less similarly sized and shaped thecal plates arrayed around the thecal axis and presumably secreted more or less simultaneously.



Text-fig. 33. Unweighted cluster analysis phenogram of the known genera and subgenera of the Holocystitidae, based on same input data as in Text-fig. 31. Subfamilies indicated as in Text-fig. 31. Again, three major groupings (recognized herein as subfamilies) are apparent.

Peristome:

epipanniculate—having a raised ambulacral platform with numerous small adjoining ambulacral facets, characteristic of the sphaeronitid subfamily Herpetocystinae.

Thecal pores:

sursumate—type of humatipore with tangential canals raised into tubercles. This morphology is characteristic of *Holocystites* (*Holocystites*) and *Pustulocystis*.

omniporate—with thecal pore structures developed over entirety of pore-bearing or all of aboral thecal plates, as in most diploporites and many eocrinoids.

partiporate—with thecal pore structures confined to only a portion of each pore-bearing or the aboral thecal plate, as in some diploporites and eocrinoids.

aporate—lacking thecal pore structures in a taxonomic group strongly characterized by their possession.

ABBREVIATIONS

Frequently-used morphological terms for diploporites are generally stated as acronyms. Those used herein are mostly the standard abbreviations of Kesling (1968), with modifications proposed by Paul (1971, 1973) either for holocystitids or for sphaeronitid peristomial features. Unique terms have letter-only acronyms. Plates in series are numbered consecutively as well, in a clockwise direction as viewed looking down the thecal axis from above, and starting with the anterior ray. Roman numerals denote rays viewed as above, numbered consecutively, but starting to the left of the posterior interray. The most frequently encountered abbreviations are:

A—presumed anus; anal opening in periproct.

CO (plural COO)—circumorals; plates bearing ambulacral facets and forming peristomial frame in Sphaeronitidae.

G—gonopore; presumed orifice for egress of genital products.

H—hydropore; presumed entrance to water vascular system, orifice for ingress of water into the system.

M—mouth; presumed location in peristome of entrance into digestive system.

F (plural FF)—ambulacral facets; point of attachment on theca for free portions of diploporite subvective system, which are almost entirely unknown.

FA (plural FAA)—facetals; second circlet of plates, most bearing ambulacral facets, surrounding peristome in Holocystitidae.

PO (plural POO)—periorals; plates forming peristomial frame and pierced by oral pores in Holocystitidae.

Roman numerals are used for ambulacra.

TECHNIQUES AND MEASUREMENTS

Osgood diploporites have the plates preserved as calcite in either a shale or limestone matrix. Most weather free and require little preparation except cleaning with brush and detergent. Others retain matrix and were prepared using vibrotools, an air abrasive unit, and small chisels. Specimens in dolomite, such as those from the Racine Formation, normally are internal molds lacking plates, or more rarely, are external molds showing outer plate surfaces. These must be broken free of matrix, but otherwise, no preparation is possible. External molds, generally partial, were cast in latex and the cast removed and cleaned for photography.

All illustrated specimens were stained and then coated with ammonium chloride sublimate. Stereoscopic pairs were made on a universal stage tilted *ca.* 12° between positions. A pocket stereoscope might be necessary to see fully three-dimensional image. A Leicaflex 35-mm camera was used for macrophotog-

Table 17. Factors 1 to 5 and their highest correlation (loading) characters for species-level input matrix. Loading values are correlations of each character with the new axes established from the Eigen vectors. For more complete character descriptions refer to Table 12.

Factor	Characters	Correlation
1	1. Thecal shape	0.488
	2. Size of attachment base	0.858
	3. Aboral projection	0.829
	4. Mode of adult attachment	0.879
	6. Regularity of thecal plate circlets	-0.647
	7. Number of thecal plates per circlet	0.880
	10. Number of ambulacral facets	-0.476
	14. Size of perioral circlets	-0.863
	17. Humatipore type	0.834
	19. Number of humatipore canals	-0.844
	1. Thecal shape	0.596
2	8. Number of thecal plate circlets	-0.647
	9. Total number of thecal plate circlets	-0.633
	10. Number of ambulacral facets	-0.713
	11. Position of ambulacral facets	-0.634
	13. Number of periorals	-0.566
	16. Location of hydropore	0.765
	19. Number of humatipore canals	0.407
	12 X 1 66 1	0.726
3	12. Number of facetals	-0.736
	15. Location of gonopore	-0.744
	18. Humatipore packing	-0.655
	20. Humatipore "size" (diameter)	-0.453
4	5. Number of thecal plate generations	0.500
	8. Number of thecal plate circlets	0.425
	11. Position of ambulacral facets	0.401
5	9 Number of these lights similar	0.676
)	8. Number of thecal plate circlets 20. Humatipore "size" (diameter)	-0.476 -0.551
	20. Frumatipore size (diameter)	-0.))1

raphy. The close-ups were made on a Leica Aristophot system. All photographs are unretouched.

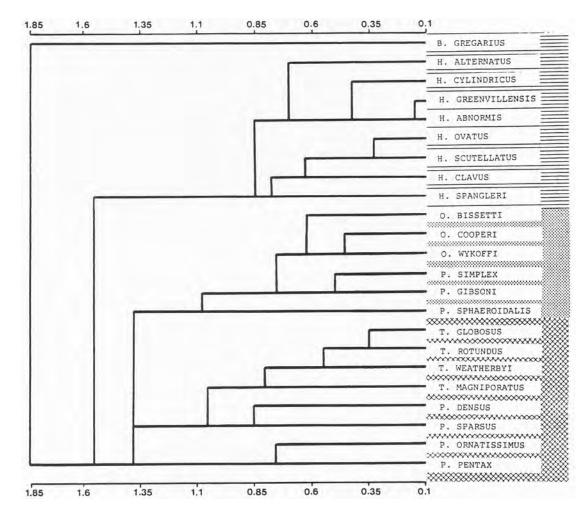
Measurements are in millimeters (mm). Larger dimensions, such as thecal proportions, required use of vernier calipers. Smaller features were measured using a Leitz Wetzlar binocular microscope fitted with a calibrated reticule eyepiece; camera lucida drawings were made using the same microscope. The techniques described by Paul (1973: 11) were used to measure diplopore size and spacing.

FORMAT

Major taxonomic subdivisions are those recognized by Kesling (1968), but families and superfamilies are based on Paul (1971). Two categories require comment. Subfamilies were introduced into diploporite taxonomy by Chauvel (1966) for the Aristocystitida. These were accepted by Paul & Kesling (1968) and Paul (1971). Usage is herein extended to the Sphaeronitida. In most primitive echinoderm classes, subgenera have not been established. However, this practice has long standing in recent echinoderm groups, as well as in fossil Crinoidea and (especially) the Diploporita (Chauvel, 1941, 1966; Kesling, 1968; Paul, 1973). We find it convenient for the Holocystitidae; both traditional and numerical taxonomic procedures recognize the distinctness of the same species groups in Holocystites s. l. Organization of the generic and specific sections largely follows the framework of Paul (1971, 1973), However, we think that genera and subgenera are based on enough characters to make a detailed breakdown into separate paragraphs on thecal, plate, pore system, peristomial, and periproctal features easier to follow, and hence we have used this format throughout.

Whenever practical, repository locations and catalog numbers of all known specimens are cited, and all illustrated material is reposited. However, because most of the specimens from Napoleon quarry were collected by amateurs, much of the material is in private collections. It was thought worthwhile,

when allowed, to examine and identify these specimens to characterize taxa better (especially the rare forms), as well as to note ranges of variation and morphology and frequencies of abnormal specimens. When counts could be made, we included these specimens in the species totals. Such figures are sometimes of necessity approximate, but many of the specimens involved will eventually be reposited.



Text-fig. 34. Unweighted cluster analysis phenogram of the known holocystitid species, based on same input data as in Textfig. 32; note that overall groupings are very similar. Distance from origin shown at base of figure; subfamilies delineated as in Text-fig. 31. Genera (from top): B, Brightonicystis; Η, Holocystites; Osgoodicystis n. gen.; P, Pentacystis; T, Trematocystis;; P, Paulicystis n. gen.; P, Pustulocystis.

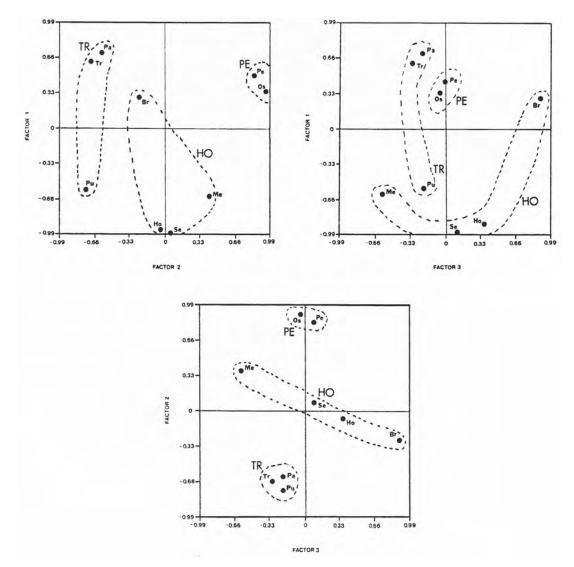
PHILOSOPHICAL CONSIDERATIONS

The Linnean binomial system of classification has been almost universally accepted by both neontologists and paleontologists for more than two centuries and is employed herein. Although modern methods of data collection and electronic storage and manipulation have suggested the possibility of other systems (Sneath & Sokal, 1973), none has achieved wide acceptance. Similarly, recent advances in evolutionary and phylogenetic theory (Eldredge & Cracraft, 1980; Wiley, 1981) have prompted proposal of major revisions to traditional, and alternative promulgations of classificatory methodology. These have so far shown no sign of displacing Linnean binomina.

Because we are interested in the study of evolutionary patterns displayed by fossil groups, we favor usage of classificatory methods emphasizing reconstruction of presumed phylogenetic relationships as a major goal. Numerical methods need not have such a goal, but generally provide a very efficient and explicit means of organizing large amounts of information. Minimally, this results in the use of more and more diverse characters for constructing phylogenies than was done with the

traditional methods of evaluating taxonomy (Dunn & Everitt, 1982). Because numerical methods do allow classification using characters coded on the basis of observed or presumed phylogenetic considerations, we regard use of methodologies combining features of both approaches as noncontradictory.

We also recognize that certain fundamental epistemological problems are frequently ignored in science, *i.e.*, that there are severe inherent limitations to the validity and scope of scientific method. As regards methods of phylogenetic inference, it is clear that one cannot assess phylogeny independent of any classification system. Use of fossil evidence presumes a preceding classification system based on concepts of general similarity derived entirely (or nearly so) from comparisons of living organisms, and hence is somewhat circular (Sokal & Sneath, 1963). However, we also agree in principle with the avowedly anarchistic position of Feyerabend (1975) that historical analysis of actual practice (as well as epistemological considerations) invalidates the notion of any completely comprehensive methodology. Our approach is based on a pragmatic acceptance of the assumptions of scientific method as the best available ana-



Text-fig. 35. Principal components analysis plot of holocystitid genera, based on data coded in Tables 10-11, 14; factor loadings in Table 16. First three factors account for most of the observed variance. Br, Brightonicystis; HO, Holocystitinae; Ho, Holocystites (Holocystites); Me, H. (Megacystites n. sgen.); Os, Osgoodicystis n. gen.; Pa, Paulicystis n. gen.; PE, Pentacystinae; Pe, Pentacystis; Pustulocystis; Holocystites (Sepulticystis n. sgen.); TR, Trematocystinae; Tr, Trematocystis.

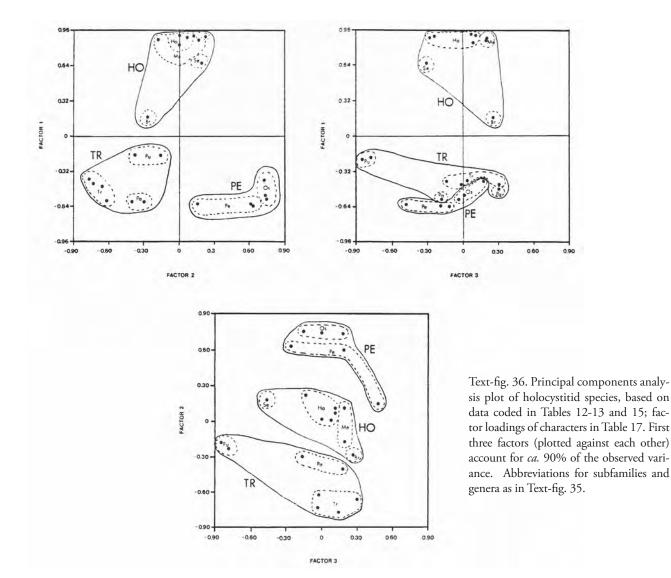
lytical method at this stage of the inherently dialectical process of accumulating and transmitting knowledge.

Even granting unreservedly the validity of the present scientific conceptual framework, one must confront the limitations of both the biological and paleontological concepts of species. We concur in the main with Hoover's (1981) analysis of assumptions and practices common among paleontologists. Some features of hard-part (preservable) morphology are presumed to reflect genetic differences between populations at taxonomically significant levels. Because diploporites are often particularly rare fossils, we accept species based on relatively few specimens, even if from a single locality, as long as some basic criteria concerning preservation and an adequate fossil record of the group concerned are met. Preservation is deemed satisfactory provided all major features found to have taxonomic significance are determinable. These include thecal shape and

plate pattern, peristomial plate arrangement and morphology (facet number and position, location of thecal orifices), and pore system morphology. Finally, to evaluate possible limits of variation and significance of taxonomically important features, statistically significant numbers of specimens of at least some closely related taxa must be available, as well as a sufficiently long and complete fossil record to determine the direction of presumed evolutionary trends. That this is the case with the diploporites dealt with herein has been convincingly argued by Paul (1982), and we have attempted to document this in more detail above.

COLLECTING LOCALITIES

Information on locations from which the *Holocystites* fauna has been collected is available in several recent papers, especially Paul (1971) and Frest *et al.* (1977). However, more modem stratigraphic information is now available, and the opportuni-



ty is taken to present a comprehensive review. This constitutes the Appendix concluding this work.

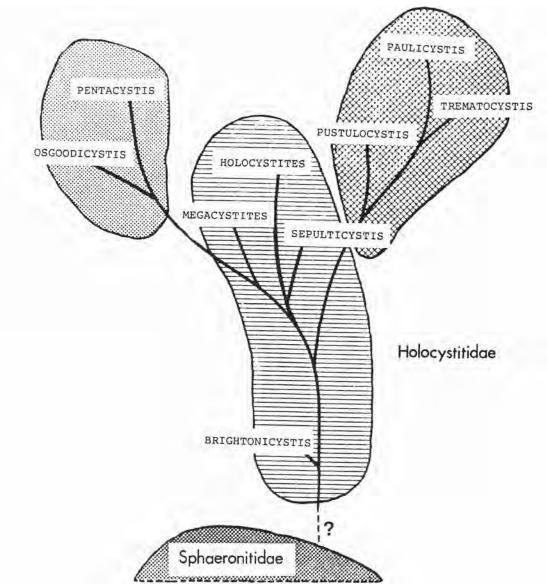
REPOSITORIES

Specimens used in this study are now mostly in the Repository, Department of Geology, University of Iowa (SUI), but some others are located in the following institutions and collections, hereafter referred to by abbreviations only: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; CAS, Chicago Academy of Science [now the Peggy Notebaert Nature Museum -Ed.], Chicago, Illinois; FMNH, Field Museum of Natural History, Chicago, Illinois; IU, Department of Geology, Indiana University, Bloomington; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MU, Department of Geology, Miami

University, Oxford, Ohio; OSU, Orton Museum, Ohio State University, Columbus, Ohio; OU, Museum of Paleontology, University of Oklahoma, Norman; UC, Department of Geology, University of Cincinnati, Cincinnati, Ohio; UMMP, Museum of Paleontology, University of Michigan, Ann Arbor; USNM, National Museum of Natural History, Washington, DC; UWBM, Burke Museum, University of Washington, Seattle; UWM, University of Wisconsin, Milwaukee; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

SYSTEMATIC SECTION

Phylum **ECHINODERMATA** Bruguière, 1791 Subphylum **BLASTOZOA** Sprinkle, 1973 Class **DIPLOPORITA** Müller, 1854



Text-fig. 37. Consensus phylogeny of the genera and subgenera of the Holocystitidae. Descent from an unknown member of the Sphaeronitidae is likely. The Holocystitinae is believed to represent the basic stock, and the Pentacystinae (dotted) and Trematocystinae (cross hatched) are independent offshoots. *Pentacystis* is a probable direct descendant of *Osgoodicystis* n. gen.; *Paulicystis* n. gen. probably was derived directly from some species of *Trematocystis*, but *Pustulocystis* and *Trematocystis* are more distantly related. Among the subgenera of *Holocystites*, *Holocystites s. s.* is overall the most advanced, but very likely is descended from a form much like *Sepulticystis* n. sgen. *Megacystites* n. sgen. and the *Holocystites-Sepulticystis* lineage probably share a common, as yet unknown, ancestor. The lineage to which *Megacystites* n. sgen. belongs probably gave rise to the Pentacystinae.

nom. transl. Paul, in Jefferies et al., 1967: 569 [ex Diploporita Bather, 1899: 920 (pro Diploporiten Müller, 1854: 249)].

Diagnosis.—Blastozoan echinoderms with exothecal porestructures (dipores) that consist of a single thecal canal; with globular to cylindrical theca commonly composed of a large number of randomly to regularly arranged plates that are usually all pierced by pore structures; generally without a true stem; with ambulacral appendages uniserial (but rarely preserved) (slightly modified from Paul, 1972: 24; Broadhead, 1980b: 126).

Remarks.—Long ranked as an order along with the Rhombifera in the class Cystoidea von Buch, 1846 (e.g., Kesling, 1968), the Diploporita were raised to class status by

	Taxonomic Level									
Feature	Order	Superfamily	Family	Genus	Species					
Thecal shape	-	-	-	X	X					
Aboral projection	-	-	-	X	X					
Facet number	-	-	-	X	X					
Facet size	-	-	-	X	X					
Facet location	-	-	X	X	X					
Gross diplopore morphology	-	X	X	X	X					
Detailed diplopore morphology	-	-	X	X	X					
Change in thecal plate number	-	-	-	X	X					
Change in plate circlet number	-	-	-	-	X					
Peristomial plate number	-	-	-	X	X					
Peristomial plate type	-	-	X	X	X					
Peristomial morphology	-	-	X	X	X					
Ambulacral number	-	-	X	X	X					
Food grooves or rays	-	-	X	X	X					
Presence/absence of stem	-	-	X	X	X					

Table 18. Comparison of relative values of some morphologic features with taxonomic significance in the Sphaeronitida.

Paul (in Jefferies et al., 1967: 566; 1968a: 727; 1972: 24), a move that has met with wide acceptance (Sprinkle, 1973, 1980, 1987; Breimer & Ubaghs, 1974; Regnéll, 1975; Chauvel & le Menn, 1979, but not Chauvel & Meléndez, 1978; Clarkson, 1979; Broadhead, 1980b; Chauvel, 1980; Haugh & Bell, 1980; Paul & Bockelie, 1983; Bockelie, 1984; Paul, 1984). More recently, Paul (1988) has argued that relationships of some diploporite superfamilies to other blastozoans are obscure, implying that the class might be polyphyletic. Nevertheless, because no plausible alternative classification has been suggested, we maintain class status for the Diploporita herein. In any case, the relationships of the Sphaeronitida are comparatively clear (Paul, 1988).

Diplopore distribution

Because the subvective appendages are so poorly known, the Diploporita was not assigned to a definite subphylum by Sprinkle, although he argued for blastozoan affinities (Sprinkle, 1973: 186-187). Placement in the Blastozoa is now generally accepted (Breimer & Ubaghs, 1974; Regnéll, 1975; Sprinkle, 1976; 1980, 1987; Paul, 1977, 1979; Broadhead, 1980b; Bockelie, 1984), although not universally (Meyer, 1982). Recently, higher classification in the Echinodermata has again become controversial, particularly at the level of class and subphylum (e.g., Paul, 1988, Paul & Smith, 1984; Smith, 1984, 1986, 1988). Although the proliferation of extinct classes can be viewed reasonably as regrettable and excessive (first two references cited above), it is equally so that no completely worked out alternative at the same level has been presented. It could be worth noting that the number of "classes" pruned by Smith or

Paul is roughly equal to the number of groups formerly thought to be monophyletic, which one or both now consider to be polyphyletic [e.g., Echinoidea (bothriocidarids), "Cystoidea" (Diploporita, Paracrinoidea), Ophiuroidea, Ophiocistioidea, Asteroidea]. Until a more satisfactory phylogenetic classification is presented, class status for the Diploporita is reasonable.

X

X

X

Broadhead (1980b: 126) felt that the currently recognized four superfamilies "should be elevated to ordinal status following Paul's (in Jefferies et al. 1967) elevation of Diploporita from an order to a class." Because Paul (1968: 727; 1972: 24) did formalize ordinal taxa within the Rhombifera, there is some justification for recognizing orders within Diploporita. Still, the Dichoporita sensu Paul, 1968, contains two superfamilies; Broadhead's diploporite orders each contain one. Thus, ordinal and superfamilial diagnoses would be identical, rendering the orders unnecessary (C. Paul, pers. obs.). But, whatever the merits of this step, the logically following step of raising families to superfamilies was not made by Broadhead, perhaps fortunately, as nearly all would have had only the nominate family as a member. Subfamilial classification has been proposed only in the Aristocystitida (Chauvel, 1966) and in the families Sphaeronitidae and Holocystitidae (herein) as yet, so that further proliferation of familial or higher taxonomy without benefit of new information or major new infusions of lowlevel taxa might be premature. This is especially true in light of recent suggestions that "dismembered" the Rhombifera and Diploporita (Paul, 1988).

The classification of the Sphaeronitidae adopted herein

Table 19. Outline classification and generic composition of the Sphaeronitida.

Kesling (1968: S166, S242-S250): This paper: Superfamily Sphaeronitida Neumayr, 1889 Superfamily Sphaeronitida Neumayr, 1889 Family Sphaeronitidae Neumayr, 1889 Family Sphaeronitidae Neumayr, 1889 Sphaeronites Hisinger, 1828 Subfamily Sphaeronitinae Neumayr, 1889 Allocystiies Miller, 1889 Sphaeronites (Sphaeronites) (Hisinger, ? Barbieria Termier & Termier, 1950 1828) Paul, 1973 Bulbocystis Ružička, 1939 Sphaeronites (Peritaphros) Paul, 1973 Carpocystites Oehlert, 1886 Sphaeronites (Ataphros) Paul & Bockelie, Codiacystis Jaekel, 1899 1983 Eucystis Angelin, 1878 Archegocystis Jaekel, 1899, Haplosphaeronis Jaekel, 1926 ? Barbieria Termier & Termier, 1950 Palaeosphaeronites Prokop, 1964 Bulbocystis Ružička, 1939 Proteocystites Barrande, 1887 Diplosphaeronis Paul, 1973 Tholocystis Chauvel, 1941 Eucystis Angelin, 1878 Glyptosphaerites Müller, 1854 Tetreucystis Bockelie, 1984 Haplosphaeronis Jaekel, 1926 Subfamily Herpetocystinae Termier & Termier, 1972 Herpetocystis Termier & Termier, 1972 Codiacystis Jaekel, 1899 Finitiporus n. gen. Tholocystis Chauvel, 1941 Family Parasphaeronitidae Bockelie, 1984 Parasphaeronites Bockelie, 1984 Pachycystis Bockelie, 1984 Family Holocystitidae Miller, 1889 Subfamily Holocystitinae n. subfam. Holocystites (Holocystites) Hall, 1864 Holocystites (Megacystites) n. subgen. Holocystites (Sepulticystis) n. subgen. Brightonicystis Paul, 1971 Subfamily Trematocystinae n. subfam. Trematocystis Jaekel, 1899 Paulicystis n. gen. Pustulocystis Paul, 1971 Subfamily Pentacystinae n. subfam. Pentacystis Paul, 1971 Osgoodicystis n. gen.

differs from that of the last comprehensive revision (Kesling, 1968), reflecting major partial revisions in the last decade, especially the addition of the Holocystitidae to the order and removal of the Aristocystitida by Paul (1971), revision of the British Ordovician sphaeronitids by Paul (1973, 1984), and other changes suggested herein (summarized in Table 19). Higher taxonomy is essentially that of Paul (1972, 1973), which emphasized dipore and ambulacral system morphology,

rather than that of the *Treatise*. Paul's system has gained some acceptance (Clarkson, 1979), and our additional taxa fit well in his framework.

Superfamily **SPHAERONITIDA** Neumayr, 1889

nom. transl. Paul, 1973: 18 [ex Sphaeronitidae Neumayr, 1889: 412; non superfamily Sphaeronitida (Jaekel, 1918) nom. transl.
Regnéll, 1945: 161, pro order Sphaeronita Jaekel, 1918: 103].

Diagnosis.—Stemless Diploporita with variable-shaped theca, almost all plates commonly pierced by diplopores; peristome covered by six plates (palatals), below which food grooves pass to the mouth from four or five ambulacra; food grooves narrow, uncovered, generally short but extending over theca in some species; periproct covered by a pyramid of triangular plates; circular gonopore and generally slit-like hydropore between peristome and periproct, but offset to the left of a direct line between the two.

Remarks.—The above definition is modified very slightly from that of Paul (1973: 18). A few sphaeronitid taxa, notably Finitiporus n. gen., but also Herpetocystis Termier & Termier, 1970, some species of Haplosphaeronis (e.g., H. sparsipora Paul, 1973: 33), and Eucystis (e.g., E. angelini Regnéll, 1945, and E. raripunctata Angelin, 1878; Regnéll, 1945: 175-180), do not have diplopores distributed uniformly over the theca, that is, they are partiporate. Where diplopores are absent, it is generally the aboral portion of the theca that lacks them.

Paul's definition is more substantial than previous attempts (Kesling, 1968: S204) and is accepted essentially *in toto* herein. As defined above, the Sphaeronitidae contains two families, *viz* the Sphaeronitidae and Holocystitidae; the Aristocystitidae now are included in their own superfamily (Paul, 1971). In the same work, Paul demonstrated conclusively the separate familial status of the genera now constituting the Holocystitidae. The latter "is closely related to, and probably evolved from, the Sphaeronitidae" (Paul, 1973: 18), as has been argued above. The main features separating the two are the pore structures and ambulacral facets. Sphaeronitids have diplopores and small, frequently multiple ambulacral facets, whereas holocystitids have humatipores and large single facets in each ambulacrum, the latter perhaps representing brachiole-bearing trunks (pinnate arms) versus sphaeronitid simple brachioles.

Bockelie (1984) has recently erected another family, Parasphaeronitidae, for two Scandinavian Upper Ordovician genera, Parasphaeronites Bockelie, 1984, and Pachycystis Bockelie, 1984. Although he placed the family in the Sphaeronitida, existing evidence is equivocal. The pore structures are reminiscent of those of the Aristocystitida (Bockelie, 1984: 59). Peristomial plating is imperfectly known, but apparently eight POO (and/or COO) surround the mouth. Bockelie (1984: 59) suggested that this group is ancestral to the Holocystitidae "at least as far as the oral area is concerned." This statement rests on the assumption that the peristomial plates are POO, which, as argued above, is not certain. For example, the facets in Parasphaeronitidae are radial in position. Although Bockelie's assignment of his family to the Sphaeronitida is provisionally accepted (Table 19), because of uncertainties about some basic morphologic features, the group is not further considered here.

Family **SPHAERONITIDAE** Neumayr, 1889

Diagnosis.—"Sphaeronitida with diplopores; peristome surrounded by six circumoral plates with a small additional plate (CO7) between the peristome and periproct but not in contact with the former; four or five ambulacra with one or more ambulacral facets each" (Paul, 1973: 18-19).

Range.—Lower-Upper Ordovician (Tremadocian-Ashgillian), Asia (China)-Europe (widespread), northern Africa (Morocco, Libya, Algeria); Upper Silurian (Wenlockian), North America (Indiana); Lower-Middle Devonian (Gedinnian-Givetian), Europe (Bohemia, France), northern Africa (Morocco, Algeria, Central Sahara), North America (Oklahoma).

Included genera.—Sphaeronites Hisinger, 1828; Archegocystis Jaekel, 1899; ?Barbieria Termier & Termier, 1950; Bulbocystis Ružička, 1939; Codiacystis Jaekel, 1899; Diplosphaeronis Paul, 1973; Eucystis Angelin, 1878: Finitiporus n. gen.; Glyptosphaerites Müller, 1854; Haplosphaeronis Jaekel, 1926; Herpetocystis Termier & Termier, 1970; Oehlertocystis Chauvel, 1980; Paleosphaeronites Prokop, 1964; Tetreucystis Bockelie, 1984; Tholocystis Chauvel, 1941.

Remarks.—Paul's diagnosis differs considerably from that of Kesling (1968: S241) and is accepted herein. In particular, the arrangement of circumoral plates is considered a family characteristic. The peristome of the highly specialized epipanniculate Finitiporus n. gen. and closely related genera (Tholocystis, Herpetocystis, and Codiacystis) appears to have the same arrangement as in better-known genera (e.g., Regnéll, 1945; Prokop, 1964; especially Paul, 1973), hence these genera are included in the Sphaeronitidae.

All well-known genera of the Sphaeronitidae appear to possess a seven-plate circlet (circumorals), six forming the peristomial frame surrounding the mouth and one smaller plate not in contact with the peristomial frame. Paul (1973) presented peristomial interpretations emphasizing this arrangement for the genera Sphaeronites (Peritaphros Paul, 1973), Eucystis, Haplosphaeronis, Archegocystis, and Diplosphaeronis. Paul & Bockelie (1983) demonstrated this arrangement in Sphaeronites (Sphaeronites), but existing material of Sphaeronites (Ataphros Paul & Bockelie, 1983) only permits confirmation that six plates (COO) make up the peristomial border (Paul & Bockelie, 1983: 732; Text-fig. 16). Bockelie (1984) illustrated the typical arrangement for Tetreucystis. Existing illustrations of Codiacystis and Bulbocystis (Prokop, 1964: figs 4, 14) and of Oehlertocystis (Chauvel, 1980: fig. 3a) might be interpreted similarly, and we present similar illustrations for Finitiponis n.

gen., Codiacystis, and Tholocystis herein. Paul (1988: 65) reassigned Glyptosphaerites to the Sphaeronitida and has interpreted peristomial plating accordingly.

Termier & Termier (1972) erected a separate family (Herpetocystidae) for *Tholocystis* and their genus *Herpetocystis* from the Ashgillian of Morocco (Termier & Termier, 1970). Chauvel (1980), in redescribing *Tholocystis*, accepted this family, but it is here regarded as a subfamily of Sphaeronitidae. As originally defined, the Herpetocystidae is characterized solely "par la forme de ses sillons brachiolaires" (Termier & Termier, 1972: 1645), but as discussed earlier, the ambulacral morphology of *Herpetocystis* appears to fall within the range displayed by other sphaeronitids with epipanniculate peristomes. Other reasons for placement of both *Tholocystis* and *Herpetocystis* in the Sphaeronitidae are discussed under the subfamily and individual generic headings below.

Accepting the sphaeronitid relations of Herpetocystis, the genus shares with Tholocystis, Codiacystis, and Finitiporus n. gen. an advanced variant of epipanniculate peristomial morphology in which the ambulacral facets are numerous, small, contiguous in at least each ambulacrum (commonly the ambulacra are in contact laterally except in the CD interray), and regularly arranged. These features suggested to Termier & Termier (1972) convergence with the diploporitan superfamily Asteroblastida and the class Blastoidea. Suggestions of a closer, i.e., phylogenetic, relationship between these two groups, although persistent (e.g., Schmidt, 1874; Termier & Termier 1948; Bergounioux, 1953) are without foundation and more than likely are a result of convergence rather than recent common ancestry (e.g., Cuénot, 1953; Moore, 1954). In particular, the notion that echinoderms with trigonally symmetrical stems are closely related (Termier & Termier, 1972), is not supported by any other features. Aside from the groups cited by the Termiers, some crinoid columns are either triangular in cross section or have a trigonally symmetrical lumen, as do some Rhombifera (e.g., Brett, 1978).

As noted previously, the tendency to concentrate the ambulacral facets on the plate circlet surrounding the peristomial opening is widespread in the Sphaeronitidae and could have evolved independently in several only distantly related diploporite lines. Some genera with epipanniculate peristomes are therefore included in both the Sphaeronitinae and Herpetocystinae. The genera of the Herpetocystinae, however, are the only sphaeronitids with paired food grooves in all rays. Genera with single food grooves (facets single to multiple; if the latter, generally fan-like, but asymmetrical) constitute the Sphaeronitinae.

Subfamily SPHAERONITINAE Neumayr, 1889, emend.

nom. transl. ex Sphaeronitidae Neumayr, 1889: 412.

Diagnosis.—Sphaeronitidae with a single food groove in each ray; facets single to multiple, often added clockwise in fan-like, asymmetrical arrangement; peristome simple to epipanniculate; theca generally globular, directly attached (without stem). Diplopores generally numerous and plates and theca usually omniporate, or rarely partiporate.

Range.—Lower-Upper Ordovician (Tremadocian-Ashgillian) Europe (widespread), northern Africa (Morocco, Libya, Algeria); Lower-Middle Devonian (Gedinnian-Givetian), Europe (Bohemia, France), northern Africa (Morocco, Algeria, Central Sahara), North America (Oklahoma).

Included genera.—Sphaeronites Hisinger, 1828; Archegocystis Jaekel, 1899; ?Barbieria Termier & Termier, 1950; Bulbocystis Ružička, 1939; Diplosphaeronis Paul, 1973; Eucystis Angelin, 1878; Glyptosphaerites Müller, 1854; Haplosphaeronis Jaekel, 1926; Oehlertocystis Chauvel, 1980; Paleosphaeronites Prokop, 1964; Tetreucystis Bockelie, 1984.

Remarks.—Overemphasis on details of ambulacral morphology has probably resulted in oversplitting of the Sphaeronitida. Bockelie (1978) demonstrated that ambulacral facets were added during growth in two sphaeronitid genera with multiple facets (*Eucystis* and *Haplosphaeronis*) and suggested that variation in the number of facets resulted from a combination of ontogeny, true variability within age groups, ecological conditions, and phyletic changes. Other sphaeronitinid genera with many facets per ambulacrum (*e.g.*, *Glyptosphaerites*) quite likely added facets during ontogeny. There is, however, a fairly consistent adult number in a given species, although the number in each ray might not be equal.

Facets are usually added in Eucystis and Haplosphaeronis in a clockwise fashion, i.e., with the oldest in each ray to the left, except sometimes in ambulacrum V, which is near to the periproct. In some genera, a fan-like arrangement is common, and in most cases, the array is asymmetrical, with the longest grooves connected to last-added facets (i.e., those to the right). Sphaeronitinid genera displaying this characteristic are Eucystis, Tetreucystis, Haplosphaeronis, Bulbocystis, and apparently Oehlertocystis. Carpocystites Oehlert, 1887, has often been included in the Sphaeronitidae (e.g., Kesling, 1968), but was synonymized with Eucystis by Regnéll (1945). Chauvel (1980) redescribed and illustrated Oehlert's specimen and removed the genus from the Sphaeronitidae. His disposition (leaving the genus unassigned) seems justified by the material; certainly, it is unlike any other sphaeronitid. In particular, the presence of a triradiate ambulacral system and stem facet warrants exclusion from the Sphaeronitida. The pore-system morphology (Chauvel, 1980: 16, pl. 4, figs 5-6) is reminiscent of that of weathered specimens of Amygdalocystites Billings, 1854,

Oklahomacystis Parsley & Mintz, 1975, Implicaticystis Frest & Strimple, 1982b, or Comarocystites Billings, 1854, suggesting that the genus could be a paracrinoid. Regnéll's (1945: 175) synonymy of Carpocystites with Eucystis is completely unwarranted, as pointed out by Chauvel (1980). Barbieria, questionably included by Kesling (1968) in the family, is too poorly known to evaluate, but is probably best included provisionally in the Spaeronitinae.

We concur with Regnéll (1945) and Paul (1973) in regarding Proteocystites Barrande, 1887, as a synonym of Eucystis. Recent revision of the British species of *Eucystis* by Paul (1973) has considerably elucidated the status of Proteocystites. Paul restudied the type species of both genera, demonstrated that they are congeneric, and accepted Eucystis as the oldest available name. The Osgood Allocystites Miller, 1889, remains problematic. Reasonably classed as a sphaeronitid by Kesling (1968) on the basis of Miller's (1889) description, it was not covered in Paul's (1971) revision of the Holocystites fauna and was later explicitly rejected as a diploporite by him (1972: 23). Sprinkle (1973: 186) tentatively referred the genus to the Paracrinoidea. This assignment was explicitly rejected by Parsley (1975: 349, 357) and Parsley & Mintz (1975: 12). No new specimens have been found at Napoleon or elsewhere to our knowledge; reexamination of the unique holotype (FMNH UC 6006) in 1975 in our opinion supports placement in the Paracrinoidea. The specimen is now apparently lost (M. Nitecki, pers. comm., 1982). Austrocystites Brown, 1963, from the Silurian of New South Wales (Brown, 1963), "is not sufficiently well known to be certain of its affinities" (Paul, 1972: 23) and is here considered unassignable below the class level.

Members of Oehlertocystis closely resemble some species of Archegocystis, but details of diplopore and peristomial morphology could support recognition as a separate genus. Oehlertocystis is unusual in that ambulacrum III has the smallest number of facets; in other genera (e.g., Eucystis, Haplosphaeronis), ambulacrum IV has the smallest number (Bockelie, 1978: 36). Oehlertocystis has an ambulacral platform and no diplopores between ambulacra (Chauvel, 1980); Archegocystis is similar, but retains a few pores (Paul, 1973: text-fig. 23A). Both genera have epipanniculate peristomes. As in Archegocystis and Diplosphaeronis, the periproct is widely separated from the peristome, and like the latter (Paul, 1973: 51, text-fig. 32A). Oehlertocystis has extra plates between the circumorals and the periproct. This feature could justify separate subfamilial status for all three, although the precise arrangement of plates around the periproct in Archegocystis is not known.

The remaining sphaeronitid genera fall into two groups. *Sphaeronites, Diplosphaeronis, Paleosphaeronites,* and some species of *Eucystis* and *Tetreucystis* have only one or two typically small ambulacral facets per ray. It has been argued previously that there is an evolutionary trend in some Sphaeronitidae toward increase

in the number of ambulacral facets. Because these genera have single food grooves entering the peristomial opening, they are best regarded as primitive Sphaeronitinae. Glyptosphaerites has recently been transferred into the Sphaeronitida by Paul (1988). His interpretation of morphology and relationships is reasonable and is accepted herein. Cited features (Paul, 1984: 65) include six peristome-surrounding circumorals, five of these radial in position, narrow, apparently open food grooves, and palatals covering the peristome. This genus is somewhat interesting in that general morphology clearly suggests a relationship with the Sphaeronitinae as defined in this work. However, some species can have up to seven rather widely spaced, small brachiole facets per ambulacrum (Kesling, 1968), spread over the upper half of the theca. In view of the degree of facet morphological and number variation shown in Eucystis, the genus is best regarded as a sphaeronitinid. There is, however, a need for detailed redescription of Glyptosphaerites in the light of Paul's interpretation. The second group is here placed in the Herpetocystinae and is discussed below.

Subfamily **HERPETOCYSTINAE** Termier & Termier, 1972

nom. transl. ex Herpetocystidés Termier & Termier, 1972: 1645.

Diagnosis.—Sphaeronitidae with double food grooves in five rays; facets small, numerous; ambulacral apparatus nearly perfectly symmetrical; peristome epipanniculate; theca globular to cylindrical, directly attached (without stem). Diplopores few to numerous, simple, often confined to adoral part of theca (theca partiporate).

Range.—Middle-Upper Ordovician (Llandeilan - Ashgillian), Europe (France, Bohemia, ?Spain), northern Africa (Morocco); Asia (China); Upper Silurian (Wenlockian), North America (Indiana).

Included genera.—Herpetocystis Termier & Termier, 1950; Codiacystis Jaekel, 1899; Finitiporus n. gen.; Tholocystis Chauvel, 1941.

Remarks.—The unusual (then thought unique among sphaeronitids) symmetry of the peristome of *Tholocystis* led Kesling (1968: S250) to suggest there "might be sufficient ground to erect a separate family" for the genus. The inclusion of additional taxa clarifies the position of *Tholocystis* among diploporites somewhat, but does not completely subsume the distinctness of it and closely related taxa. We feel that at least separate subfamilial status is warranted and easily accommodated within the higher taxonomy erected (albeit for different reasons) by previous authors, *i.e.*, by redefinition and transfer of the Termiers' family Herpetocystidae.

The subfamily comprises sphaeronitids with advanced peristomial morphology, *i.e.*, strongly pentagonal, symmetrical, and regularly-arranged, double, multifaceted ambulacra, usually with facets adjoining except in the posterior interray. In two genera (*Herpetocystis* and *Finitiporus* n. gen.), diplopores are much reduced in number and confined to the adoral position of theca. *Tholocystis* is a globular, large-based form; the other herpetocystinids have cylindrical thecae, also, in our opinion, an advanced feature.

None of the component taxa are represented by an abundance of specimens. The nominate genus is based on scanty material from the Upper Ordovician of Morocco originally ascribed to Asteroblastus Eichwald, 1852 (Termier & Termier, 1950: 97, pl. 231, figs 1-2, ?3-12). As reconstructed by Termier & Termier (1970: 2), the genus has a long, curved ("serpentiforme"; Chauvel, 1980: 15) recumbent theca with three symmetrical, Y-shaped, double ambulacra at the oral pole, diplopores largely confined to the adoral tenth of the theca, and a radix-like distal portion with cirri. Their photographs of the adoral pole illustrate a diploporite with numerous small facets and small, simple diplopores (Termier & Termier, 1970: 1, figs 1-2), very similar in morphology to those in Finitiporus n. gen. (Text-figs 18, 19C) and *Tholocystis* (Chauvel, 1980: pl. 4, figs 1-3; Text-fig. 19B). Almost certainly, the genus is a sphaeronitid closely related to the cited genera, and we have few reservations about our disposition of the genus. It is more probable, however, that *Herpetocystis* had five (or possibly four) ambulacra, as do all other sphaeronitids, and we suspect that the illustrated cirrate peduncle fragments belong to another echinoderm, possibly a hemicosmitid rhombiferan. We conjecture that the triradiate axial canal of the peduncle (?probably actually a holdfast; see Termier & Termier, 1970: pl. 1, fig. 5) could have influenced the peristomial reconstruction. As noted by Paul (1973: 19), no definite sphaeronitid has a true stem.

Tholocystis was originally described in 1941 (Chauvel, 1941), but has been redescribed recently and reillustrated (Chauvel, 1980). Although first accepted as a sphaeronitid (Chauvel, 1941: 88-89), the later work transferred it to the Herpetocystidae. Chauvel's (1980: 4, 11-15, figs 1-4, 5a-d) excellent later description and photographs demonstrated *Tholocystis* to be a globular sphaeronitid with an epipanniculate, five-rayed peristome, numerous thecal plates of one generation arranged in several definite circlets, all pierced by numerous diplopores, and a broad aboral attachment base. We concur with Kesling (1968: S249) and Chauvel (1941), and maintain the genus in the Sphaeronitidae. Both Chauvel (1980) and Termier & Termier (1972) have discussed the unusual aspects of the peristomial morphology of *Tholocystis* and noted its close resemblance to Herpetocystis. Their reasoning is convincing, and, in our interpretation, supports recognition of a separate subfamily within the Sphaeronitidae including both.

The unusually symmetrical (for a sphaeronitid) peristome suggested to Chauvel (1941: 95-96) a possible relation to the Blastoidea. We regard the resemblances as superficial and due to convergence. As a result, our interpretation of peristomial plating (Text-fig. 19B) differs considerably from that of Chauvel (1941: figs 36, 37A) in that we do not recognize separate "lancet" plates between ambulacral branches, or "peristomials" (?possible palatals). Although details are obscure, the peristomial opening, as noted by Chauvel (1980: 12) is clearly surrounded by six plates (here interpreted as circumorals); five are large and radial in position, and one is smaller, and interradial (*CD*) in position. A small plate beneath the *CD* circumoral (CO6), in contact with the periproct and flanked by CO1 and CO6, is most likely CO7 (Text-fig. 19C).

The peristomial morphology of *Tholocystis* suggested to Kesling (1963b, 1966) a possible relationship with the Cyclocystoidea, i.e., descent of both from a common diploporite ancestor. Cited points of comparison were the more or less circular disposition of brachiole facets, facets borne on quadrangular plates very much thicker than other thecal plates, and the large, circular, flexible base (Kesling, 1966: U202). Chauvel's (1941, 1980) descriptions and illustrations indicate that the last two items are not present in *Tholocystis*. Remaining resemblances might better be explained as cases of convergence, like most recent authors (e.g., Paul, 1979; Sprinkle, 1980; Smith & Paul, 1982), we prefer to regard the class Cyclocystoidea as having echinozoan, rather than blastozoan, affinities. Aside from the type species, Chauvel (1980: 15) suggested that one poorly known Chinese species, originally described as Sphaeronis jenhochiaoensis Sun, 1948, is a Tholocystis. To judge from the photographs, Chauvel was probably correct and we transfer the species to *Tholocystis* herein; minimally, this diploporite is certainly a herpetocystinid.

Codiacystis is also a member of the Herpetocystinae. It was originally described under the preoccupied name Craterina Barrande, 1887; the present name was proposed by Jackel (1899). The genus was poorly understood until the critical Bohemian species were revised by Prokop (1964), who also published a plate diagram of the peristome. Prokop's plate diagram is herein reinterpreted (Text-fig. 19A) using the terminology of Paul (1973). The double ambulacra strongly indicate herpetocystinid affiliation. The genus has an ambulacral platform and epipanniculate peristome with relatively few facets (three per half ray in the type species). Prokop (1964: 17) recognized four European species; more recently, the genus has been reported from Morocco and Libya (Chauvel, 1966; Prokop, 1973).

This subfamily is as yet too poorly known to suggest phyletic relations. *Herpetocystis* lacks an ambulacral platform, has numerous diplopores between the rays, and apparently does not have the facets of adjoining rays in contact, whereas *Finitiporus*

n. gen. has a distinctly protrusive peristome, no between-facet diplopores, and facets in contact laterally except in the posterior interray. Tholocystis is intermediate in all cited characters between Herpetocystis and Finitiporus n. gen., as is Codiacystis, but the last has a relatively small number of ambulacral facets. The globular thecal shape of Tholocystis and Codiacystis is here interpreted as an ancestral (primitive) character; the cylindrical Herpetocystis and Finitiporus n. gen., both of which also have large aboral stem-like projections, are more advanced in this respect. Applying the criteria employed earlier for the Holocystitidae, Finitiporus n. gen. is clearly the most morphologically advanced herpetocystinid and occupies a position similar to that of Haplosphaeronis in the Sphaeronitinae. Aside from features already discussed, its simplified thecal plating, much-reduced diplopores, strongly partiporate theca, and Silurian provenance are unique. The remaining Herpetocystinae are essentially contemporaneous (Middle-Upper Ordovician) and nearly cosmopolitan (outside of North America), but no occurrences with diploporite diversities approaching that of the Holocystites fauna are yet known. Lack of definite ancestors and Lower Silurian forms indicate that many more taxa remain to be discovered.

> Genus *Finitiporus* Frest & Strimple, n. gen. Text-figs 18, 19C, 38-41; Pl. 1, Figs 6-17

Etymology.—Combining Latin *finitus* (of limited extent) with Greek *porus* (pore, pored).

Type species.—Finitiporus boardmani n. gen., n. sp., by original designation herein. The genus is monotypic.

Diagnosis.—Herpetocystinae with cylindrical theca composed of a few circlets of a small number of large, thin plates; with sparse, oval diplopores confined to adoral portion of theca (theca partiporate); ambulacral platform on adoral part of circumorals; with five double ambulacra having numerous small facets in each; subcircular epipanniculate peristome; periproct between circumorals and next (aboral) thecal plate circlet.

Range.—Upper Silurian (early Wenlockian); Osgood Member, Salamonie Dolomite, U.S.A. (Indiana).

Description.—Theca large and cylindrical, with raised ambulacral platform and sizeable aboral projection.

Plates very thin except for circumorals and distalmost part of distal circlet near the attachment area; relatively few, large, elongate plate circlets with few plates (6-7 in *Finitiporus boardmani* n. gen., n. sp.) of one generation in each, arrayed in partly offset circlets, but not strictly alternating.

Diplopores regular, simple, oval, with shallow peripores

surrounded by narrow rim; in type species, arranged with long axes mostly in adoral direction, confined to circumorals and adoral part of underlying plate circlet.

Peristome almost symmetrical, but interrupted by CO6; numerous small ambulacral facets forming continuous peristomial border except in posterior interray; peristome small, epipanniculate, on adoral halves of circumorals, subcircular in outline; opening circular; diplopores absent from peristome proper. Palatals unknown; ambulacral groove system complex, with separate grooves for each facet uniting into two main adjacent grooves per ray.

Periproct moderately distant from peristome, but bordered by circumorals adorally and two large plates of following circlet aborally; periproct pentagonal, with narrow sunken rim for attachment of anals (unknown).

Gonopore a small circular opening, not raised into tubercle, divided across suture CO1:CO7, beneath ambulacral platform just outside peristomial border.

Hydropore madreporite-like, on shallow tubercle extending across suture CO6:CO1 on ambulacral platform.

Attachment direct, by moderate-sized flat area at aboral pole, terminating in elongate aboral stem-like projection.

Remarks.—Differentiating characters of this genus have been discussed above, and will be dealt with in more detail under the type species description below.

Finitiporus boardmani Frest & Strimple, n. sp. Text-figs 18, 19C, 38-41; Pl. 1, Figs 6-17

Etymology.—The species is named for Darwin Boardman (Ohio University), who collected the holotype and generously donated it to the authors.

Diagnosis.—*Finitiporus* n. gen. with large cylindrical theca with strongly protruded ambulacral platform; theca composed of a few (4 or more) circlets of smooth or finely granulose, scarcely staggered elongate plates, generally seven per circlet; diplopores confined to lower circumorals (aboral part below ambulacral platform summit) and next plate circlet; large (wide and elongate) aboral projection, attachment direct.

Occurrence.—Osgood Member, Salamonie Dolomite (early Wenlockian), Napoleon quarry of New Point Stone Company, Ripley County, Indiana.

Material.—Nine reposited specimens: holotype SUI 48175; figured paratypes SUI 48173, 48174, 48178-48181; unfigured paratypes SUI 48139, 48190; other material in private collections.



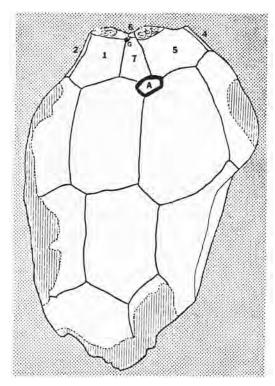
Text-fig. 38. Finitiporus boardmani n. gen., n. sp., holotype SUI 48175. (A-C) Lateral views illustrating thecal morphology; note the very thin plates (except adorally), absence of diplopores except near the top of the theca. Maximum dimension = 43.4 mm. (D) Lateral view of damaged peristome, maximum dimension 28.3 mm. (E-F) Enlargements of adoral portions of two circumorals, showing simple diplopores with raised peripore rims, width of field of view = 4.4mm. All specimens coated with ammonium chloride sublimate.

Description.—Theca large, elongate cylindrical with elongate, gradually tapering, or cylindrical aboral extremity (Pl. 1, Figs 10-12, 14-17) and constricted summit (Text-fig. 38B).

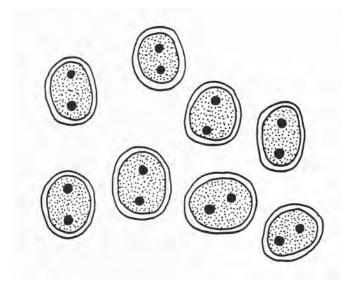
Plates elongate, regular in shape, to twice as high as wide, apparently only of one generation, disposed in circlets, generally of seven plates each (one aboral extension, SUI 48189, has only six), mostly six-sided but not regularly hexagonal; succeeding circlets offset approximately one quarter of average width (Text-fig. 38B); four circlets present on incomplete holotype (Text-figs 38A-C). All plates with very fine tubercular

ornament (Text-figs 18E, H, 38E); most extremely thin and fragile (Text-fig. 38); thicker plates at both thecal poles.

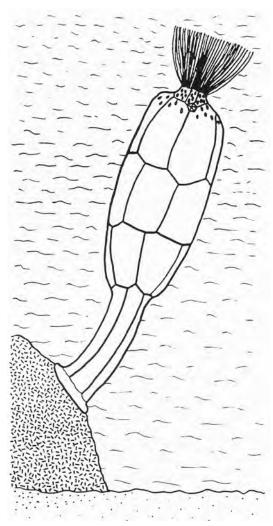
Diplopores with shallowly excavated peripores surrounded by narrow, slightly raised rim (Text-figs 18, 38E-F, 40); sparsely distributed on adoral part of theca only, most dense adorally on circumorals, rapidly decreasing in number aborally and not extending far below level of periproct on circlet underlying circumorals (Text-fig. 39). Most diplopores oriented with long axis parallel to major thecal axis, but some more randomly oriented (Text-figs 38E-F, 40).



Text-fig. 39. Interpretation of thecal plating in holotype of *Finitiporus boardmani* n. gen., n. sp., SUI 48175. Thecal plates white; areas with diplopores indicated by fine stipple; lined portions covered by bryozoan; periproct border as heavy black line; circumorals numbered. Symbols as outlined under Abbreviations, p. 52. Compare with Text-fig. 38B.



Text-fig. 40. Camera lucida drawings of diplopores of *Finitiporus boardmani* n. gen., n. sp., SUI 48175. Pores of perpendicular canals black, peripores dotted, peripore rims white. Adoral direction is to right of figure. Maximum dimension of largest diplopore = *ca.* 0.6 mm.



Text-fig. 41. Restoration of *Finitiporus boardmani* n. gen., n. sp., in life position. Note large attachment base and limited area with diplopores. Fine grill-like ambulacral appendages are conjectural.

Peristome subcircular in outline, but with slightly indented margin between half-rays, giving subdued pentagonal appearance when viewed from above (Text-figs 19C, 38D). Epipanniculate portion flat, forming top of ambulacral platform, covering between one-third and one-half of total circumoral length; no diplopores between rays. Diameter 12.9 mm in holotype, approximately one-third maximum thecal width. COO 1-5 subequal; CO6 a thin, sliver-like plate completely on the flat summit of ambulacral platform; CO7 a small, irregularly pentagonal plate on platform flanks (Text-figs 19C, 38B, 39). Ambulacral platform prominent, involving very large, nearly erect distal halves of circumorals and adoral halves of next plate circlet (Text-figs 38B, 39). Peristomial opening apparently small, circular; diameter unknown. Ambulacral facets numerous; seven per half-ray in all rays except half-rays flanking CO6 and CO7, which have three facets, but five grooves, on large specimen (Text-figs 18E, H); facets erect in side view, forming platform border. Each facet rectangular, with central opening connected to narrow ambulacral grooves flanked laterally by paired pits (Text-figs 18A-B, E, H). Main ambulacral grooves two per ray, separate peristomial opening, with tributary grooves given off toward lateral edges only, forming asymmetrical, fanlike array in each half-ray (Text-figs 18B, H, 19C).

Periproct small; pentagonal opening on side of ambulacral platform, of diameter 5.5 mm, with recessed edge for attachment of anals (not preserved; Text-figs 19C, 38B, 39). Border formed by CO5, CO7, and two lower thecal plates of next circlet.

Gonopore a very small circular opening on inconspicuous tubercle on ambulacral platform flank just below peristomial border on suture between CO1 and CO7 (Text-figs 19C, 38B); diameter 0.8 mm on holotype. Internally, gonoduct expanding beneath exterior surface, then contracting again to narrow interior opening (Text-figs 18D, F-G, I).

Hydropore exterior expression as narrow, slightly elevated slit adorally, aborally also a series of fine pores (Text-figs 18C, H). Viewed laterally, preserved part of stone canal duct in circumoral showing as a funnel-like opening on internal plate surface (Text-figs 18C, F), then expanding rapidly before dividing into series of small, tube-like, single elongate canals situated adorally (Text-figs 18D, G, I). Length of slit and diameter of porous area equal, approximately 1.0 mm on paratype SUI 48174.

Attachment by very elongate, subcylindrical stem-like process consisting of single series of plates (usually seven, but six in SUI 48189). Attachment area circular; plates often fused into basal disc somewhat expanded beyond diameter of thecal base where plates remain separate (Pl. 1, Figs 6-12). On one specimen (SUI 46180), traces of covered (presumably secondarily infilled by calcite by animal) diplopores preserved immediately above fused basal disk.

Remarks.—No complete specimens have been encountered, because of the extreme thinness and fragile construction of most thecal plates. The reconstruction made here (Text-fig. 41) is based on the holotype, a crushed partial theca held together in part by encrusting Bryozoa (Text-fig. 38). An interpretation of thecal plating in this specimen is given in Text-fig. 39; it shows at least four circlets of large, very thin plates.

Isolated circumorals and aboral projections are not rare in the Upper Shales at Napoleon. These are always associated with "bioherms" or masses of skeletal debris. Reposited specimens and others in private collections indicate that *Finitiporus* n. gen. invariably attached to large, more or less smooth, flat surfaces, such as stromatoporoids, and not to shelled invertebrates (*e.g.*, nautiloids, brachiopods, and corals) as did some holocystitids. No intact separate plates from the central portion of the theca

have been found, again most likely because of their fragility. Apparently the boring organism, which produced *Tremichnus*, ignored the genus. Differential thickening of plates at thecal poles has been reported in one other sphaeronitid, *Codiacystis* (Jaekel, 1899, Prokop, 1964), and can occur in other genera with ambulacral platforms and prominent circumorals (*e.g.*, *Haplosphaeronis*).

The thin plating in Finitiporus n. gen. could be in partial compensation for the very reduced number of diplopores and the strongly partiporate theca. Paul (1972, 1973) and Paul & Bockelie (1983) demonstrated a trend toward increase in size and reduction in number of diplopores in the genus Sphaeronites that they interpreted (Paul 1976, 1977; Paul & Bockelie, 1983) as selection toward fewer, more efficient diplopores maintaining a respiratory rate more or less directly related to thecal volume. Similar trends in the evolution of endothecal pore structures (e.g., the pectinirhombs of Rhombifera) are reasonably interpreted as progressively more efficient compromises between two vital functions, protection of soft tissues and respiration (Paul, 1979). The problem of protection is more critical in diploporites, which potentially had highly efficient pore-structures (Paul, 1977: 145), but depended on external, soft-tissue structures only rarely strongly calcified (Paul, 1973; R. Lewis, pers. comm., 1981; known instances were reviewed by Bockelie, 1984) and not protected by spines or other calcified exothecal structures. It is of interest that one of the few diploporite families with strongly calcified exothecal pore structures, the Holocystitidae, was also one of the most successful and is as yet the only diploporite family known to have flourished in the Silurian.

From a point of view emphasizing respiratory efficiency, it seems probable that *Finitiporus* n. gen. competed with the coextensive holocystitids by downgrading the role of diplopores and relying on direct diffusion of dissolved oxygen through the thecal plates. To judge from the arguments of Farmanfarmaian (1966) and Paul (1968), these were thin enough in *Finitiporus* n. gen. to allow significant diffusion if the postulated extensive internal water vascular system (Paul, 1968, 1972) was maintained despite the loss of diplopores.

Echinoderm pore structures reached an early Paleozoic peak in taxonomic and morphologic diversity during the Ordovician. During this period, blastozoans thrived, and a significant number of Crinozoa (e.g., Carabocrinidae, Porocrinidae, Paleocrinidae, Acolocrinus; for discussion of these forms see Kesling & Paul, 1968, 1971, and Sprinkle, 1982) also developed thecal respiratory structures, perhaps because of (?temporary) low-oxygen tenor in shallow tropical seas (Paul, 1976: 553; 1980). Specialized respiratory structures are less common in the diverse echinoderm faunas of the extensive epeiric carbonate platforms of the Silurian (*Paracolocrinus*, for example, lacks them), but still persist in some classes, notably

the Rhombifera and Diploporita. Trends toward reduction in area, increased efficiency, and better protection are evident in Silurian forms (Paul, 1968, 1972, 1977). It is likely that the reduced diplopores and thin thecal plating of *Finitiporus* n. gen. are coordinated adaptations to enable the genus to compete successfully with contemporaneous blastozoans with morphologically advanced and efficient respiratory systems, in particular Rhombifera (*e.g.*, Caryocrinitidae and Callocystitidae, both present in the Osgood) and Diploporita (Holocystitidae), rather than indicators of the overall trend in Silurian echinoderms toward loss of thecal respiratory structures.

Because no complete specimens are known, thecal size of *Finitiporus* n. gen. can only be guessed at, but the genus was probably one of the largest Diploporita so far reported. One aboral stem projection (SUI 48181) is nearly 7 cm in length, and still larger fragments have been observed. Existing material suggests a thecal shape very like that of some *Holocystites* spp., especially *H. cylindricus* (see Paul, 1971: fig. 26). If so, the total thecal length might well have exceeded 30 cm, rivaled only by the Ordovician aristocystitid *Calix* Roualt, 1851, which could have reached lengths of 40 cm (Chauvel, 1977a, b).

Our reconstruction of the ambulacral apparatus of Finitiporus n. gen. (Text-fig. 41) is largely conjectural, because no traces of the appendages have been found. It is in line however, with what other authors have suggested for echinoderms with similar peristomial morphologies. The small, closelyspaced facets of Haplosphaeronis indicated to Paul (1973: 29) an arrangement in which "the appendages formed five open-ended grilles which gathered food in a manner analogous to that of a phoronid lophophore" (see also Paul, 1972; Text-fig. 12). Reconstructions of *Tholocystis* by Chauvel (1941: fig. 36C; 1980: fig. 4) and Kesling (1968: fig. 41-3) are along similar lines. Also comparable is the "ambulacral spout" of the probable paracrinoid Bockia (Hecker, 1938: fig. 32), although this genus has biserially pinnate biserial "arms" (brachiolar trunks in our view; Bockelie, 1981; this author interprets Bockia as an eocrinoid, but see Frest & Strimple, 1981a).

Finitiporus n. gen. is a highly specialized genus showing several advanced features, which indicate that the taxon occupies a position in the Herpetocystinae analogous to that of Haplosphaeronis in the Sphaeronitinae. Both have well-developed, compact, symmetrical, epipanniculate peristomes, with a relatively large number of small ambulacral facets. Both have raised ambulacral platforms, with the platforms confined only to the adoralmost part of the circumorals (for Finitiporus n. gen., see Text-fig. 19C; for Haplosphaeronis, see Paul, 1973: 29, pl. 2, figs 7, 12). Both also possess atypically few, constant and regular plate circlets with only a small number of plates per circlet. Haplosphaeronis carries the tendency of plate reduction to an extreme unique among Diploporita (excepting possibly the enigmatic Ascocystis Chauvel, 1941): the hemispherical to

pyriform theca has only two circlets of seven plates each. The nearly contiguous facets and reduced diplopores of *Finitiporus* n. gen. are not, however, paralleled in the Ordovician genus, which is omniporate.

Family **HOLOCYSTITIDAE** Miller, 1889

Diagnosis.—"Sphaeronitida with humatipores, a relatively large peristome generally surrounded by six or ten perioral plates, then a circlet of six, eight, or ten facetal plates; four or five ambulacra with one large ambulacral facet each" (Paul, 1971: 68).

Range.—Upper Ordovician (Ashgillian), Europe (United Kingdom, Spain, Sweden); Upper Silurian (Wenlockian), USA (Wisconsin, Illinois, Indiana, Ohio, Kentucky, Tennessee, ?Arkansas).

Included genera.—Holocystites Hall, 1864; Brightonicystis Paul, 1971; Osgoodicystis n. gen.; Paulicystis n. gen.; Pentacystis Paul, 1971; Pustulocystis Paul, 1971; Trematocystis Jaekel, 1899.

Remarks.-The family name Holocystitidae was first used (without definition) by Miller (1889: 215). It was generally ignored as unfounded and the nominate genus considered an aristocystitid (e.g., Bassler, 1938; Bassler & Moodey, 1943; Regnéll, 1945; Kesling, 1963a, 1968). Paul (1971) revised the constituent taxa and reconstituted the family on a formal basis. His work and procedures (Paul, 1971: 3-4, 68-72) are exceptionally sound, and are accepted in toto herein. In particular, his case for recognition of Holocystites cylindricus as type species, based on Miller's (1889: 253) subsequent designation, is convincing, and we have little to add on that point. Holocystites was originally described (Hall, 1861) from internal molds which seldom preserve some features now regarded as diagnostic taxobases, especially the humatipore morphology. Sufficient circumstantial evidence now exists to allow ascription of some well-preserved Osgood specimens (which frequently show the vital pore morphology) to Hall's Racine Dolomite (s. l.) species.

Paul (1971) demonstrated that the peristomial features of the Holocystitidae ally that family more closely with the Sphaeronitida than with the Aristocystitida. As defined by Paul (1971: 45), the latter have a small mouth at the junction of two broad long ambulacral grooves roofed in life by numerous small ambulacral covering plates. Sphaeronitids have a large peristomial opening ("mouth" s. l.), four or five small short ambulacral grooves, and the oral area is covered by six, large, thin plates termed palatals (Paul, 1971: 7). The oral area of holocystitids is similar to that of the latter superfamily (Text-fig. 16), supporting assignment to the Sphaeronitida.

Dipores (Paul, 1968: 700) of varying morphology are characteristic of Diploporita. The specialized type characteristic of the Sphaeronitidae, termed diplopores (Paul, 1968), are similar to those of many Aristocystitida (Paul, 1973). Dipore morphology of holocystitids does not resemble that of the other Sphaeronitida. As first pointed out by Regnéll (1945: 183), the most distinctive feature of Holocystites is the calcified dipores which Paul (1968) termed humatipores. Our work and that of Paul show humatipores to be ubiquitous to Holocystites and related taxa and warrant recognition of those genera possessing them as a separate family. Nearly as distinctive to the Holocystitidae are the large (to 2 cm length in *Paulicystis* n. gen.) ambulacral facets, which, as proposed earlier, might have borne uniserial, brachiolate ambulacral trunks, instead of themselves representing very large, but small in number, biserial or uniserial brachioles. Derivation of the family from the Sphaeronitidae, as advocated previously by Paul (1971: 7), perhaps from the large, single-faceted genus Diplosphaeronis, seems likely.

Paul (1971) recognized five genera in the family. The Napoleon material impels us to recognize two additional genera, subdivide *Holocystites* on the basis of humatipore morphology into three subgenera, and erect three subfamilies within the Holocystitidae. Subfamilial characters are the size and presence/ absence of the perioral circlet, the position and number of the ambulacral facets, and the location of the hydropore. Like Paul (1971: 71-72), we use humatipore morphology, number of periorals and facetals, and number of plate generations in conjunction with lesser variations of the subfamilial characters to define genera. In summary, the classification of the Holocystitidae used herein is as follows:

Subfamily Holocystitinae (6-10 prominent POO; 10-8 FAA; 5

FF; FF on facetals and periorals; hydropore on POO).

Brightonicystis: 10 POO, 10 FAA, 5 FF.
Holocystites: 6 POO, 8 FAA, 5 FF.
(Holocystites): pustular, complex humatipores with three-dimensional tangential canals.
(Megacystites n. sgen.): sunken, simple humatipores with two-dimensional tangential canals.
(Sepulticystis n. sgen.): sunken, complex humatipores with three-dimensional tangential canals.
Subfamily Pentacystinae (0-6 vestigial POO; 8 FAA; 5 FF; FF on facetals only; hydropore obscure or on FAA).
Pentacystis: no POO, 8 FAA, 5 FF.
Osgoodicystis n. gen.: 2-6 POO, 8 FAA, 5 FF.
Subfamily Trematocystinae (6 reduced POO; 6-8 FAA; 4 FF; FF on facetals or lower thecal plates; hydropore on POO).
Trematocystis: 6 POO, 8 FAA, 4 FF, facets on facetals only.

Paulicystis n. gen.: 6 POO, 8 FAA, 4 FF, facets overrunning

Pustulocystis: 6 POO, 6 FAA, 4 FF, facets on facetals only.

facetals.

Subfamily **HOLOCYSTITINAE** Miller, 1889

nom. transl. ex Holocystitidae Miller, 1889: 215.

Diagnosis.—Holocystitidae with pyriform to cylindrical theca; plates smooth or pustular, of one to three generations, in many circlets with 8 to many plates each; humatipores with flat or curved tangential canals; POO prominent, 8 or 10; 8-10 FAA; 5 FF developed equally on POO and FAA; gonopore on FA1 or FA2; hydropore on PO1:PO6 suture; aboral projection present.

Range.—Upper Ordovician (Ashgillian), Europe (United Kingdom, Sweden); Upper Silurian (Wenlockian), North America (Wisconsin, Illinois, Indiana, Ohio, Kentucky, Tennessee, ?Arkansas).

Included genera.-Holocystites Hall, 1864; Brightonicystis Paul, 1971.

Remarks.—Holocystites and Brightonicystis differ in several important respects, such as number of periorals and facetals and details of humatipore morphology. Separate subfamilies will probably eventually be necessary for each. This step is not yet taken, however, because the wide stratigraphic gap between the two forms hampers speculation as to their actual relationships. The plethora of Wenlockian holocystitid forms might imply equally diverse and variable predecessors. Subfamilial groupings are thought to be relatively secure for the Wenlockian taxa largely because enough specimens are available to discriminate between individual, specific, and higher ranges of variation.

The following key summarizes major morphologic discriminations within the subfamily:

KEY TO THE SPECIES OF HOLOCYSTTTINAE

1.	10 periorals and 10 facetals
	genus Brightonicystis 2
	6 periorals and 8 facetals
	genus <i>Holocystites</i> 3
	Theca globular, humatipores with up to 10 tangential
	canals
	Theca pyriform, humatipores with 2-4 tan-
	gential canals
3.	Humatipores flat
	Humatipores raised into pustules
	subgenus <i>Holocystites</i> 6
4.	Humatipores essentially two-dimensional
	subgenus Megacystites n. sgen 5

Genus *Holocystites* Hall, 1864 Text-figs 16, 22, 26-27, 42-43; Pl. 1, Figs 1-5; Pls 2-3; Pl. 4, Figs 1, 3-4, 6; Pl. 5, Figs 4-9; Pls 6-8

Caryocystites Hall, 1861: 23; 1862: 431 (non Von Buch, 1846). Holocystis Haeckel, 1896: 60 (non Lonsdale, 1849). Holocystites Hall, 1864: 7; 1868: 311; Miller, 1878: 129; 1889: 253; Zittel, 1879: 416; Grabau & Shimer, 1910: 460; Foerste, 1920a: 207-208; 1920b: 48; Bassler & Moodey, 1943: 167; Regnéll, 1945: 183; Kesling, 1963a: 115; 1968: S254; Paul, 1971: 72-73.

Megacystis Angelin, 1878: 29; Bather, 1900: 47; 1919a: 73. Megacystites Hall, 1868: 380; Shimer & Shrock, 1944: 125. *Type species.—Caryocystites cylindricum* Hall, 1861; subsequent designation by Miller (1889: 253).

Diagnosis.—Holocystitidae with cylindrical or pyriform to subglobular theca; six periorals; eight facetals; five ambulacral facets; gonopore in FA1 or FA2; slit-like hydropore on P01:P06 suture; smooth or pustular plates of one to three generations; humatipores with many planar or non-planar tangential canals arranged in a radiate pattern; attachment area small to medium, usually small.

Range.—Upper Silurian (Wenlockian), North America (Wisconsin, Illinois, Indiana, Ohio, Kentucky, Tennessee, ?Arkansas).

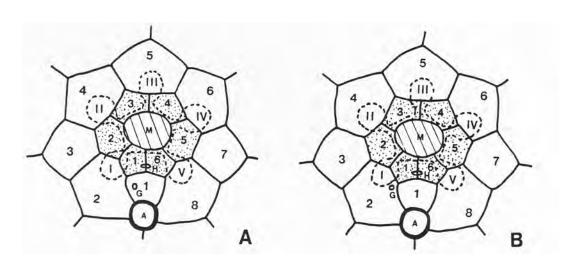
Description.—Theca typically cylindrical, fusiform in Holocystites greenvillensis, distinctly pyriform in H. spangleri and H. scutellatus, ovate or subglobular in H. ovatus; small to ca. 15 cm in length.

Plates smooth to pustular, one to three distinct generations, generally many circlets, eight plates in primary circlets. Total number of thecal plates large, often exceeding 120.

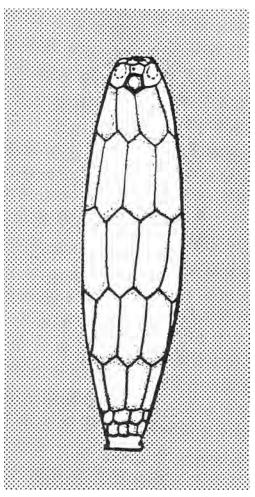
Humatipores generally with numerous (> 4) tangential canals, either arrayed in a single or several planes, flat or sursumate, not densely packed.

Peristome invariably pentagonal; five circular ambulacral facets developed on two or three plates, equally on periorals and facetals; 6 POO, 8 FAA, less regularly arranged than in other holocystitids; peristomial border pitted by numerous oral pores; periorals prominent; peristome frequently offset to one side of cylindrical thecae (Pl. 6, Fig. 3); palatals poorly known.

Periproct pentagonal or, rarely, hexagonal with prominent indented border forming shelf for articulation of anals. Anal pyramid composed of 5 (?) thin triangular plates. Anus round.



Text-fig. 42. Diagrammatic representations of the oro-anal areas of *Holocystites* (*Holocystites*) *alternatus* (A), with gonopore in FA1, and *H.* (*H.*) *clavus* n. sp. (B), with gonopore in FA2. Symbols as outlined under Abbreviations, p. 52.



Text-fig. 43. Restoration (posterior lateral view) of adult *Holocystites* (*Megacystites* n. sgen.) *greenvillensis*; composite based largely on SUI 42732 and lectotype USNM 80875b.

Gonopore round, in elevated tubercle, invariably on single plate, either FA1 (usually) or FA2 (*H. clavus* n. sp.).

Hydropore slit-like or occasionally oval, in low tubercle across PO1: PO6 border.

Attachment direct as juvenile and also some adults, by small to medium-sized, gradually tapering aboral process in most; attachment area commonly small.

Remarks.—Restudy of five species formerly (Paul, 1971: 77) ascribed to the genus and of new material from Napoleon suggests the propriety of subdivision of the genus based on humatipore morphology, as discussed above. In addition, previously unknown material from the Cedarville Dolomite of Ohio substantiates the validity of Holocystites greenvillensis and allows ascription to Megacystites n. sgen. Our resurrection of this name requires discussion. Hall (1864), recognizing major differences from typical Caryocystites von Buch, 1846, to which he first (Hall, 1861) referred Racine holocystitids, chose

the name *Holocystites* (1864: 7). After becoming aware of Lonsdale's (1849) use of the name *Holocystis* for a Cretaceous coral, he suggested the alternative name *Megacystites* (1868: 380). Current ICZN rules permit acceptance of both names, so *Megacystites* Hall, 1868, is a junior objective synonym of *Holocystites* Hall, 1864 (Paul, 1971). Hall himself did not select a type species for either name, and *Holocystites* has enjoyed much greater usage. Miller (1889) did designate a type species for *Holocystites*, but none was ever chosen for *Megacystites* despite use of the name and its variant *Megacystis* Angelin, 1878, by several authors (Hall, 1868; Angelin, 1878; Bather, 1900, 1919a; Shimer & Shrock, 1944). Because the species we propose to include in *Megacystites* have long been accepted as *Holocystites*, we prefer to validate the name rather than propose a totally new one.

Paul (1971: 72-102) provided detailed descriptions of the then-known taxa based on all available material. His work is very careful and comprehensive and need be supplemented only in minor ways despite the large increase in specimens from Napoleon. Opportunity is taken here to add to his descriptions where possible and also to incorporate new occurrence and stratigraphic data, as well as that published separately by Frest *et al.* (1977). One additional *Holocystites* species, *H. clavus* n. sp., is added from Napoleon, and *H. ovatus* is recognized as a separate species.

Subgenus *Holocystites* Hall, 1864 (new rank) Text-figs 16, 22, 27-29, 42; Pl. 1, Figs 1-5; Pls 2-3; Pl. 4, Figs 1, 3-4, 6; Pl. 5, Figs 4-9; Pl. 6

Diagnosis.—Holocystites with cylindrical to ovate theca; pustulate plates with sursumate humatipores; prominent aboral projection, with small attachment area, theca fixed or free as adult.

Range.—Upper Silurian (Wenlockian), North America (Wisconsin, Illinois, Indiana, Ohio, Kentucky, Tennessee, ?Arkansas).

Description.—As for genus except where superceded by above diagnosis.

Remarks.—The sursumate humatipores of Holocystites (s.s.) mark this as the most advanced subgenus. Perhaps not by coincidence, it is also the most diverse, abundant, and widespread. We consider the following taxa as bona fide members of Holocystites s. s.: H. cylindricus; H. alternatus, H. clavus n. sp.; H. ovatus, H. scutellatus.

Holocystites (Holocystites) cylindricus (Hall, 1861) Text-figs 16A, 27; Pl. 1, Fig. 5; Pl. 5, Figs 4-9

Caryocystites cylindricum Hall, 1861: 23; 1862: 431.

Holocystis cylindrica. Haeckel, 1896: 60.

Holocystites cylindricus. Hall, 1864: 7; 1868: 311; 1870: 354; Chamberlin, 1883: 191; Nicholson & Lydekker, 1889: 455; Grabau & Shimer, 1910: 461; Foerste, 1917: 204; 1920a: 207-208; 1920b: 51; Bassler & Moodey, 1943: 50, 168; Paul, 1971: 79.

Megacystites cylindricum. Shimer & Shrock, 1944: 125.

Diagnosis.—*Holocystites* (*Holocystites*) with cylindrical theca and plates of one generation.

Occurrence.—The lectotype from Grafton, Wisconsin, is probably from the Manistique Formation of present usage and not from the Racine Dolomite as previously cited (Paul, 1971: 81; see also Frest *et al.*, 1977: 92). Additional specimens are from the Joliet Dolomite (Illinois), Maddox Member, Wayne Formation (Tennessee), and Osgood Member, Salamonie Dolomite (Indiana).

Material.—Approximately 30 specimens; lectotype AMNH 2018a, paralectotypes AMNH 2018b-c; other specimens in AMNH, FMNH, USNM, SUI (illustrated specimens SUI 48172, 48177), UWBM, and private collections.

Description.—See Paul (1971: 81-83), with the following addition: Humatipores raised in moderate tubercles, which vary from 0.6-1.1 mm diameter; 4-12 tangential canals (average 7), radially arranged.

Remarks.—As interpreted herein, true Holocystites cylindricus ranges no higher than middle Wenlockian (Text-fig. 4), not being found in the Racine Dolomite (s. s.). Previously, all internal molds with a single generation of plates and cylindrical to elongate-oval thecae were referred to this species (Paul, 1971: 83), but the addition of H. clavus n. sp. to the subgenus necessitates caution in making such assignments, because small specimens with a single plate generation could be the latter.

The species was not formerly reported from the Indiana Osgood, but is not uncommon in the Upper Shales at Napoleon; we have examined over a dozen undoubted examples. The humatipore description is based on these specimens, several of which are now reposited under SUI 46321, 48172, and 48177. Osgood specimens of *Holocystites clavus* n. sp. and *H. cylindricus* are readily separated; the former has more prominent, smaller tubercles and a relatively slender, thin-plated theca (compare Pl. 1, Figs 4-5), as well as two generations of plates in most examples. More importantly, the gonopore is on FA2 in *H. clavus* n. sp. and on FA1 in *H. cylindricus* and

all other normal *Holocystites* species. Generally, the plates of *H. cylindricus* are more equidimensional than those of *H. clavus* n. sp., even in specimens with only two plate generations (compare Pl. 1, Fig. 5, with Pl. 1, Fig. 4 and Pl. 2, Fig. 11), so that even internal molds can be referred to one or the other with some confidence.

In the Indiana Osgood, *Holocystites cylindricus* seems to be restricted to the Upper Shales (Zone 1b). Specimens have been seen from Osgood (Locality 11 of Paul, 1971, and herein) as well as Napoleon (Locality 12b). The species appears to change little in shape throughout ontogeny, as far as is known. Small specimens (*i.e.*, < 5 cm length) have a flat, unexpanded basal disk at the end of the aboral projection and were probably attached. No large specimen retains the basal disk, and they were probably not attached; the aboral process is rounded at the terminus.

One abnormal (?) specimen (SUI 48172), which has only six plates per circlet, is provisionally assigned to this species. The facetal plate arrangement (Text-fig. 27) is suggestive of *Pustulocystis*, and the specimen can be interpreted, as was done earlier, as an intermediate form. It should be noted, however, that *Pustulocystis* has up to 20 plates (Paul, 1971: 132) per circlet, although of one generation, like *Holocystites cylindricus* and unlike most holocystitids. SUI 48172 appears to have only six plates in lower plate circlets as well (Pl. 5, Figs 4-9), but the specimen is poorly preserved. Should better material prove to exhibit the same characteristics, separate specific or generic status might be appropriate.

Holocystites (Holocystites) alternatus (Hall, 1861) Text-fig. 42A; Pl. 1, Figs 1-3

Caryocystites alternatum Hall, 1861: 23; 1862: 431.

Holocystites alternatus. Hall, 1864: 8; 1868: 312; 1870: 355; Foerste, 1917: 233; 1920a: 207-208; 1920b: 51, 53; Chauvel, 1941: 126; Bassler & Moodey, 1943: 49-50, 167; Regnéll, 1960: 776: Kesling, 1968: S254; Paul, 1971: 83-84.

Holocystites baculus Miller, 1879: 105; Bassler & Moodey, 1943: 43, 168.

Holocystites colletti Miller, 1891: 16; 1892a: 626; Bassler & Moodey, 1943: 43, 168.

Holocystites perlongus Miller, 1878: 132; Bassler & Moodey, 1943: 44, 170.

Megacystis alternata. Haeckel, 1896: 60.

Megacystis alternatus. Grabau & Shimer, 1910: 461.

Megacystites alternatus. Shimer & Shrock, 1944: 125.

Diagnosis.—*Holocystites* (*Holocystites*) with elongate cylindrical theca; plates of two or three generations; gonopore in FA1; aboral projection long, tapering; basal disk small.

Occurrence.-See Paul (1971: 84) and the Appendix. In the Osgood the species is frequent in the Upper Shales at

Napoleon, Osgood, Big Creek, and other localities and occurs also in the upper Laurel Member at St. Paul (FMNH, SUI).

Material.—At least 100 specimens. Lectotype AMNH 2020a; Holocystites baculus holotype FMNH 8762; H. colletti holotype FMNH 8758; H. perlongus holotype FMNH 6007. Other specimens in AMNH, FMNH, SUI (including illustrated SUI 48176), IU, UMMP, USNM, UWBM, UWM, and private collections.

Description.—The description by Paul (1971: 84-89) need be supplemented only in the following particulars: Plates of two or three generations, three in adults. Attachment by long gradually tapering aboral projection much like that of *Holocystites* (H.) cylindricus; basal disk small, flat on small specimens, rounded or broken off on large ones.

Remarks.—The addition of Holocystites (H.) clavus n. sp. to the subgenus necessitates some modification of Paul's diagnosis. In the Osgood, H. (H.) alternatus is readily distinguishable from H. (H.) clavus n. sp. by the position of the gonopore. Also, similarly-sized specimens generally have three generations of plates in H. alternatus and only two in H. clavus n. sp. One young specimen of H. alternatus (SUI 48176; Pl. 1, Figs 1-3), 27.5 mm length, already has three plate generations, whereas the smallest H. (H.) clavus n. sp., SUI 46317, 46 mm length, has only two. Thus, even specimens without the oral area can often readily be assigned to one or the other species. All large specimens, i.e., those > 70 mm length, have three plate generations and gonopores in FA1 (Text-fig. 22), so that it appears that H. (H.) alternatus frequently attained larger size.

Internal molds from the Racine Dolomite and from formations with similar preservation might present problems, because the position of the gonopore is seldom detectable. Cylindrical internal molds can be divided into two groups, one with fairly regular plate arrangement and the other with plate arrangement much less regular. These have traditionally been placed in *Holocystites* (*H.*) *alternatus* for the latter, and *H.* (*Megacystites*) *abnormis* for the former. Molds of *H.* (*H.*) *clavus* n. sp. might well be indistinguishable from those of *H.* (*M.*) *abnormis* unless the matching external mold is also retained. However, *H.* (*M.*) *abnormis* frequently has secondaries developed only aborally, so that most specimens are indeed determinable even on incompletely preserved molds.

The smallest observed specimen of *Holocystites* (*H*.) *alternatus* (SUI 48176; Pl. 1, Figs 1-3) has a distinctly pyriform rather than cylindrical theca, recalling that of *H*. (*H*.) *scutellatus*. This could indicate that the pyriform shape is less advanced phylogenetically. This same specimen preserves a complete aboral process with a flat attachment disk. Large specimens are almost invariably incomplete at the aboral pole, but one speci-

men examined (now in a private collection) has a rounded-off aboral extremity, suggesting that adults, unlike juveniles, might have been unattached.

Aside from the specimens used by Paul, *ca.* 50 additional Napoleon specimens have been seen, indicating that the species was uncommon in the Upper Shales. The species ranges throughout the whole of Zone 1 (*Holocystites* Zone; Text-fig. 10), and also occurs in the uppermost 1.5 m of the Laurel Member, Salamonie Dolomite, near St. Paul, Indiana (see section and detailed description of occurrence by Frest, 1975: 83-84, fig. 1; Frest *et al.*, 1977: 87-88: see Appendix for details on collecting localities). Upper Laurel specimens are in FMNH and SUI collections.

Holocystites (Holocystites) clavus Frest & Strimple, n. sp. Text-fig. 42B; Pl. 1, Fig. 4; Pl. 3; Pl. 4, Fig. 4

Derivation of name.—Latin *clavus* (club), in reference to the-cal shape.

Diagnosis.—*Holocystites* (*Holocystites*) with elongate cylindrical theca; plates of one or two generations; gonopore in FA2; aboral process long, gradually tapering; basal disk small.

Occurrence.—Upper Shales (Zone 1b; Pentacystinid subzone), Osgood Member, Salamonie Dolomite (Wenlockian), Napoleon Quarry locality, Ripley County, Indiana.

Material.—At least 13 specimens. Holotype SUI 46317; figured paratypes SUI 46318, 46319, 48165; unfigured paratype SUI 46320. Other specimens are in private collections.

Description.—Theca cylindrical to elongate pyriform, gradually tapering aborally.

Plates of one generation in some juveniles, generally two generations with secondaries (usually 15 per circlet) distributed regularly over theca. Plates without impressed sutures (Pl. 3), with faint granular ornament as well as tubercles (Pl. 4, Fig. 4).

Humatipores raised in prominent tubercles varying from 0.5-0.9 mm in diameter, 7-12 radial canals (average 9), radially arranged (Pl. 3, Figs 8-9, 11).

Peristome mostly rounded pentagonal to oval, 4-7 mm across, set within pentagonal peristome sometimes protruded and/or set to one side of theca (Pl. 3, Fig. 3), bearing five short food grooves. Ambulacral facets equal, five, often equally developed on periorals and facetals, circular to oval, slightly concave, 3-4 mm in diameter. Facets divided into two equal areas by faint median ridge (Pl. 4, Fig. 4). Palatals unknown.

Periproct pentagonal, with rounded anus 3-4 mm in diameter set within periproct, leaving moderately wide border for

attachment of (unknown) anals.

Gonopore small, circular, 0.5 mm in diameter, within prominent tubercle in FA2 (Text-fig. 42B; Pl. 4, Fig. 4).

Hydropore oval to slit-like, set in prominent elongate tubercle 1.2 mm by 0.4 mm across POI:PO6 suture in paratype SUI 48165.

Attachment: No complete aboral area known; aboral stemlike projection present; morphology and rate of taper of preserved portions as in *Holocystites* (*H.*) *alternatus*.

Remarks.—Features distinguishing this taxon from the two previously discussed species have been mentioned above. Available specimens have proportionately finer tubercles and smaller facets, peristome, mouth, and orifices at the same "size" (length), but a larger sample would be necessary to establish the value of these differences. Very small specimens with only two generations of plates might be difficult to distinguish from Holocystites (H.) cylindricus if the peristome is not preserved. Osgood specimens of H. (H.) cylindricus do, however, consistently have slightly less elongate (more baculate) thecae and thicker, more regularly hexagonal plates. Like the preceding two species, H. (H.) clavus n. sp. does not seem to be preferentially associated with mud mounds, "bioherms," or debris piles.

Paul (1971: 83-84) synonymized several of S. A. Miller's species with *Holocystites* (*H.*) *alternatus*. Review of Miller's papers (1878, 1879, 1891) and of the FMNH holotypes [cited above, and illustrated photographically by Paul (1971: figs 29D, 30C, 31)], indicate that three of these have the gonopore in FA1, and two of these (*H. perlongus* Miller, 1878, and *H. baculus* Miller, 1879) have three plate generations; all three are accepted as synonyms of *H.* (*H.*) *alternatus*, necessitating a new name for the specimens placed here in *H.* (*H.*) *clavus* n. sp. As far as is presently known, *H.* (*H.*) *clavus* n. sp. is confined to the Upper Shales, with a range coincident with *H.* (*H.*) *cylindricus*, *i.e.*, Zone 1b (Pentacystinid subzone).

Holocystites plenus Miller, 1878, could conceivably be conspecific with *H.* (*H.*) clavus n. sp., but the type is apparently lost (Paul, 1971: 84, 150). According to Miller's somewhat confusing description (1878: 135, pl. 6, figs 2, 2a), the specimen is the adoral portion of a large cylindrical holocystitid with offset peristome, five ambulacral facets, gonopore in FA1 (?), and more than two plate generations. As noted by Paul, these characters could fit either *H.* (Sepulticystis n. sgen.) spangleri or *H.* (*H.*) alternatus. Paul (1971: 84) apparently considered the species provisionally a synonym of *H.* (*H.*) alternatus. The "slightly granulose" plate surfaces reported by Miller (1878) could render ascription to what is here called *H.* (*H.*) clavus n. sp. possible, particularly if our interpretation of Miller's description of the gonopore location is mistaken — which is quite possible given Miller's rather unorthodox interpretation of

thecal orifices, which apparently derives from that of Billings (1870; see also Paul, 1971: 28). For the present, consideration of the species as unrecognizable, as was done by Paul (1971: 150) is the wisest course. Miller's name would of course have priority if the gonopore could be shown to be in FA2 and the humatipores have the characteristic morphology of *H.* (*H.*) rather than *H.* (*Sepulticystis* n. sgen.).

Holocystites (Holocystites) scutellatus Hall, 1864 Pl. 2; Pl. 4, Figs 1, 3, 6

Holocystites faberi Miller, 1889: 254; Bassler & Moodey, 1943: 44,

Holocystites jolietensis Miller, 1882: 223; Bassler & Moodey, 1943: 50, 169.

Holocystites parvulus Miller, 1891: 18; 1892a: 628; Butts, 1915: 206; Bassler & Moodey, 1943: 44, 170.

Holocystites scutellatus Hall, 1864: 10; 1868: 314; 1870: 357; Foerste, 1917: 235; 1920a: 207-208; 1920b: 49; Fisher, 1925: 48; Bassler & Moodey, 1943: 50, 170; Paul, 1971: 94-101 (partim).

Holocystites splendens Miller & Gurley, 1894: 7; Miller, 1897: 747; Bassler & Moodey, 1943: 44, 170.

Diagnosis.—Holocystites (Holocystites) with pyriform theca, short aboral stem-like projection and plates of two generations.

Occurrence.—Zone 1 (a-c: Holocystitinid subzone — Holocystites (H.) alternatus subzone: Table 3), basal Laurel Member and Upper Shales and upper unit (a) of Middle Osgood Limestone (Text-figs 9-10), Osgood Member, Salamonie Dolomite, Indiana, Kentucky, and Tennessee; Joliet Dolomite, Illinois; Manistique Dolomite, Wisconsin.

Material.—Over 1,000 complete thecae, and in excess of 150 internal molds. Lectotype AMNH 2010a, selected by Paul (1971: 95); = *H. jolietensis* Miller, 1882, holotype CAS 2538; *H. faberi* Miller, 1889, holotype FMNH 8764; *H. parvulus* Miller, 1891, holotype FMNH 6009; *H. splendens* Miller & Gurley, 1894, holotype FMNH 5998. Other specimens in AMNH, BMNH, CAS, FMNH, IU, MCZ, OSU, UC, USNM, UWBM, UWM, YPM, and private collections.

Description.-See Paul (1971: 96).

Remarks.—This species is by far the most abundant and variable member of the *Holocystites* fauna, both at Napoleon and elsewhere. Somewhere between one and two thousand specimens are reported to have been collected over a five-year period at Napoleon. Despite the wealth of new material, Paul's (1971) description remains essentially sound; our treatment does differ in a few respects.

Paul (1971: 99-100) recognized two forms, both among Osgood specimens and internal molds from Illinois. One (common in the Osgood, rare in the Joliet) is small and distinctly pyriform, whereas the other (rare in the Osgood, common in the Joliet; both are equally rare in the Manistique but present in roughly equal numbers) is larger and more globular. He (1971: 101) considered and rejected the hypothesis that the two represent two species. Detailed examination of several hundred additional specimens convinces us that the two are indeed distinct, even though Holocystites (H.) scutellatus is certainly quite variable. Among previously described "species," the holotypes of H. scutellatus, H. jolietensis, H. faberi, H. parvulus, and H. splendens in our opinion are conspecific and members of the small pyriform-subcylindrical morph, whereas those of H. ovatus and H. pustulosus Miller, 1878, represent the larger, globular morph.

At the time of Paul's work (1971: 149), the holotype of *Holocystites ovatus* was missing and he considered the species unrecognizable. Subsequent location of the holotype led to its redescription, and it was then considered "almost certainly conspecific with *H. scutellatus* Hall, 1864" (Frest, *et al.*, 1977: 86). Because the name is the first available one for the globular form, the species is recognized here. Although strict application of page priority would have required use of *H. ovatus* for both forms (if considered conspecific), Paul (1977: 86), as first revisor, legitimately chose *H. scutellatus* even though he considered the two as possible synonyms. *Holocystites ornatus* Miller, 1878, is a possible synonym of *H. scutellatus* as construed herein, but the type is still lost, and the form is best considered unrecognizable, as was done by Paul (1971: 150), rather than synonymized with *H. scutellatus* (see Paul, 1971: 94).

As we define Holocystites scutellatus, the thecal shape varies between elongate pyriform and baculate; no truly cylindrical specimens were encountered. On first examination, the species seems to fall into two groups even as restricted here. One is pyriform, has small rounded pustules, a shallow broad peristomial border with shallowly concave facets, and the ornament around the peristome is mostly fine granules (e.g., Pl. 2, Figs 1-7). The second, rarer form is baculate, has coarse, coalescent pustules, a narrow peristomial border, more deeply sunken facets, and coarse pustulate ornament around the peristome (Pl. 2, Figs 8-13). It is possible that these forms represent separate species, but a few intergrades are known, so we consider each merely extremes of a broad range of variation. Among "species" here relegated to synonymy, all are assignable to the pyriform morph with the exception of the holotype of *H. parvulus*, which would be the first available name for the baculate morph should the two forms be later proven distinct.

Despite the abundance of specimens, none with major deviations in morphology (other than those mentioned above) was encountered, *i.e.*, all had 5 FF, 6 POO, 8 FAA, gonopore

in FA1, and hydropore on the PO1:PO6 suture. Some variation in hydropore shape was noted; most had a slit-like hydropore on a prominent elongate tubercle (e.g., Pl. 2, Fig. 9), whereas some had a small, circular opening in the proper location (Pl. 2, Fig. 7), barely elevated above the regular plate surface. Neither hydropore type seems preferentially associated with either of the two extremes of variation, or morphs, described above. No extremely small specimens were found. The smallest (SUI 46322, length 27.3 mm) has a shape similar to larger adults, except that the aboral process is proportionately broader. Small specimens also frequently have disk-like (flat) terminations; nearly all large specimens have rounded-off aboral poles (Pl. 2, Fig. 6), suggesting that adults might not have been attached. Juveniles (small specimens) of *Holocystites* (*H*.) scutellatus and H. (H.) ovatus are, if anything, more distinct than adults, because large specimens of H. scutellatus tend to become somewhat more broad proportionately than small ones (compare Pl. 2, Figs 3 and 6). Young specimens of H. scutellatus closely resemble those of H. alternatus (Pl. 1, Figs 1-3), but the latter characteristically have the small secondaries inserted in fairly regular, distinct circlets, whereas even young H. scutellatus tend to have variable-sized secondaries, some as large as the primaries, so that the plate configuration looks more or less irregular at first glance.

Holocystites (Holocystites) ovatus Hall, 1864 Text-fig. 22; Pl. 6

Holocystites ovatus Hall, 1864: 9; 1868: 313; 1870: 356; Chamberlin, 1883: 191; Bassler & Moodey, 1943: 50, 169; Paul, 1971: 149; Frest et al., 1977: 85.

Holocystites pustulosus Miller, 1878: 134; Bassler & Moodey, 1943: 44, 170.

Holocystites scutellatus Hall, 1864 (Paul, 1971: 94-101), pars.

Diagnosis.—*Holocystites* (*Holocystites*) with ovoid to globose theca, small aboral process, and two plate generations.

Occurrence.—Manistique Formation, Wisconsin; Upper Shales [Zone 1b (Pentacystinid subzone), Text-fig. 10], Osgood Member, Salamonie Dolomite, Indiana; Joliet Dolomite, Illinois.

Material.—Approximately 60 complete thecae and internal molds; holotype AMNH 2021; illustrated specimens SUI 48187, 48188. Other specimens in AMNH, SUI, USNM, and private collections.

Description.—Theca ovoid, with very short narrow aboral process.

Plates of two generations, secondaries intercalated irregularly and of variable size. Primaries and secondaries to 10 mm

across, with impressed sutures. Most regular specimens show at least 13 circlets.

Humatipore raised in distinct rounded pustules to 1.1 mm in diameter at base and approximately one-half that in height (Pl. 6, Figs 2-5); 7-10 tangential canals, radially arranged.

Peristome elongate-pentagonal (Pl. 6, Fig. 1), to 9 mm width; border broad, 1-2 mm wide, pitted with oral pores; peristomial opening rounded, 7 mm in width. Facets five, circular to oval in shape, 3.5-5 mm in diameter, developed on two or three plates (facetals and periorals). Palatals unknown.

Periproct pentagonal or hexagonal, width 7 mm, with narrow border for insertion of anals. Anus rounded, to 6 mm in diameter; anals unknown.

Gonopore small, circular, at summit of prominent, round tubercle in FA1 (Pl. 6, Fig. 1).

Hydropore a narrow slit on low tubercle across suture PO1:PO6; length to 1.8 mm, width *ca.* 0.5 mm (Pl. 6, Fig. 1).

Attachment by short, narrow (6.5 mm in SUI 48187, compared to maximum thecal width of 30 mm) aboral process, with rounded-off terminus in adults.

Remarks.—Thecal shape and the small, indistinct aboral process (barely noticeable on young specimens, e.g., SUI 46323) distinguish the species from Holocystites (H.) scutellatus. This species also commonly reaches a greater maximum size, i.e., ca. 50-60 mm or more, compared to 30-40 mm for H. (H.) scutellatus. The two Osgood specimens illustrated here (Pl. 6) are approximately the same size as most H. scutellatus to facilitate comparison.

Like *Holocystites* (*H.*) scutellatus, the holotype of this form is an internal mold from the Manistique Formation at Waukesha, Wisconsin; this formation has yielded relatively few specimens compared to the Osgood and Joliet. Thecal orifices are described from Osgood specimens, several of which (e.g., SUI 48187, 48188, 46323, 48191) are recently collected Napoleon individuals. Confirmation of the identity of the internal molds is possible due to fortunate preservation of some plates on one Waukesha specimen (SUI 42741A), which shows the two-generation, highly pustular plates with impressed sutures, i.e., the same morphology as the Osgood material. Other specimens in this lot (SUI 42741B, C) show traces of two tubular structures, interpreted as the gonoduct and stone canal, connected to the probable gonopore and hydropore, much as Paul (1971: 32) described for *H.* (*H.*) scutellatus.

We have not seen or collected any Salamonie specimen from the upper part of the Middle Osgood limestone or lower Laurel (Text-fig. 9), but the species is considerably less common than *Holocystites scutellatus*, and its range in the Osgood could be coincident with that of *H.* (*H.*) scutellatus.

One specimen of Holocystites (H.) ovatus has a definitely

abnormal peristome and is illustrated here (Text-fig. 22; Pl. 6, Figs 6-10). The thecal shape is normal (Pl. 6, Figs 7-10), but it has only four, equally-spaced ambulacral facets (Pl. 6, Fig. 6) and a quadrilateral peristome. In our interpretation, the ambulacra are I, II, III, and V. The normal complement of facetals is present, but there are only four periorals (Text-fig. 22). These might be PO1, PO2, combined PO3-PO4, and PO5 in the usual nomenclature. Although a number of holocystitids have four facets (*i.e.*, members of Trematocystinae), these are reasonably interpreted as being equivalent to I, II, IV, and V of normal *Holocystites*, so that this specimen could be merely aberrant. Interestingly, it also lacks definite hydropore and gonopore openings.

Subgenus *Megacystites* Frest & Strimple, n. sgen. Text-fig. 43; Pl. 7

non Megacystites Hall, 1868: 380 (nom. nud.); Shimer & Shrock, 1944: 125.

non Megacystis Angelin, 1878: 29; Bather, 1900: 47; 1919a: 73 (nom. van.).

Derivation of name.—Combining *mega* (Greek: large, great) with standard *-cystites* ending.

Type species.–Holocystites abnormis Hall, 1864, by original designation herein.

Diagnosis.—*Holocystites* with cylindrical theca, smooth plates, flat (oriented tangential to plate surfaces), tangential humatipore canals, and small attachment area.

Range.—Upper Silurian (Wenlockian), North America (Wisconsin, Illinois, Indiana, Ohio).

Description.—Theca elongate cylindrical, with one or both ends gradually tapering.

Plates smooth, of one or two generations; sutures impressed or not impressed; normally, eight plates in primary circlet and moderate number of circlets (7-9); where present, secondaries developed irregularly, confined to aboral portion of theca.

Humatipores buried, but tangential canals on same plane; 4-8 tangential canals radially arranged.

Peristome pentagonal, with distinct peristomial border, pitted with numerous oral pores. Peristomial opening oval, surrounded by six periorals and then eight facetals. Ambulacral facets five, oval or circular, slightly concave.

Periproct rounded or pentagonal, with narrow border for insertion of anals; anals unknown.

Gonopore small, circular, set within shallow tubercle in FA1.

Hydropore oval or slit-like, in slight tubercle across PO1:PO6 suture.

Attachment direct, by small, gradually tapering attachment area; adults probably not attached. Aboral process distinct in *Holocystites* (*Megacystites* n. sgen.) *abnormis*, not well marked from theca in *H.* (*M.* n. sgen.) *greenvillensis*.

Remarks.-Osgood specimens with smooth plates can be ascribed to two groups: one (containing only Holocystites spangleri) has impressed sutures, a distinctly pyriform shape with large, flat attachment area, short aboral process, and irregular plate arrangement with plates of two generations. More importantly, this taxon has sunken humatipores with numerous tangential canals arrayed collectively more or less around a hemisphere (Text-fig. 20B; Pl. 8, Fig. 6). Holocystites abnormis has a cylindrical theca with secondaries developed only aborally, a small attachment area at the base of a gradually tapering aboral projection, and, most significantly, sunken humatipores with tangential canals just beneath and tangential to the outer plate surface, as in most other holocystitids, but not in Holocystites s. s. The difference in humatipore morphology is to us sufficient to warrant separate subgenera for the sunken "flat" and sunken "three-dimensional" species groups. Based on material additional to that available to Paul (1971), we also regard H. greenvillensis as a species of Megacystites n. sgen. Further discussion of the relationships of H. spangleri, H. abnormis, and H. greenvillensis is deferred to the individual specific descriptions. Because H. greenvillensis is known mostly from internal molds, details of the subgenus are based largely on H. abnormis.

Holocystites (Megacystites n. sgen.) abnormis Hall, 1864

Holocystites abnormis Hall, 1864: 8; 1868: 312; 1870: 355; Chamberlin, 1883: 191; Foerste, 1917: 233; 1920a: 207-208; 1920b: 79; Bassler & Moodey, 1943: 50, 167; Paul, 1971: 89-92.

Holocystites canneus Miller, 1889: 253; Bassler & Moodey, 1943: 43, 168.

Diagnosis.—Holocystites (Megacystites n. sgen.) with cylindrical theca; smooth, flat plates of two generations, with secondaries developed only aborally and without impressed sutures; adoral pole rounded; aboral pole prolonged into distinct aboral projection with small (1/3-1/2 thecal diameter) attachment area.

Occurrence.—Silurian (Wenlockian); Racine Dolomite and Manistique Formation, Wisconsin; Upper Shales and Middle Osgood Limestone, Osgood Member, Salamonie Dolomite, Indiana; basal meter of Laurel Member, Salamonie Dolomite, Indiana.

Material.—Approximately 20 specimens. Lectotype AMNH 2016a, paralectotype AMNH 2016b. Additional specimens AMNH, FMNH, SUI, UMMP, and private collections.

Description.-See Paul, 1971: 92.

Remarks.—Additional material has basically served to confirm Paul's description. Specimens that we have examined always have two plate generations, with the secondaries found only on the aboral portion of the theca and then in incomplete circlets. The small number of tangential canals (4-8, commonly 4) does seem to typify the species, as does the essentially planar tangential canal morphology. The lectotypes are internal molds, but the thecal morphology is distinctive and can be confirmed and detailed readily from Osgood specimens. Like other cylindrical Osgood Holocystites species, a number of specimens show offset peristomes and appear to have fallen over late in life; one such collected in place by the authors had the peristome oriented uppermost. Very likely the species lived in the same manner as H. (H.) cylindricus, but very few specimens have been seen which retain the whole aboral process.

The unusual (for the genus) plate and humatipore morphology recall *Pentacystis* and *Osgoodicystis* n. gen., but these taxa do not offset the peristome and have large attachment areas. We suspect that *Holocystites* (*Megacystites* n. sgen.) *abnormis* was not attached as an adult, unlike members of the other two mentioned genera. As noted by Paul (1971: 92), the only form with which this species could be confused is *H. spangleri*, but the addition of new Osgood material has not blurred the distinctions between the two forms; on the contrary, differences noted by Paul (1971) are quite constant.

The species is of uncommon but persistent occurrence in the Upper Shales at Napoleon. Material that we collected was found in areas with little skeletal debris and no biohermal development. One specimen was also found in the lowermost meter of the Laurel at Napoleon, and at least two internal molds from the Manistique Formation of Wisconsin (FMNH UC 3380) are very likely *Holocystites* (*Megacystites* n. sgen.) *abnormis*.

Holocystites (Megacystites n. sgen.) greenvillensis Foerste, 1917 Text-fig. 43; Pl. 7

Holocystites greenvillensis Foerste, 1917: 203; Chauvel, 1941: 126; Bassler & Moodey, 1943: 49, 169; Busch, 1943: 106; Larocque & Marple, 1958: 72; Regnéll, 1960: 776; Paul, 1971: 101-102

Diagnosis.—Holocystites (Megacystites n. sgen.) with spindle-shaped theca (tapering at both ends), smooth, tumid plates of one generation, indistinct aboral projection with small attachment area.

Occurrence.—Upper Silurian (Wenlockian); Cedarville Dolomite and Huntington Dolomite, Ohio.

Material.—Approximately 20 specimens, mostly internal molds. Lectotype USNM 87075b; paralectotype USNM 87075a, c; illustrated specimens SUI 42732, 48192-48195. Other specimens: OSU, SUI, USNM.

Description.—Theca cylindrical, but tapering equally and gradually at both ends to give spindle shape (Pl. 7, Figs 9-10).

Plates of one generation in most (?all) examples, arranged in five (small specimens) to nine (largest) circlets of eight elongate hexagonal plates each. Exterior surface of plates smooth, shallowly tumid, without impressed sutures (Pl. 7, Figs 9-10).

Humatipores poorly preserved on existing material, on all plates, apparently with flat tangential canals.

Peristome centered at oral pole, apparently narrow (details obscure). Ambulacral facets five; six periorals and eight facetals, as in other *Holocystites* species.

Periproct located in position typical for genus, pentagonal (Pl. 7, Fig. 7). Anus rounded, 4-5 mm in diameter; anals unknown.

Gonopore on FA1 in SUI 48195; details not preserved.

Hydropore apparently on PO1:PO6 suture; detailed morphology unknown.

Attachment direct, by small attachment area less than ½ maximum thecal diameter on SUI 42732 (Pl. 7, Figs 9-10), a medium-sized specimen.

Remarks.—Enough specimens are now known to validate Foerste's species as distinct. The unusual thecal shape is consistent, as is the number of plate generations. In a few large specimens, aboralmost plates remain quite small, but because this is a feature of several holocystitid taxa, they are regarded as primaries. As is evident from the preceding, the species description remains incomplete; only a portion of an external mold (SUI 4273IE), showing a few smooth plates is yet known and some critical details of the peristome in particular are poorly preserved.

Ascription to *Megacystites* n. sgen. rather than *Sepulticystis* n. sgen. is based on partial and indirect evidence, because the tangential canals are not preserved on the only known external mold. The thecal plates are thin compared to those of *Holocystites* (*S.*) *spangleri* and infillings of the perpendicular canals on some internal molds are long enough to extend nearly through the plates. It is thus unlikely that enough space remains for branching into a three-dimensional array of tangential canals, as in the latter species.

Precise age of the cystoid-bearing Ohio dolomite localities is not presently known, as the Ohio Silurian section requires further detailed study. Most reasonably well-documented specimens are from the Cedarville Dolomite, but Busch (1943: 107) recorded the species from a quarry near Rockford, Ohio. According to Pinsak & Shaver (1964: 33), the strata in this quarry are equivalent to the Louisville Limestone in Indiana and thus could represent the Huntington Dolomite (Paul, 1971: 101, 165).

Subgenus *Sepulticystis* Frest & Strimple, n. sgen. Text-fig. 26; Pl. 8

Type species.–Holocystites spangleri Miller, 1891, by original designation herein.

Diagnosis.—A subgenus of *Holocystites* with pyriform theca, smooth plates, tangential canals arrayed in three dimensions, and moderate attachment area.

Range.—Upper Silurian (Wenlockian), North America (Wisconsin, Illinois, and Indiana).

Description.—Theca pyriform to pyriform-cylindrical, with short aboral projection.

Plates of two generations, irregularly arranged; externally smooth, with impressed sutures.

Humatipores on all thecal plates with 9-12 arcuate tangential canals; central members nearest plate surface, peripheral members more deeply buried and longer.

Peristome pentagonal, large, not protrusive; peristomial border broad, pitted with many oral pores. Peristomial opening oval, surrounded by six prominent periorals, then eight facetals. Ambulacral facets five, slightly concave, circular, largely developed equally on periorals and facetals.

Periproct pentagonal, with broad border around circular anal opening.

Gonopore small, circular, within distinct tubercle, normally on FA1.

Hydropore slit-like, within elevated ridge across PO1:PO6

Attachment direct, by large flat basal disc at terminus of short aboral projection.

Remarks.—The unique humatipore morphology of *Sepulticystis* n. sgen. can be seen on all three Osgood specimens, but is especially obvious on SUI 48197. Internal molds are easy to identify because of the type species' unusual thecal shape and plate arrangement. The subgenus is monotypic.

Holocystites (Sepulticystis n. sgen.) spangleri Miller, 1891 Text-fig. 26; Pl. 8

Holocystites spangleri Miller, 1891: 16; 1892a: 626; Bassler & Moodey, 1943: 44, 170; Paul, 1971: 93-94.

Diagnosis.-As for subgenus.

Occurrence.—Racine Dolomite, Wisconsin and Illinois; lower limestone unit (c) of Middle Osgood limestone (Text-fig. 9), Osgood Member, Salamonie Dolomite, Indiana.

Material.—Three complete thecae, seven internal molds. Holotype FMNH 6008; illustrated specimen (Pl. 8) SUI 48197; other specimens at FMNH.

Description.—Theca large (to at least 11 cm high), pyriform-cylindrical in small specimens (*e.g.*, holotype, Paul, 1971: fig. 35), pyriform in large examples (SUI 48197) and several internal molds.

Plates of two generations, thick (to 3 mm) with especially variable-sized secondaries disrupting basic regular pattern of primaries (eight per circlet). Total number of circlets exceedes 16. Outer plate surfaces smooth, sutures slightly impressed (Pl. 8, Figs 1-5).

Humatipores densely packed with 8-12 (generally 10) radially-arranged canals delineating a hemiellipsoid or hemisphere between two perpendicular canals (Pl. 8, Fig. 6; Paul, 1971: fig. 35b).

Peristome, periproct, gonopore, hydropore: see Paul (1971: 94).

Attachment direct, by moderate-sized flat basal disk approximately 1/3 greatest thecal diameter in SUI 48197.

Remarks.-The provenance of two of the four Osgood specimens is known. Apparently the species is restricted in the Osgood to the so-called Lower limestone Band (Foerste, 1897: 257), i.e., Zone Id [Sepulticystis subzone; see Text-fig. 10, along Big Creek (localities 74-76 of Foerste, 1897; 3-5 of Paul, 1971; see Frest *et al.*, 1977: 88-91 and Appendix for details)]. Paul (1971: 94) noted that the holotype of Holocystites plenus could be conspecific with H. spangleri. As discussed previously, this is unlikely, but if it proves to be the case, the former name takes precedence should the type specimen be located. SUI 48197 is definitely attributed to H. (S.) spangleri even though it is probably an abnormal specimen. As indicated diagrammatically in Text-fig. 26 (see also Pl. 8, Figs 2, 5), the peristomial opening is surrounded by eight (instead of six), irregularly sized and shaped periorals, and the gonopore is in FA2. Because all other peristomial and thecal features are the same as those of the holotype, the specimen is unquestionably H. (S.) spangleri.

Subfamily **TREMATOCYSTINAE**

Frest & Strimple, n. sfam.

Diagnosis.—Holocystitidae with globular to pyriform theca; plates of one generation, in up to ten circlets, usually with numerous plates in each; humatipores with flat tangential canals; 6 small POO; 6-8 FAA; 4 ambulacral facets on facetals or on facetals and lower thecal plates; gonopore on FA1 or FA2; hydropore on PO1:PO6 suture; attachment direct, by medium to large attachment area; aboral projection small or absent.

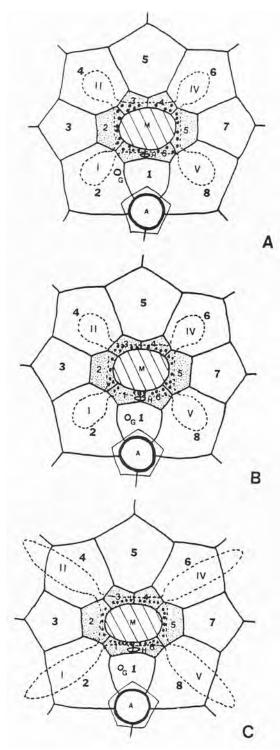
Range.-Upper Silurian (Wenlockian), North America (Indiana).

Included genera.—Trematocystis Jaekel, 1899; Paulicystis n. gen.; Pustulocystis Paul, 1971.

Remarks.—The Trematocystinae are among the most abundant diploporites in the Osgood, but the subfamily is entirely endemic to the Osgood Member, and then only in the southeastern Indiana outcrop area, unlike the Aristocystitidae and Holocystitinae. This is most likely due to limited ecological tolerance, as argued earlier; all Trematocystinae appear to have been attached throughout life, and all are rather small for the *Holocystites* fauna as a whole, *i.e.*, less than 50 mm in width and height. The subfamily shows a narrower range of variation in several features (thecal shape, size of aboral process, thecal plate generations) than do the Holocystitinae, or even the Pentacystinae (Text-figs 13-14).

Even within the Osgood, the Trematocystinae are remarkably uneven in distribution. *Trematocystis* is represented by two common species in Zone 2 (Lower Shales *Trematocystis* Zone; Text-fig. 10) confined mostly to a single six-inch silt-stone bed ("main cystoid layer" of Foerste, 1897; Text-fig. 9). One other species is of rare occurrence in the Upper Shales, and *Paulicystis* n. gen. is common in the same unit (lower half of Zone 1b (Pentacystinid subzone; Text-fig. 10) at Napoleon. The type species of *Pustulocystis* is common in Zone 2, and it and *Trematocystis globosus* and *T. rotundus* constitute the entire known diploporite fauna of this zone (*Trematocystis* Zone). In the Upper Shales, the Trematocystinae are a subordinate component (in terms of both abundance and diversity) of a large and varied, holocystitinid-dominated fauna (Table 3).

All known Trematocystinae, with the exception of *Pustulocystis pentax*, have just four ambulacral facets (ambulacrum III is not developed), and small periorals pitted with a moderate number of oral pores (Text-fig. 44). Generally, they have small, globular thecae and a moderate number of thecal plates of a single generation, with both plates and plate circlets moderately numerous. Despite narrow but definite stratigraphic separation of their diversity/abundance acmes, *Trematocystis*



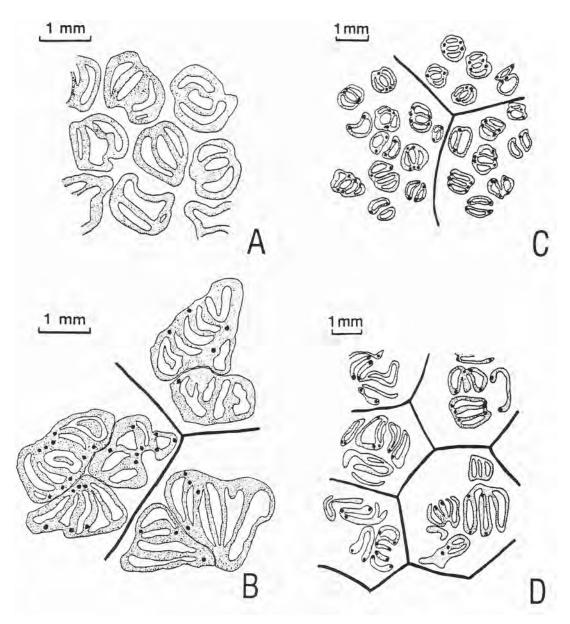
Text-fig. 44. Diagrammatic representations of oro-anal areas of members of Trematocystinae. (A) Arrangement in *Trematocystis globosus*; 4 facets of Trematocystinae, facets on facetals only, gonopore on FA2. (B) Arrangement typical of *T. rotundus*, *T. wetherbyi*, and *T. magniporatus* n. sp.; as in *T. globosus*, but gonopore on FA1. (C) Arrangement in *Paulicystis* n. gen.; 4 elongate facets overrunning facetals, gonopore on FA1. Symbols as outlined under Abbreviations, p. 52; black dots are oral pores.

and *Paulicystis* n. gen. are more closely related than either is to *Pustulocystis*. The last genus has sursumate humatipores resembling those of *Holocystites* (s. s.), but containing only two to four tangential canals that are *not* radially arranged (Paul, 1971: 132). The other two trematocystinid genera have flat, radially arranged canals (Table 9). Ambulacral facets of *Pustulocystis* are circular to slightly oval, again like those of the Holocystinitinae, whereas *Trematocystis* and *Paulicystis* n. gen. have distinctly (or in the case of the latter, exaggerated) elliptical facets. All three genera tend to have definite median ridges dividing the ambulacral facets, although existing evidence as a whole supports the evolution of *Pustulocystis* from *Trematocystis* (necessitating independent evolution of sursummate humatipores); separate evolution from holocystitinid predecessors is also possible.

At present, approximately eight species are here regarded as definite Trematocystinae. One other, *Pustulocystis* sp. Paul, 1971, is included in the following key, but might represent a distinct genus; only one, poorly preserved specimen has yet been found, however (Paul, 1971: 141-142, fig. 61).

KEY TO THE SPECIES OF TREMATOCYSTINAE

1. Humatipores flat, 8 FAA
2. 5 ambulacral facets
3. Globular theca
4. Tumid plates in incomplete and complete circlets, facets overrunning FAA genus <i>Paulicystis</i> n. gen 5 Smooth plates in complete circlets, facets on facetals genus <i>Trematocystis</i> 6
5. Humatipores small, sparsely packed with regular outlines
6. Gonopore in FA2
7. Plates in circlets of 15-16 plates <i>T. wetherbyi</i> Plates in circlets of 12 or less plates 8
8. Humatipores large, very densely packed



Text-fig. 45. Camera lucida drawings of humatipores in members of Trematocystinae. (A) Trematocystis globosus, AMNH 2156b; redrawn from Paul (1971: fig. 51A). The humatipores of T. rotundus are very similar. (B) T. magniporatus n. sp., holotype SUI 48198. (C) Paulicystis sparsus n. gen., n. sp., holotype SUI 48164. (D) P. densus n. gen., n. sp., paratype SUI 46310. Tangential canals with dot stipple, pores (openings of perpendicular canals) black; plate sutures indicated by heavy black lines.

Genus *Trematocystis* Jaekel, 1899 Text-figs 44A-B, 45A-B; Pl. 5, Figs 1-3; Pl. 9

Trematocystis Jaekel, 1899: 413: Kesling, 1963a: 115; 1968: S258; Paul, 1971: 115-120.

Type species.—Holocystites subglobosus Miller, 1889 (H. globosus Miller, 1878), by original designation (Jaekel, 1899: 413).

Diagnosis.—Trematocystinae with globular theca, smooth plates of one generation, flat humatipores, peristome with six periorals, eight facetals, and four ambulacral facets, large attachment area and short aboral process.

Range.-Upper Silurian (Wenlockian), North America (Indiana).

Description.—Theca generally globular to inverted pyriform; small for the fauna (usually 5 cm or less in diameter).

Plates of one generation, generally smooth, with sutures impressed slightly or not at all, arranged in several circlets of 16 or fewer plates; total number of thecal plates generally small, often less than 70.

Humatipores with tangential canals on a single plane just beneath plate surface, small to moderate in number (2-7), equally developed on all thecal plates.

Peristome quadrangular; four elliptical, slightly raised am-

bulacral facets with median ridge developed on facetals 2, 4, 6, and 8, representing ambulacra I, II, IV, and V respectively; periorals moderate in size, often slightly protrusive; peristomial border pitted by moderate number of oral pores; peristome roofed by six palatals in *Trematocystis globosus* (see Paul, 1971: fig. 50c).

Periproct pentagonal or hexagonal, with wide deeply indented border for insertion of anals (five in *Trematocystis globosus*; Paul, 1971: fig. 50c).

Gonopore round, in prominent elevated tubercle, either in FA1 (three species) or FA2 (*T. globosus*).

Hydropore oval or slit-like, in elongate tubercle across POl:P06 suture.

Remarks.—Paul (1971: 117-118) resuscitated Jaekel's (1899) genus under a restricted definition and transferred it to the Holocystitidae; most previous authors (e.g., Jaekel, 1899; Kesling, 1963a, 1968) had regarded it as an aristocystitid. The name Trematocystidae had been suggested previously as a family name (Paul, in Jefferies et al., 1967: 566) but because the name was not then or subsequently defined, it is not accepted here as an available name.

Trematocystis species are currently defined on relatively minor characters [e.g., position of the gonopore (Text-figs 44A-B), size and number of humatipore canals (Text-figs 45A-B)], but because a comparatively large number of specimens are now known (ca. 120), we feel that enough is known of the range of variation in the genus to constitute a good case for the validity of the chosen criteria. Variation in Trematocystis seems limited to the number of plates per circlet (generally 8 in T. globosus and T. rotundus, but varying from 7?-12; to 16 in T. wetherbyi), and some details of peristomial plate arrangement. Paul (1971: figs 54B, C) illustrated two atypical examples of T. rotundus with double FA1, and one of T. globosus with a double gonopore (Paul, 1971: fig. 50B).

Trematocystis globosus (Miller, 1878) Text-figs 44A, 45A

Holocystites globosus Miller, 1878: 133; ?Parks, 1913: 132; Bassler & Moodey, 1943: 44, 169.

Holocystites scitulus Miller, 1891: 14; 1892a: 624; 1897: 747; Bassler & Moodey, 1943: 44-170.

Holocystites subglobosus Miller, 1889: 255; Bassler & Moodey, 1943: 44, 170.

Megacystis subglobosus. Müller, 1963: 287.

Trematocystis globosus. Paul, 1971: 120-124.

Trematocystis hammelli Jaekel, 1899: 409.

Trematocystis subglobosus. Jaekel, 1899: 414; Kesling, 1968: S251.

Diagnosis.—A species of *Trematocystis* with gonopore in FA2; humatipores with 3-7 (usually 4) tangential canals, 1.1-

1.4 mm long, moderately packed and with more or less regular outlines; 8-14 plates per circlet.

Occurrence.—"Main cystoid layer" (Foerste, 1897), Trematocystis Zone, Osgood Member, Salamonie Dolomite, Jefferson and Ripley counties, Indiana.

Material.—At least 60 complete thecae, AMNH, BMNH, FMNH, SUI, UC, UMMP, USNM.

Description.-See Paul, 1971: 123-124.

Remarks.—As noted by Paul (1971: 124), the main distinguishing feature between *Trematocystis globosus* and *T. rotundus* is the position of the gonopore, but the former also generally has a few more thecal plates if specimens of the same size are compared.

Trematocystis rotundus (Miller, 1879) Text-fig. 44B; Pl. 9, Fig. 7

Holocystites gorbyi Miller, 1891: 14; 1892a: 624; Bassler & Moodey, 1943: 44, 168.

Holocystites commodus Miller, 1891: 14; 1829a: 624; Bassler & Moodey, 1943: 44, 168.

Holocystites indianensis Miller, 1891: 15; 1892a: 625; Bassler & Moodey, 1943: 44, 169.

Holocystites parvus Miller, 1891: 16; 1892a: 626; Bassler & Moodey, 1943: 44, 169.

Holocystites papulosus Rowley, 1903 (non Miller, 1891): 166.

Holocystites rotundus Miller, 1879: 107; Bassler & Moodey, 1943: 44, 170.

Holocystites turbinatus Miller, 1880: 259; 1889: 255; Bassler & Moodey, 1943: 44, 171.

Trematocystis rotundus. Paul, 1971: 126-129.

Diagnosis.—A species of *Trematocystis* with gonopore in FA1, no more than 12 plates per circlet; humatipores as in *T. globusus*.

Occurrence.—As for type species (Trematocystis globosus).

Material.—At least 60 specimens, AMNH, BMNH, FMNH, MCZ, ROM, SUI, UC, USNM.

Description.-See Paul, 1971: 127-129.

Remarks.—This species is equally as abundant as Tremato-cystis globosus, with which it occurs.

Trematocystis wetherbyi Miller, 1878

Holocystites wetherbyi Miller, 1878: 131; Bassler & Moodey, 1943: 44, 171.

Trematocystis wetherbyi. Paul, 1971: 129-131.

Diagnosis.—A species of *Trematocystis* with gonopore in FA1; up to 16 plates per circlet; humatipores moderately densely packed, with 3-6 tangential canals, 0.8-1.1 mm long, often elliptical in outline.

Occurrence.—Osgood Member, Salamonie Dolomite; Osgood, Ripley County, Indiana; precise horizon unknown.

Material.-A single specimen, holotype FMNH 6005.

Description.-See Paul, 1971: 129-131.

Remarks.—Although based on a single specimen, the larger average number of plates and elliptical, small humatipores are distinct, and we concur with Paul (1971: 131) in accepting this as a valid species. No additional specimens turned up at Napoleon or at other sites we collected.

Trematocystis magniporatus Frest & Strimple, n. sp. Text-fig. 45B; Pl. 5, Figs 1-3; Pl. 9, Figs 1-6, 8-9

Derivation of name.—Combining Latin magnus (great, large) with porus (pored, pore-bearing), in reference to humatipore size.

Diagnosis.—A species of *Trematocystis* with gonopore in FA1; 8 plates per circlet; humatipores densely packed, with 4-9 (usually 5) tangential canals, diameter 1.3-2.0 mm, with irregular outlines.

Occurrence.—Upper Shales (Zone 1b, Text-fig. 10), Osgood Member, Salamonie Dolomite: the holotype is from Big Creek (see Frest *et al.*, 1977: 88-91, and Appendix for precise locality) and the paratype from Napoleon.

Material.–2 specimens, holotype SUI 48198, paratype SUI 48171.

Description.—Theca compressed pyriform to subglobose, slightly wider than high.

Plates of one generation, generally 8 per circlet, smooth and without impressed sutures, and with prominent humatipores. Plates arranged in 5-6 circlets of nearly equidimensional, hexagonal elements (Pl. 5, Figs 1-2; Pl. 9, Figs 2-5).

Humatipores buried, densely packed, with 5-9 tangential canals each (often 5 or more): outlines irregular, maximum

length to 2.0 mm or more, minimum 1.3 mm (Pl. 9, Figs 8-9).

Peristome quadrangular, with oval peristomial opening 5 mm across; peristomial border narrow, pitted with oral pores, generally 4-6 per perioral. Periorals small, slightly protuberant; ambulacral facets elliptical, each developed on a single facetal, four in number, dimensions *ca.* 4.5-5.0 mm length and 2.0-2.5 mm maximum width, distinctly elevated above thecal surface, with slight rim, but slightly concave in centers, with median ridge (Pl. 5, Fig. 3; Pl. 9, Fig. 1). Palatals unknown.

Periproct pentagonal, *ca.* 3 mm in diameter, with very narrow periproctal border around rounded anal opening *ca.* 2.8 mm in diameter; anals unknown.

Gonopore small, circular, 0.3 mm in diameter on left side of FA1; not on tubercle in holotype SUI 48198, but this is probably preservational.

Hydropore slit-like, dumbbell-shaped on eroded holotype, raised into elongate tubercle on paratype SUI 48171 (compare Pl. 5, Fig. 3 with Pl. 9, Fig. 1), *ca.* 1.5 mm long.

Attachment direct, by large, flat attachment area one-half maximum thecal diameter; no aboral projection.

Remarks.—Aside from previously noted differences, the comparatively thin, flat plates without impressed sutures could prove a constant and significant character if more specimens are found. Most specimens of other *Trematocystis* species have thicker, slightly tumid plates with barely impressed sutures. The paratype lacks a gonopore, a condition noted occasionally on specimens of both *T. globosus* and *T. rotundus* (see Paul, 1971: 29); one specimen of *T. globosus* has a double gonopore (Paul, 1971: 124). Apparently, gonopore development in the genus is sufficiently variable that its absence in an occasional specimen might not be significant.

Genus *Paulicystis* Frest & Strimple, n. gen. Text-figs 44C, 45C-D; Pl. 4, Fig. 2; Pls 10-11

Derivation of name.—The generic name honors C. R. C. Paul, University of Liverpool.

Type species.–Paulicystis densus n. gen., n. sp., by original designation herein.

Diagnosis.—A genus of Trematocystinae with globular theca; tumid plates with impressed sutures, of one generation disposed in numerous, sometimes incomplete circlets of 20 or more plates per circlet; gonopore in FA1, facets large, irregularly elongate, elliptical, overrunning onto next one or two thecal circlets; attachment area very large, three-quarters or more of maximum thecal diameter, its plates fused.

Range.-Upper Silurian (early Wenlockian), North America (Indiana).

Description.—Theca generally globular to squat pyriform, seldom over 50 mm in height, generally slightly higher than wide.

Plates tumid, with distinctly impressed sutures and granular ornament, disposed in numerous circlets, some incomplete aborally, of one generation and with 20 or more plates per circlet. Thecal plate shape irregularly polygonal, plates often wider than high, grading regularly in size from smallest aborally to larger adorally.

Peristome quadrilateral around oval central opening, which is surrounded by 6 periorals and then 8 facetals. Peristomial border narrow, pitted by moderate number of oral pores, peristome slightly elevated. Ambulacral facets 4 (Ambulacra I, II, IV, and V present), much longer than wide, developed on facetals 2, 4, 6, and 8, but then overrunning these plates onto one or (usually) two lower plate circlets. Median ridges well developed; transverse ridges at regular intervals dividing facet into barely concave quadrilateral areas. Facets irregularly elliptical, distal portions wandering irregularly over thecal plates. Facets strongly concave, surrounded by slight rim and elevated above thecal plates. Palatals unknown.

Periproct pentagonal, with narrow border around rounded anal opening; anals unknown.

Gonopore on rounded, barely developed tubercle on FA1; a small, circular opening *ca.* 0.5 mm in diameter.

Hydropore slit-like, on prominent elevated elongate tubercle across PO1:PO6 suture.

Attachment direct, by large generally flat attachment area just under maximum thecal diameter, offset from main thecal axis. Plates of basal disc fused, outflaring slightly from preceding thecal plate circlet.

Remarks.—The very numerous tumid thecal plates, very large attachment area, and bizarre, elongate ambulacral facets differentiate this genus from *Trematocystis*. Paulicystis n. gen. is a fairly common diploporite in the Upper Shales at Napoleon, definitely associated with bioherms or with skeletal debris patches, and clearly attached throughout life. The thecal shape, like that of *Trematocystis*, is consistent for the genus (Text-fig. 13), and recalls that of *Sphaeronites* (Peritaphos) sp. B of Paul (1973: fig. 21).

Two species are presently distinguished on details of humatipore morphology. Most specimens examined are *Paulicystis densus* n. gen., n. sp.; all of the rest, except two, are here referred definitely to *P. sparsus* n. gen., n. sp. The other two partial thecae (SUI 46327) with only 5 or 6 plate circlets and large (to 9.0 mm) plates are tentatively placed in *P. sparsus* n. gen., n. sp., but could well constitute a third species. The critical peristo-

mial area, however, is incompletely preserved on both.

Paulicystis densus Frest & Strimple, n. sp. Text-fig. 45D; Pl. 10, Figs 1-7, 9-10

Derivation of name.—The specific epithet refers to the humatipore distribution.

Diagnosis.—A species of *Paulicystis* n. gen. with densely-packed, large humatipores with irregular outlines and from 3-8 (usually 5) deeply buried tangential canals.

Occurrence.—Upper Shales (Zone 1b, Text-fig. 10), Osgood Member, Salamonie Dolomite, Napoleon Quarry, Ripley County, Indiana.

Material.—At least 30 specimens: holotype SUI 46311; figured paratypes SUI 46310, 46312, 46315; unfigured paratypes SUI 46324, 46325. Other specimens: OU 4846, private collections.

Description.—Theca globular, maximum diameter (SUI 46315) *ca.* 40 mm; usually asymmetrical, with attachment area offset to one side (Pl. 10, Fig. 3).

Plates tumid, with impressed sutures, irregularly polygonal, all densely covered with humatipores; slightly granular surface on best-preserved specimens. Plates disposed in 8-12 circlets of from 20-35 plates; some circlets incomplete aborally; these developed on longest side of theca (Pl. 10, Figs 3-4); plate circlets increasing in size adorally, apparently not increasing in number during ontogeny.

Humatipores densely packed, distributed equally over theca, well developed except on basal attachment disc (Pl. 10, Fig. 9), irregular in shape, 0.8-1.6 mm in diameter. Tangential canals 4-8, usually 5 or more, deeply incised into theca, giving incomplete appearance except on deeply weathered specimens (Pl. 10, Fig. 10).

Peristome quadrangular; 6 elevated periorals around oval peristomial opening *ca.* 4-5 mm in diameter, with narrow border, pitted with oral pores, often arranged in linear fashion around periphery. Ambulacral facets 4; morphology as described under genus.

Periproct pentagonal, as described above.

Gonopore and hydropore as for genus above.

Attachment direct, by large, often flat attachment area at least two-thirds of maximum thecal diameter (SUI 46315; Pl. 10, Fig. 9), but generally three-quarters or more, (*e.g.*, SUI 46311; Pl. 10, Fig. 5).

Remarks.—This species closely resembles *Paulicystis sparsus* n. gen., n. sp. except for humatipore morphology. On average,

thecal plates are smaller and more numerous in this form, but the small number of specimens of *P. sparsus* n. gen., n. sp. that are now available could mean that these features are not constant. Maximum humatipore size varies little on material that we have seen.

Most specimens show the impression of the fossil or object to which they were attached, but some (e.g., SUI 46315; Pl. 10, Fig. 9) have exposed very lengthy (to 15 mm) perpendicular canals. Retention of such canals on a cystoid attachment surface could support Paul's (1988) contention that such surfaces were covered by epidermis, and hence that attachment was not necessarily extremely solid. We have collected crinoid root systems that expose canals (not part of a thecal pore system, but more likely offshoots of the axial canal system) in parts of the Waldron. However, some of these were still firmly attached to a hardground surface (the discontinuity locally present at the top of the Laurel Member). It is difficult to imagine how such canals in diploporites could remain functional if a part of the respiratory system; perhaps they served another purpose in this case.

The presence of incomplete plate circlets in this species is interesting. Because we suspect that both *Paulicystis* species were fixed as adults, the most probable interpretation of the extra plates was that they serve to orient the peristome directly upward. Such plates are always added only on the longest lateral side. As far as we are aware, this phenomenon has not been reported definitely from other diploporites, but it is probably common. It is readily detectable in this species because the plate circlets are normally regular in number and disposition. We have not noted it in curved thecae of *Holocystites*, which simply elongates some plates in particular circlets preferentially on one side to achieve the same result.

Paulicystis sparsus Frest & Strimple, n. sp. Text-fig. 45C; Pl. 10, Fig. 8; Pl. 11

Diagnosis.—A species of *Paulicystis* n. gen. with moderately packed, small humatipores with regular outlines and from 2-7 (usually 4) shallowly buried tangential canals.

Occurrence.—Upper Shales (Zone 1b; Text-fig. 10), Osgood Member, Salamonie Dolomite, Napoleon Quarry, Ripley County, Indiana.

Material.—At least 6 specimens: holotype SUI 48164; illustrated paratype SUI 46314; unfigured paratype SUI 46326. Other specimens: SUI 46327, private collections.

Description.—Theca globular to stout pyriform, maximum observed diameter (SUI 46326) ca. 30 mm; theca generally asymmetrical, with basal attachment disc generally not normal

to aboral-oral axis (Pl. 11, Figs 3-5).

Plates tumid, irregularly polygonal, all except fused basal-most circlet with evenly distributed humatipores. Sutures impressed, fine granulose prosopon evenly developed over outer surfaces (Pl. 11, Fig. 11). Plates disposed in 8-12 circlets of from 20-30 plates; more (incomplete) circlets sometimes found on longest side of theca (compare Pl. 11, Figs 2, 5); number of complete circlets constant through known ontogeny. Plates increasing in size evenly from bottom to top of theca, often wider than high; maximum size to 9.0 mm.

Humatipores moderately packed, distributed over theca except on basal disc, regular in shape (nearly circular to slightly oval in outline), 0.5-0.9 mm in diameter. Tangential canals shallowly buried, 3-7 in number (most often 4), with canals radially arranged (Pl. 11, Fig. 11).

Peristome 4-sided, elevated above general thecal level (Pl. 11, Figs 1-2); peristome with wide border pitted with oral pores around elongate, oval peristomial opening. Facet morphology and distribution as noted for genus.

Periproct rounded pentagonal, with extremely narrow border for insertion of anals, diameter *ca.* 4-5 mm; diameter of circular anal opening only slightly less.

Gonopore round, *ca.* 0.3 mm in diameter, not at all or only slightly elevated.

Hydropore slit-like, morphology as for genus, on prominently elevated tubercle across PO1:PO6 suture in SUI 46314.

Attachment direct. Attachment area formed by fusion of lowermost thecal plates, which do not bear pores; diameter three-quarters or more of maximum thecal diameter. Base outflaring slightly aborally.

Remarks.-This species is much less common than the preceeding one, with which it occurs at Napoleon. As mentioned above, some minor features (not used in the diagnosis) which seem to distinguish this form from Paulicystis densus n. gen., n. sp. might be small-sample artifacts; another that might be cited is the seeming absence of humatipores from the base of this species, but not in *P. densus* n. gen., n. sp. Most specimens have from 8-12 thecal plate circlets, but two with only 5 or 6 have sparse irregular humatipores with fewer canals and are accepted only provisionally as P. sparsus n. gen., n. sp. With these specimens (by no means the largest) excluded, maximum plate size is ca. 7.0 mm. The slightly outflaring, solidly fused base of this and the preceding species resembles that described for Tholocystis kolihai Chauvel, 1980. As with P. densus n. gen., n. sp., the incomplete plate circlets occur only on the longest lateral side of the theca.

Genus *Pustulocystis* Paul, 1971 Text-figs 28-29

Pustulocystis Paul, 1971: 131.

Type species.–Holocystites ornatissimus Miller, 1891, by original designation.

Diagnosis.—A genus of Trematocystinae with pyriform theca; granular plates of one generation; raised (sursummate) humatipores; peristome with 6 periorals and 6 facetals; 4 or 5 ambulacral facets; small attachment area and short aboral process.

Range.-Upper Silurian (Wenlockian), North America (Indiana, Tennessee).

Description.—Theca generally pyriform to fusiform, of small to moderate size for the fauna (to 4 cm diameter).

Plates of one generation, generally with fine granular ornament and coarser pustular humatipores, often with impressed sutures. Arranged in several circlets of 20 or fewer plates; total number of thecal plates moderate, between 70 and 100.

Humatipores with tangential canals arrayed three-dimensionally but not radially, small to moderate in number (2-4, usually 4), equally developed on all thecal plates. Humatipores sursummate, raised into prominent tubercles, larger than those of *Holocystites*.

Peristome quadrangular in *Pustulocystis ornatissimus*, pentangular in *P. pentax*. Ambulacral facets prominent, planar, variable in shape, circular to oval, with distinct median ridge; developed on facetals 2, 4, 6, and 8 (ambulacra I, II, IV, V) in *P. ornatissimus*, also on facetal 5 (ambulacrum III) in *P. pentax*. Peristome slightly protrusive, with border distinct, pitted by oral pores. Periorals moderate in size.

Periproct pentagonal or quadrangular, with narrow border.

Gonopore round, very variable in position, but usually on low tubercle across suture and commonly on various combinations of PO1, FA1, and FA2.

Hydropore slit-like, on elongate tubercle across suture PO1:PO6.

Attachment direct throughout life, by small aboral process that gives theca a pyriform appearance. Attachment area medium-sized.

Remarks.—Placement of this genus in the Trematocystinae is based on several lines of reasoning. The single plate generation, with number of plates per circlet relatively high, could suggest either pentacystinid or trematocystinid affinities, but not holocystitinid. Thecal shape, periorals reduced in number and size (but persistent), reduced facetals, a comparatively small

aboral process, and direct attachment all suggest genera such as *Trematocystis*. The number of ambulacral facets (four) in the type species (*Pustulocystis ornatissimus*), the only taxon known from a sizeable number of specimens, also indicates trematocystinid affinities. However, it must be noted that one species, *P. pentax*, does possess five. It is unfortunate that this taxon is known from a single specimen; possibly, the specimen is abnormal, or better assigned to another new genus or subgenus. For the present, however, it is assumed that five facets is a normal feature of the species, but it is retained in *Pustulocystis*.

The sursummate humatipores of the genus are not a feature of any other trematocystinid, and recall those of *Holocystites*. This, plus the five-facet condition of *Pustulocystis pentax*, could suggest that the genus is in these respects a transitional form between typical holocystitinids and trematocystinids. However, the large size of the humatipore tubercles, small number of tangential canals, and their nonradial arrangement are all atypical of holocystitinids. These features could just as readily indicate an independent evolution of the sursummate condition. On the whole, *Pustulocystis* does not appear to be closely related to either *Trematocystis* or *Paulicystis* n. gen. and probably represents a largely unknown line of trematocystinid evolution of coequal status with that which gave rise to *Trematocystis* itself. Derivation of the trematocystinids from early holocystitinids appears plausible.

The most unusual feature of *Pustulocystis* is the small number of facetals (six), a feature that marks this holocystitid genus as relatively advanced, if our perceptions of trends in holocystitid plate evolution are correct. Balancing this are the subspherical thecal shape and direct attachment, characteristic of Group 2 taxa. As far as is known, the genus is confined to the *Trematocystis* zone, *i.e.*, the upper part of the Lower Osgood Shales. It occurs with *Trematocystis* species in Indiana, but is much less common than the latter. Like most Group 2 taxa, the genus is an Osgood endemic.

Another unusual feature of *Pustulocystis* is the variable position of the gonopore. In *P. ornatissimus*, this orifice is usually situated on a plate suture and close to ambulacral facet I, but it can also be located within a single plate. Reported combinations (Paul, 1971: 138) include FA1:FA2, FA1:PO1, FA2:PO2, junction of FA1, FA2, and PO1, within PO1, and within FA2.

Pustulocystis ornatissimus (Miller, 1891)

Holocystites affinis Miller & Faber, 1892: 87; Bassler & Moodey, 1943: 43, 167.

Holocystites asper Miller & Gurley, 1895: 84; Bassler & Moodey, 1943: 43, 168.

Holocystites ornatissimus Miller, 1891: 17; 1892a: 627; Bather, 1919b: 257; Bassler & Moodey, 1943: 44, 169.

Holocystites papulosus Miller, 1891: 18; 1892a: 628; Bassler & Moodey, 1943: 44, 169.

Holocystites subovatus Miller, 1891: 17; 1892a: 627; 1892c: 680;Foerste, 1931: 206; Bassler & Moodey, 1943: 44, 170.Pustulocystis ornatissimus (Miller, 1891). Paul, 1971: 134.

Diagnosis.—A species of *Pustulocystis* with four-sided peristome, four ambulacral facets, variable gonopore position, and stout pyriform theca; plate sutures moderately impressed; 50-80 thecal plates in circlets of up to 17 plates; attachment area small.

Occurrence.—"Main cystoid layer"" (Foerste, 1897): Trematocystis Zone, Osgood Member, Salamonie Dolomite, Jefferson and Ripley counties, Indiana, and near Pegram, Tennessee.

Material.–17 undoubted specimens; AMNH, FMNH, USNM.

Description.-See Paul, 1971: 135-138.

Remarks.—Paul (1971: 138) commented on the resemblance of this species to *Holocystites* (*H*.) scutellatus in thecal shape and ornament. It differs in peristome shape and plating, and number of ambulacral facets. Pustulocystis ornatissimus also has only a single plate generation, and the humatipore tubercles are larger and more widely spaced. The humatipores also have fewer tangential canals, which are *not* radially arrayed.

Pustulocystis pentax Paul, 1971

Pustulocystis pentax Paul, 1971: 138.

Diagnosis.—A species of *Pustulocystis* with five-sided peristomial and five ambulacral facets, gonopore on FA1:FA2 suture, elongate fusiform theca with distinct aboral projection, and moderate attachment area. Plate sutures slightly impressed; thecal plates in 10 circlets of *ca.* 10 plates each.

Occurrence.—Probably Trematocystis Zone, Osgood Member, Salamonie Dolomite; the holotype is from the old quarry dump at Newsom Station, Tennessee.

Material.-1 specimen, holotype MU 884.

Description.-See Paul, 1971: 138-140.

Remarks.—As noted by Paul (1971), the thecal shape and morphology of the aboral projection, as well as the peristomial morphology (shape and number of facets) are distinctive. Even if the facet number exhibited by the holotype should prove abnormal, there is little doubt that this is a valid species.

Subfamily **PENTACYSTINAE** Frest & Strimple, n. sfam.

Diagnosis.—A subfamily of Holocystitidae with globular to cylindrical theca; plates usually of one generation, in many circlets with numerous plates in each; humatipores with flat tangential canals, often sparsely packed and with relatively few tangential canals; POO vestigial or absent (6, 2, or none); 8 FAA; 5 ambulacral facets developed on facetals only; gonopore on FA2 (usually) or FA1 (rarely); hydropore cryptic or on FA1:FA8 suture; attachment direct, by medium to large attachment area; aboral projection absent.

Range.—Upper Silurian (early Wenlockian), North America (Indiana).

Included genera.—Pentacystis Paul, 1971; Osgoodicystis n. gen.

Remarks.-The Pentacystinae are among the rarest members of the Holocystites fauna. The subfamily has not yet been reported outside of the Osgood Member in southeastern Indiana, and all species for which provenance is known are from the Upper Shales, with the exception of Osgoodicystis wykoffi, said by Foerste (1897), on the authority of John Hammel, to have come from the lower bed of the Middle Osgood Limestone. We have found no new specimens of the previously described *Pentacystis* species (Paul, 1971), and their provenance is problematic. To judge from the preservation of the specimens, the source is very likely the Upper Shales. As with the Trematocystinae, all members were probably attached throughout life and thus required a delicate balance between incoming sedimentation and hard substratum availability (on a predominantly soft bottom) to survive. Maximum thecal size is comparable to the Holocystitinae, as is the range in thecal shape (Text-figs 13-14). The number and arrangement of ambulacral facets also recalls the Holocystitinae, and evolution of the subfamily from a form much like *H. (Sepulticystis) spangleri*, but with flat tangential canals, is probable. The principal differentiating features are the much-reduced (or absent) periorals, numerous plates per circlet, mostly of one generation, and the large attachment base.

Humatipore morphology is also simpler. No pentacystinids with sursummate humatipores are known (Table 9), and the tangential canals are generally few in number. Humatipore morphology is essentially similar in both pentacystinid genera.

The vestigal or absent periorals are the most obvious point of difference between the Pentacystinae and Holocystitinae. Judging by the general stability of peristomial plate arrangement in both the Sphaeronitidae and Holocystitidae as well as other, less closely related families (*e.g.*, Gomphocystitidae; Bockelie, 1979), the diminution and eventual loss of a major element is

of considerable phylogenetic significance, and on its own justifies separate subfamilial status for these diploporites. The other two holocystitid subfamilies, despite the unusual diversity of both (for diploporites) show essentially no internal variation in prominence and development of periorals. However, within the Pentacystinae, a range of forms with complete (although much reduced), incomplete, or totally absent periorals is now known. Even here, however, no specimens have been seen with anything like the full development characteristic of the other holocystitid subfamilies.

We segregate those forms with complete or partial PO circlet as a new genus (Osgoodicystis n. gen.) and retain Pentacystis primarily for pentacystinids that lack this circlet entirely. One new form, P. gibsoni n. sp. has only the posterior periorals (PO1 and PO6). Because this species also has oral pores, Osgoodicystis n. gen. is defined sufficiently broadly to include it. As noted by Paul (1971), there is a correlation between possession of periorals and development of oral pores. Pentacystis lacks them, so we prefer to link P. gibsoni n. sp. with Osgoodicystis n. gen., and for the present do not feel that a separate subgenus or genus is justified for the taxon. Loss or reduction or periorals might be related to one other morphological peculiarity of the Pentacystinae, the location of the hydropore. This thecal orifice is on the PO1:PO6 suture in all other holocystitids, but is cryptic or located on the FA1:FA8 suture in Pentacystinae, even in those species that still have periorals (Text-fig. 46). It is only detectable with certainty on exceptionally well-preserved specimens, as it is not developed on a tubercle, but rather seems to be located on an irregular plate suture. Bather (1919c) originally suggested that there is an irregular suture on PO1:PO6 which might have functioned as a hydropore in *Pentacystis* (also reported from Brightonicystis; Paul, 1971: 145, fig. 46; 1973: 57; Text-fig. 19B), and the hydropore of O. wykoffi is reported (Paul, 1971: 114) to be slit-like and on PO1:PO6 in USNM S8063a. We think we can detect an irregular suture (probable hydropore) on FA1:FA8 in P. sphaeroidalis (Miller & Gurley, 1895) (see Paul, 1971: fig. 40A), P. gibsoni n. sp., and P. simplex Paul, 1971, and also O. wykoffi (Text-fig. 46D; see also Paul, 1971: fig. 40B). We were unable to locate the hydropore in existing material of O. cooperi n. gen., n. sp. or O. bissetti n. gen., n. sp. Jaekel (1899) advanced the possibility that cystoids lacking a distinct hydropore might have combined it with the gonopore; however, as pointed out by Paul (1971: 30) "this seems very unlikely since the gonopore is fundamentally an exit and the hydropore is basically an entrance." We have not yet found any isolated pentacystinid FA1 or FA8 plates, which might settle the problem; for now, Paul's suggestion of the possibility of a "hidden hydropore" developed in soft tissue within the peristome (Paul, 1971) in some species should be seriously considered.

A key to the presently well-characterized species of

Pentacystinae follows:

KEY TO THE SPECIES OF PENTACYSTINAE

- 1. Perioral circlet present . . . genus *Osgoodicystis* n. gen.; 2 Perioral circlet absent genus *Pentacystis*; 4
- 3. Humatipores incomplete, 2 or more perpendicular canals with 2-3 tangential canals O. wykoffi Humatipores complete . . O. bissetti n. gen., n. sp.

Genus *Pentacystis* Paul, 1971 Text-figs 46A-B, 47A, C, E; Pl. 12, Figs 5-10; Pl. 13, Figs 2-3

Pentacystis Paul, 1971: 102-105.

Type species.—Pentacystis simplex Paul, 1971: 102, by original designation.

Diagnosis.—A genus of Pentacystinae lacking periorals and oral pores; theca globular to cylindrical, plates of one generation; numerous circlets and many plates per circlet; humatipores flat, simple, with few tangential canals; gonopore in FA1 or FA2; hydropore cryptic or (?) on FA1:FA8 suture.

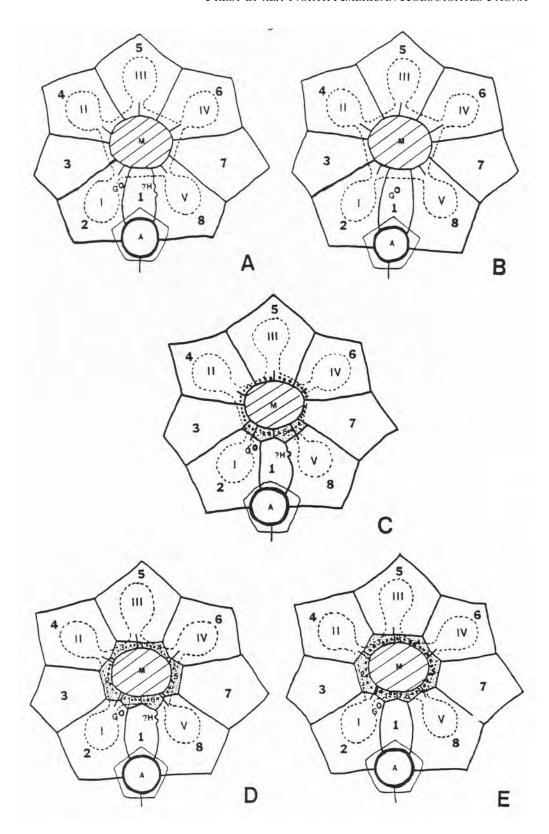
Range.—Upper Silurian (early Wenlockian), North America (Indiana).

Description.—Theca globular or depressed pyriform, with broad base of attachment; large, reaching diameter and length of 60 mm or more.

Plates numerous, of one generation, total number from *ca.* 120 to > 200, arranged in 8-12 or more circlets of from 13-30 or more plates; plates smooth or with granular prosopon.

Humatipores flat; tangential canals just beneath plate surfaces; 2-5 tangential canals, moderately to densely packed, outlines regular to irregular.

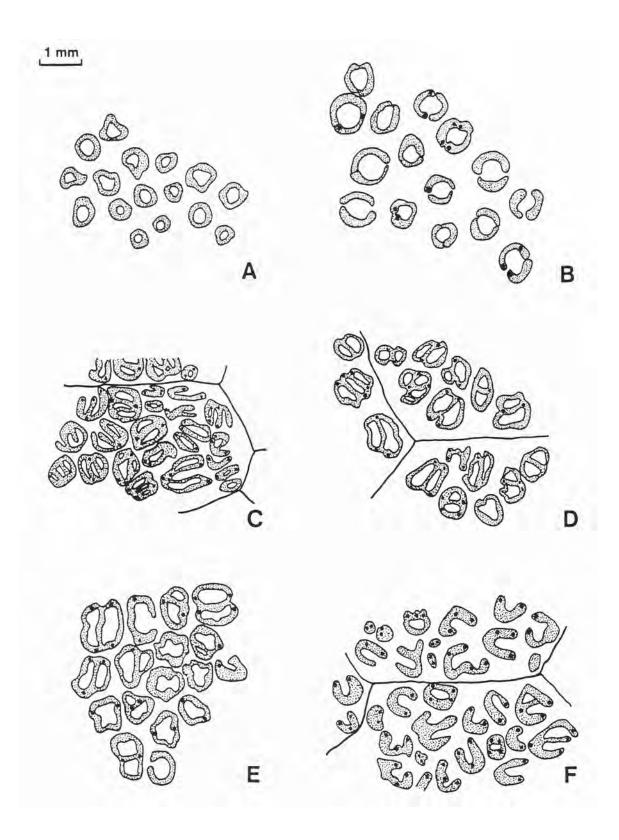
Peristome pentagonal, always subcentral (not offset); peristomial opening circular, surrounded by 8 facetals; 5 ambulacral facets, round or oval, distinctly concave, with sizable raised



Text-fig. 46. Diagrammatic representations of the oroanal regions in members of Pentacystinae. (A) Pentacystis sphaeroidalis; no periorals, gonopore in FA2, probably hydropore on FA1:FA8 border. (B) P. simplex and P. gibsoni n. sp.; no periorals, gonopore in FA1, no evident hydropore. (C) Osgoodicystis cooperi n. gen., n. sp.: oral pores around wide peristomial border, only PO1 and PO6 present. (D) O. wykoffi; complete, but small perioral circlet, gonopore in FA2, possible hydropore on FA1:FA8 border. (E) O. bissetti n. gen,, n. sp.; as in O. wykoffi, but no trace of hydropore. Symbols as outlined under Abbreviations, p. 52.

rims, developed each on single facetals (FAA 2, 4, 5, 6, and 8). Palatals unknown.

Periproct pentagonal, with substantial rim for (unknown) anals. Anal opening round.



Gonopore in FA1, round, always on prominent tubercle. Hydropore on irregular FA1:FA8 suture (?) or cryptic. Attachment direct, by large, flat attachment area commonly over one-half greatest thecal diameter; aboral process absent.

Remarks.—Pentacystis, as construed herein, shows less variation than Osgoodicystis n. gen. in thecal shape and humatipore morphology. The short, rotund theca of most species could be considered more primitive, but the complete absence of periorals makes it among the most advanced Holocystitidae. Overall, the thecal shape and plating and the large base of attachment give the genus a close resemblance to Trematocystis and Paulicystis n. gen. It occurs in close association with the latter at Napoleon, and is probably ecologically convergent with it. There is no evidence that Pentacystis was able to modify its life position. Our observations confirm those of Paul (1971: 103-104) that a large solid object for attachment was a must for Pentacystis at all growth stages and that it remained upright and stationary for all of its life.

Pentacystis simplex Paul, 1971 Text-figs 46B, 47A

Pentacystis simplex Paul, 1971: 105-108.

Diagnosis.—A species of *Pentacystis* with globular to inverted pyriform theca; smooth gently convex plates arranged in *ca.* 8 circlets of roughly 24 plates each; gonopore in FA1; humatipores with 2 or 3 tangential canals, sparsely to moderately packed; attachment area approximately one half greatest thecal diameter.

Occurrence.—Osgood Member, Salamonie Dolomite, at Big Creek (see Paul, 1971; Frest *et al.*, 1977; and Appendix for locality details), Jefferson County, Indiana.

Material.–5 specimens: holotype AMNH 20271a; paratypes BMNH E23111, BMNH E23112, USNM 5306a, and UMMP.

Description.-See Paul, 1971: 107.

Remarks.—The small, sparsely to moderately packed humatipores of this species resemble those of Osgoodicystis cooperi n. gen., n. sp. most closely and represent the simplest known humatipore to date. Paul (1971: fig. 40A) showed the gonopore in FA2; this appears to have been an oversight, because the gonopore is described as being in FA1 in the text (Paul, 1971: 105, 107), and certainly it is in the holotype, rather near to the FA1:FA2 suture. Presumably, the cited figure is Pentacystis sphaeroidalis. At present, all known species of Pentacystis have the gonopore in FA1 or FA2, but all Osgoodicystis spp. have it in FA2. Gonopore location is merely a specific trait in Holocystites s. s. and in Trematocystis, and might well be in the Pentacystinae also.

Pentacystis sphaeroidalis (Miller & Gurley, 1895) Text-figs 46A, 47C

Holocystites sphaeroidalis Miller & Gurley, 1895: 85; Bather, 1919b: 258; Foerste, 1920b: 52; Bassler & Moodey, 1943: 44, 170. Pentacystis sphaeroidalis. Paul, 1971: 108-111.

Diagnosis.—A species of *Pentacystis* with globular theca; scarcely convex, smooth plates arranged in *ca.* 8 circlets of up to 27 plates each; humatipores densely packed and with irregular outlines; gonopore in FA2; attachment area large, exceeding one half maximum thecal diameter.

Occurrence.-As for Pentacystis simplex.

Material.—Approximately 8 specimens: holotype FMNH 6000; other specimens FMNH, UC, and AMNH.

Description.-See Paul (1971: 108-111).

Remarks.—There is little variation in humatipore morphology among available specimens, and this feature, plus the gonopore location, supports recognition as a distinct species. Pentacystis sphaeroidalis is the commonest Pentacystis, and closely resembles members of Paulicystis n. gen. and Trematocystis in appearance. The provenance is unknown, but is almost certainly either the Upper Shales or the Lower Shales of the Osgood. To judge by specimens of other taxa that we have col-

Text-fig. 47(at left). Camera lucida drawings of humatipores in members of Pentacystinae. (A) Pentacystis simplex, holotype AMNH 2027a, redrawn from Paul (1971: fig. 41A); humatipores comparatively sparse, average 2 tangential canals. (B) Osgoodicystis cooperi n. gen., n. sp., paratype SUI 48168; simple rounded, sparse humatipores, often with 2 tangential canals. (C) P. sphaeroidalis, holotype FMNH 6000; dense humatipores, usually with 4 tangential canals. (D) O. bissetti n. gen., n. sp., holotype SUI 48166; humatipore spacing moderately dense, 2-5 (most often 3) tangential canals. (E) P. gibsoni n. sp., holotype SUI 48170; fairly crowded, humatipores averaging 3 tangential canals. (F) O. wykoffi, holotype FMNH 6022, redrawn from Paul (1971: fig. 41B); incomplete humatipore morphology is unique to this species. Tangential canals with dot stipple, pores (openings of perpendicular canals) black, plate sutures indicated as heavy black lines.

lected along Big Creek, the latter (*i.e.*, the *Trematocystis* Zone) is more likely. *Pentacystis gibsoni* n. sp. has an elongate pyriform theca and humatipores with fewer tangential canals than this species. Humatipores of *P. sphaeroidalis* are more densely packed than in *P. simplex*. Unlike the latter and like *P. sphaeroidalis*, the gonopore of *P. gibsoni* n. sp. is in FA2.

Pentacystis gibsoni Frest & Strimple, n. sp. Text-figs 46B, 47E; Pl. 12, Figs 5-10; Pl. 13, Figs 2-3

Derivation of name.—The species is named after J. A. Gibson, of Hamilton, Ohio, who generously donated several critical Napoleon specimens to the authors.

Diagnosis.—A species of *Pentacystis* with elongate pyriform theca; single generation of plates with granular ornament, arranged in 8 or more circlets of *ca.* 14 plates each; humatipores with 2-5 (generally 3) tangential canals, moderately packed; gonopore in FA2; hydropore cryptic; basal attachment area large.

Occurrence.—Upper Shales, Osgood Member, Salamonie Dolomite; Napoleon Quarry, Ripley County, Indiana.

Material.–Holotype SUI 48172 and two paratypes SUI 46316 and 48170.

Description.—Theca elongate pyriform, greatest diameter 39 mm and length 55 mm in holotype.

Plates hexagonal, flat, of single generation, arranged in 8 or more regular circlets of 14 plates each (except facetals and around periproct), barely higher than wide, reaching maximum size (13 mm length) approximately one third of distance from peristome; all covered with shallowly-buried humatipores and granulose ornament (Pl. 12, Figs 8, 10).

Humatipores moderately to densely packed, 1.0-1.3 mm length, with irregularly circular outlines, 2-5 (usually 3) tangential canals each, evenly developed over theca (Text-fig. 47E; Pl. 12, Figs 5-6, 9-10; Pl. 13, Figs 2-3).

Peristome rounded pentagonal, composed solely of 8 facetals, arrayed around circular peristomial opening *ca.* 8 mm in diameter; distinctly protrusive (Pl. 12, Figs 5, 9); peristomial border narrow, without oral pores. Ambulacral facets 5, round to oval, length *ca.* 4.0-4.5 mm, strongly concave, with broad, smooth, poreless, elevated rims (Pl. 12, Figs 6-7) and median ridges. Preserved proximal brachials uniserial, very thin (Pl. 12, Fig. 7). Palatals unknown.

Periproct hexagonal, diameter *ca.* 7-8 mm, margin deeply inset for insertion of anals (not preserved); anal opening rounded, diameter *ca.* 6 mm.

Gonopore circular, near center of FA1, ca. 0.6 mm in diameter, atop prominent tubercle 1.1 mm in diameter at base

(Pl. 12, Fig. 7).

Hydropore not detected.

Attachment apparently direct, by sizable attachment area of one-half of thecal diameter.

Remarks.—Comparisons with related species have been made above, and only a few details need be added here. The seeming regularity of thecal plating could be an artifact of the small number of known specimens. The granular ornament is much like that of some Osgoodicystis spp. (described below). None of the specimens shows any sign of a hydropore, and the FA1:FA8 suture does not appear irregular. As with other Pentacystinae, the ambulacral facets are prominent and protrusive, although this feature seems unlikely to be a consistent subfamilial characteristic, and its functional significance is unclear. The species is associated with algal-stromatoporoid and debris mounds, which presumably offered preferred hard attachment sites.

Genus *Osgoodicystis* Frest & Strimple, n. gen. Text-figs 46C-E, 47B, D, F, 48; Pl. 12, Figs 1-4; Pl. 13, Fig. 1; Pl. 14

Derivation of name.—Provenance of known taxa (Osgood Member, Salamonie Domolite), plus standard *-cystis* ending.

Type species.—Osgoodicystis bissetti n. gen., n. sp., by original designation herein.

Diagnosis.—A genus of Pentacystinae with cylindrical or globular theca; periorals present, but circlet vestigial or incomplete; oral pores few but present; plates of 1 or 2 generations; many circlets with 10-20 plates per circlet; gonopore in FA2; hydropore cryptic or on FA1:FA8 suture; attachment area large; 5 concave ambulacral facets on slightly protrusive central peristome.

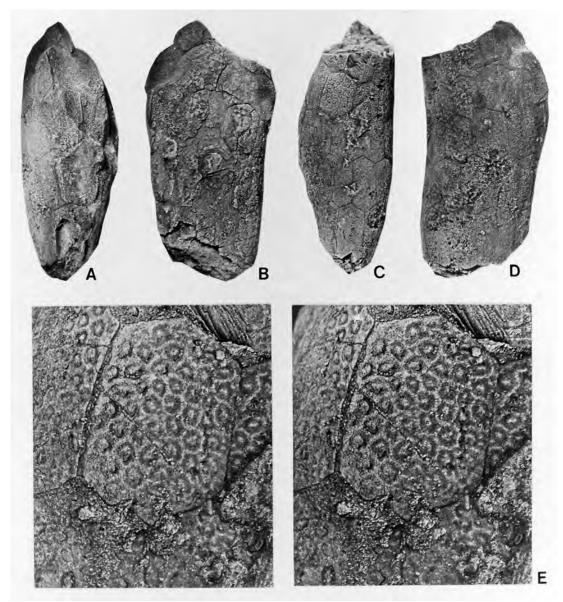
Range.-Upper Silurian (Wenlockian), North America (Indiana).

Description.—Theca cylindrical or globular, moderate-to large-sized for fauna (to at least 77 mm length in Osgoodicystis cooperi n. gen., n. sp.; 50 mm width in O. wykoffi).

Plates numerous, of 1 or 2 generations, total number ranging from *ca.* 80-160, smooth or granular, with humatipores distributed evenly over theca.

Humatipres evenly distributed over theca, sparse or moderate, with few tangential canals, complete or incomplete; tangential canals flat and barely covered by outer layer of plate stereom.

Peristome rounded pentagonal, elevated above rest of oral



Text-fig. 48. Paratype of *Osgoodicystis cooperi* n. gen., n. sp., SUI 56168. (A-D) Lateral views of small cylindrical theca missing both ends; orientation uncertain, maximum dimension = 52 mm. (E) Enlarged stereoscopic pair illustrating moderately dense simple humatipores, with more or less regular, circular outlines, generally with 2 tangential canals, width of field of view = 9 mm.

area, central, comprising very small periorals (6 or 2) and then 8 facetals; ambulacral facets circular or oval, large, distinctly concave with surrounding rim evident, on FAA 2, 4, 5, 6, and 8. Peristomial border deeply indented for reception of (missing) palatals; oral pores 4-6 per perioral, arranged evenly around peristomial border, surrounding central, almost circular peristomial opening.

Periproct rounded pentagonal; deeply incised border for attachment of anals (not preserved in any known specimen); anal opening circular.

Gonopore small, circular, on low tubercle or simply round opening, on FA2 near common junction with FA1 and PO1.

Hydropore possibly beneath irregular portion of FA1:FA8 suture in two species, not detected in another.

Attachment direct, by large flat attachment area at aboral pole.

Remarks.—Thecal shape varies more widely in Osgoodicystis n. gen. than in Pentacystis (Text-fig. 13). Two species are approximately cylindrical (?advanced shape), whereas one is globular. Osgoodicystis cooperi n. gen., n. sp. and O. bissetti n. gen., n. sp. can be distinguished on humatipore morphology and on number of periorals: O. cooperi n. gen., n. sp. retains periorals in the posterior interray, whereas O. bissetti n. gen., n. sp. has

a small, but complete circlet (Text-figs 47C-D), as does *O. wykoffi*. The humatipore morphologies of *O. cooperi* n. gen., n. sp. and *O. bissetti* n. gen., n. sp. have rough parallels as in *P. simplex* and *P. sphaeroidalis* (compare Text-figs 47A-B and C-D). The contrast is between sparsely packed humatipores with two tangential canals and more densely packed ones with 3 or commonly more. The two new taxa are both Upper Shales species.

Osgoodicystis wykoffi differs considerably from the other Osgoodicystis spp.; it has a globular theca and smooth plates of 2 generations (versus the granular ornament and single plate generation of the rest). The humatipores of this species are highly unusual in that they are frequently incomplete and have branched perpendicular canals with 2 or 3 terminal openings on each side of the humatipore (Text-fig. 47F). As in Pentacystis, the tangential canals are very near the plate surface and easily exposed by weathering. It is possible that this species should have separate subgeneric or generic status, but the small number of available specimens of Osgoodicystis n. gen. hampers evaluation, and we prefer a broad generic definition for the present.

Osgoodicystis bissetti Frest & Strimple, n. sp. Text-figs 46E, 47D; Pl. 4, Fig. 5; Pl. 12, Figs 1-4; Pl. 13, Fig. 1

Derivation of name.—The species is named after D. Bissett, Hamiltion, Ohio, in partial compensation for his aid in making this study possible by donating numerous important Napoleon specimens from his personal collection.

Diagnosis.—A species of Osgoodicystis n. gen. with subcylindrical (clavate) theca; complete perioral circlet; plates ornamented with fine granules and vermiculations; humatipores complete, moderately densely packed, with 2-5 (frequently 3) tangential canals and somewhat irregular outlines; 13 plates per circlet, 8 or more circlets; gonopore on FA2, not on tubercle, hydropore (?) on FA1:FA8 suture: attachment area large (?).

Occurrence.—Upper Shales, Osgood Member, Salamonie Dolomite; Napoleon Quarry, Ripley County, Indiana.

Material.—A single reposited specimen, holotype SUI 48166; other specimens in private collections.

Description.—Theca subcylindrical (clavate); greatest width at third circlet from peristomial opening; moderate-sized, width of holotype 35.8 mm, length 66.3 mm (Pl. 12, Figs 2-3).

Plates elongate hexagonal, disposed in 7 or more regular circlets of 13 plates each, reaching maximum size in fourth circlet from top, to 15.5 mm length; ornament consisting of fine granules ranging in shape from rounded to irregularly elongate and coalescent, giving finely vermiculate appearance (Pl. 12,

Fig. 2). All plates covered with evenly distributed humatipores.

Humatipores sparsely packed, over whole theca, with 2 or 3 (generally 2) tangential canals; often irregularly circular outlines but little size variation, *ca.* 0.8-1.0 mm in diameter; tangential canals flat, scarcely buried beneath plate surfaces (Text-fig. 47D; Pl. 12, Figs 3-4; Pl. 13, Fig. 1).

Peristome rounded pentagonal, slightly elevated above normal thecal plates (Pl. 12, Fig. 1), at apex of adoral pole (Pl. 12, Fig. 2); peristomial opening rounded (distorted on holotype; average width 4 mm) surrounded by 6 narrow (2 mm wide) POO; border pitted with oral pores (4 per POO); next circlet (FAA) also complete, composed of 8 plates. Ambulacral facets definitely concave, with elevated rims, circular to oval, average length 3.5 mm, with distinct median ridge. Preserved proximal brachials very thin, uniserial (Pl. 4, Fig. 5; Pl. 12, Fig. 1). Peristomial diameter approximately one third of ambital diameter.

Periproct pentagonal, average width *ca.* 6.5 mm, with indented 0.5 mm border around originally circular (distorted on holotype) anal opening *ca.* 5.5 mm in diameter.

Gonopore round, 0.5 mm in diameter, not mounted on tubercle, flanking ambulacral facet I on FA2 and adjacent to FA1:FA2 suture.

Hydropore obscure, apparently beneath an irregular portion of FA1:FA8 suture (Pl. 12, Fig. 1; Text-fig. 46D).

Attachment direct, by large attachment area approximately one third of thecal diameter (incomplete on holotype).

Remarks.—Although known only from a couple of specimens (only one available for reposit), the species is quite distinct from better-known taxa. Only one other pentacystinid (Osgoodicystis wykoffi) has a complete perioral circlet. Ignoring this feature, O. bissetti n. gen., n. sp. most closely resembles O. cooperi n. gen., n. sp., but the latter has a larger, truly cylindrical (rather than clavate) theca with smaller plates, more plate circlets, and characteristically simple humatipore morphology (compare Text-figs 47B and D). The holotype of O. bissetti n. gen., n. sp. has several large Tremichnus pits, evidently made while the diploporite was alive, scattered over the adoral third of the theca (Pl. 12, Figs 1-2).

Osgoodicystis cooperi Frest & Strimple, n. sp. Text-figs 46C, 47B, 48; Pl. 14

Derivation of name.—The specific epithet acknowledges the contributions of the late D. Cooper, Hamilton, Ohio, to this study, in the form of several important Napoleon specimens.

Diagnosis.—A species of *Osgoodicystis* n. gen. with large, elongate, cylindrical theca, granular plates of one generation arranged in 7 or more regular circlets of 10-14 hexagonal plates;

only periorals 1 and 6 present (perioral circlet incomplete); humatipores sparsely packed, with regular circular outlines, 2 or 3 (usually 2) tangential canals; gonopore in FA2 on low tubercle; hydropore on FA1:FA8 suture (?); attachment area not preserved.

Occurrence.—Upper Shales, Osgood Member, Salamonie Domolite; Napoleon Quarry of New Point Stone Company, Inc., Ripley County, Indiana.

Material.—Two reposited specimens: holotype SUI 48167, paratype SUI 48168. Other specimens in private collections.

Description.—Theca cylindrical, large (Pl. 14, Figs 2-5); length of holotype 73 mm, average width 35 mm.

Plates hexagonal, much higher than wide, maximum length *ca.* 14 mm; all circlets roughly equal in length on preserved portion of holotype; plate surfaces granular; humatipores evenly distributed over thecal surface, moderately deeply buried. Plates arranged in regular circlets (at least 7) of 10-14 plates.

Humatipores sparsely packed, usually with regular, circular outlines and flat tangential canals, sometimes 3 but generally 2 (Text-figs 47B, 48): maximum length varies between 0.7 and 0.9 mm; tangential canals more deeply buried than in other species of *Osgoodicystis* n. gen.

Peristome rounded pentagonal, at summit of theca, weakly protrusive; peristomial opening round, diameter 6.5 mm in holotype, surrounded by circlet of 8 facetals and 2 small periorals (Text-fig. 46C; Pl. 14, Fig. 1). Peristomial border broad (ca. 3 mm), pitted with numerous oral pores (Pl. 14, Fig. 1), ambulacral facets 5, strongly concave and deeply inset into facetals, surrounded by narrow elevated rims; outlines circular, average width 4.5 mm.

Surviving posterior penorals small, partly below peristomial border, but aboral halves elevated above, in line with adjacent facetals (Pl. 14, Fig. 1).

Periproct pentagonal, large (average width 7.4 mm), with incised border for (unknown) anals surrounding circular or oval anal opening.

Gonopore small (0.3 mm) opening on flat summit of rounded tubercle (diameter 0.7 mm) adjacent to ambulacral facet on FA2 near to FA1:FA2 suture (Text-fig. 46C; Pl. 14, Fig. 1).

Hydropore difficult to detect, but apparently on irregular portion of FA1:FA8 suture (Text-fig. 46C).

Attachment Unknown; distal areas of both known specimens missing.

Remarks.—The holotype (SUI 48167) has even circlets of 14 plates each and retains the peristome. SUI 48168 is referred to this species even though it has 10 plates per circlet and is

missing both poles because the thecal shape, plate size, and humatipore morphology (Text-fig. 48) are similar to those of the holotype and unlike those of *Osgoodicystis bissetti* n. gen., n. sp., the only other species remotely resembling the specimen. There is a chance that this specimen represents a distinct species, but better-known pentacystinid species display as wide or wider ranges of variation in number of plates per circlet.

Osgoodicystis wykoffi (Miller, 1891) Text-figs 46D, 47F

Holocystites wykoffi Miller, 1891: 15; 1892a: 625; Bather, 1919b: 258; Foerste, 1920b: 51-52; Bassler & Moodey, 1943: 44, 171

Pentacystis wykoffi. Paul, 1971: 111-115.

Diagnosis.—A species of Osgoodicystis n. gen. with large globular or inverted pyriform theca; 2 plate generations; smooth, generally convex plates with slightly impressed sutures; gonopore in FA2; hydropore cryptic; humatipores incomplete; with branched perpendicular canals and few, irregular, flat tangential canals; attachment area large; perioral circlet complete, very small.

Occurrence.—Lower unit (c) of Middle Osgood Limestone, according to Foerste, (1897); Osgood Member, Salamonie Dolomite, Big Creek, Jefferson County, Indiana.

Material.—Three thecae: holotype FMNH 6022; referred specimens BMNH E7641 and USNM 53063a.

Remarks.—We have seen no additional material of this species. Several features of Osgoodicystis wykoffi (2 plate generations; smooth convex plates with impressed sutures; globular theca; unique humatipore morphology) are sufficiently different from the remaining Osgoodicystis spp. (single plate generation; granular, flat plates; cylindrical theca; normal pentacystinid humatipore morphology) that eventually segregation as a separate subgenus or genus might be required. In particular, the incomplete, highly irregular humatipores are without parallel in the Holocystitidae. As yet, however, there are too few pentacystinid specimens and too little is known about ranges of variation to permit confident interpretation of the taxonomic significance of some morphologic features.

Ichnogenus *Tremichnus* Brett, 1985

Tremichnus Brett, 1985: 626.

Type species.–Tremichnus paraboloides Brett, 1985, by original designation.

Diagnosis.—"Circular pits or embedment structures of varying diameter (ca. 0.1-4.0 mm) occurring on the plates of echinoderms, primarily crinoids, with or without associated thickening or gall-like deformation of the plates. Pits regularly parabolic in cross section, with diameter/depth ratios variable from ca. 0.1-1.0; no internal expansion or other ramifications. Holes always oriented perpendicularly to external plate surfaces, tapering inward; generally not penetrating through plates. Adjacent pits may overlap one another" (Brett, 1985: 626).

Remarks.—Circular parabolic pits in echinoderms, interpreted variously as results of embedment, boring, or a combination of the two, either by commensal filter feeders or true parasites, have been referred to several ichnogenera. Brett (1985) provided a comprehensive review of these forms.

Morphology of the pits in diploporites is consistent with that of other described *Tremichnus* species, a conclusion reached earlier by Brett (1985; see also Paul, 1971; Frest *et al.*, 1977, for description and interpretation). Review of occurrences of *Tremichnus* in Osgood diploporite supports Brett's conclusions that the living organism producing the preserved structures was a sessile, host-specific epibiont. Pits in diploporites are generally circular in outline, occur selectively on thecal areas assumed to be uppermost in life, can occasionally overlap each other, frequently are closely similar in size on the same specimen, do not occur selectively on plate sutures, and always show evidence of stimulating secondary secretion of stereom by the host diploporite.

It seems likely from the forgoing that the pit-forming organism was a larval settler, perhaps passively, and remained on the diploporite surface for some time. As with other species of *Tremichnus*, borings that unarguably penetrated the plate are very rare, certainly less than 1% on specimens that we have examined. Host selectivity has been discussed previously (see also Table 8). It is also clear that borings occurred only while the diploporite was alive. Overgrowth of both pitted and adjacent unpitted thecal surfaces by bryozoans are common, whereas avoidance of pitted areas has not been observed, for example. It is most likely, as Brett surmised, that the organism produced pits through a combination of selective inhibition of stereom growth and some true boring (removal of previously secreted stereom).

As with one other described species, *Tremichnus cysticus*, the amount of secondary stereom secreted (forming gall-like structures) should not be ignored as a factor in producing pit architecture and depth. Diploporite galls are not as extensive as in *T. cysticus* (compare Brett, 1985: fig. 3 with Pl. 2, Fig. 2, Pl. 3, Fig. 3, Pl. 12, Fig. 2; see also Paul, 1971: figs 33b, 36a-b, 37a, 42a-b, 44b, 52a, c, f-g, 55b, 56g), but are an invariant feature.

Tremichnus cystoidiphilus Frest & Strimple, n. sp. Pl. 2, Fig. 2; Pl. 3, Fig. 3; Pl. 12, Fig. 2

Tremichnus sp. aff. puteolus Brett, 1985: 630.

Derivation of name.—Combining cystoid with Latin -philus, lover, liker.

Diagnosis.—"Large, shallow, hemispherical pits (diameter 3.5-4.0mm; maximum depth *ca.* 2 mm); resembling pits of *T[remichnus] putelous*, but lacking concentric ring, more uniform in size and ... surrounded by raised rims" (modified slightly from Brett, 1985: 630).

Occurrence.—Osgood Member, Salamonie Dolomite (Wenlockian), southeasterm Indiana and adjacent Kentucky; central Tennessee.

Material.—Many specimens in most holocystitinid and pentacystinid and a few trematocystinid taxa: FMNH, USNM, UMMP, and UI collections.

Description.-See diagnosis above.

Remarks.— All pits that we have seen on diploporites are surrounded by raised rims and show at least some degree of secondary stereom growth, often to the point of constituting galls (e.g., Paul, 1971: figs 33b, 52g). The Osgood occurrences remain the only published examples on blastozoan taxa, although occasional specimens of Caryocrinites from the Osgood are similarly affected. Large pits (3.0-4.0 mm diameter) are most frequently seen, and most affected diploporite specimens have groups roughly equal in size/diameter (Paul, 1971: fig. 33b). Less often, swarms of smaller pits are encountered (Paul, 1971: fig. 55b), or a more random scatter of pit diameters is evident (Paul, 1971: fig. 42b). Because no relation between pit diameter and diploporite taxonomy is evident, it is probable that only one ichnospecies is involved. Pit absence from certain relatively common taxa (especially the aristocystitid Triamara, but also certain trematocystinids, e.g., species of Paulicystis n. gen.) has been noted previously (Paul, 1971, and herein).

ACKNOWLEDGMENTS

Many people contributed Osgood specimens to this study. In particular, the large and generous donations of D. Bissett, the late D. Cooper, and W. Bruce Gibson (Cincinnati, Ohio), and R. H. Mapes (Ohio University) deserve special recognition. Other important specimens were contributed by Carlton E. Brett (University of Rochester), Vince Dick (University of Rochester), George McIntosh (Rochester Museum), Darwin Boardman (Ohio University), and Christina Strimple. Craig

Clement (University of Tennessee), Carlton E. Brett, and George McIntosh commented on environmental interpretations and visited the Napoleon locality. The original draft of this work was reviewed by C. R. C. Paul (University of Liverpool), Peter Hoover (Paleontological Research Institution, Ithaca, New York) and T. Guensberg (Southern Illinois University-Edwardsville), to whom we are indebted for numerous perspicacious comments. A later draft was reviewed by Carlton E. Brett. The remaining errors are our own.

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APPENDIX: HOLOCYSTITES FAUNA LOCALITIES

The diploporites constituting the *Holocystites* fauna have been collected for well over a century. Precise locality information is often unavailable for many of the specimens collected in the 19th century, and there are numerous more or less anecdotal reports of the fauna from a variety of places and horizons. Many of the older localities are no longer exposed; on the other hand, recent quarrying activity in some areas has made new material available. Previous attempts to summarize locality and occurrence data for the *Holocystites* fauna have of necessity been somewhat piecemeal. Most notable among these are Paul (1971: 162-166) and Frest *et al.* (1977: 86-104). Major references for 19th century localities are Day (1878), Foerste (1897), Greacen & Ball (1946), and Teller (1911).

In the following discussion and Table 20, we attempt to give a comprehensive, but brief, compilation of all currently accepted *Holocystites* fauna localities. This is drawn largely from the previously cited sources, but also includes some new information on stratigraphy and occurrences unavailable through 1977. Only localities known to have produced reposited specimens are cited. Where possible, information is provided on the source unit, genera found, and current accessibility. For more detailed information, see Paul (1971), Frest *et al.* (1977) and the references cited therein.

ILLINOIS

- (1) Joliet. Several quarries in the Markgraf and Romeoville Members, Joliet Dolomite, appear to have produced diploporites, but the precise localities remain unknown. Older quarries are mostly inaccessible, but active quarrying is still being carried out.
- (2) Romeoville. According to Fisher (1925), the fossils collected by A. W. Slocum, which include *Holocystites* and *Triamara*, were from two quarries located near the Illinois and Michigan Canal (SW1/4 NE1/4 sec. 35, T37N R10E; and NE1/4 NW1/4 NE1/4 sec. 2, T36N R10E, Romeoville 7½" quadrangle), Will County. Neither is now collectable.
- (3) Lemont. W side of Sanitary and Ship Canal between SW1/4 SE1/4 SW1/4 sec. 35, T37N R10E and SW1/4 NW1/4 NE1/4 sec. 25, T37N R10E, Romeoville 7½' quadrangle, Will County. The spoil banks are still accessible, but no specimens have been found recently.
 - (4) Bridgeport Reef. Abandoned quarry (now mostly refuse-

filled) two blocks W of Halsted at 27th Street, sec. 29, T39N R10E, Englewood 7½ quadrangle, Cook County. No longer accessible.

Indiana

- (1) Marble Hill. Locality 18 of Foerste (1897): section line between sections 20 and 29, T2N R10E, Bethlehem 7½ quadrangle, Jefferson County.
- (2) North Madison. This locality produced a number of specimens in old collections, but has not been positively relocated. For discussion, see Paul (1971: 163).
- (3-5) Big Creek. Localities 74-76 of Foerste (1897). Two-mile stretch of creek bottom along Big Creek, Jefferson Proving Grounds, SE1/4 of San Jacinto 7½"quadrangle, Jefferson County. This locality is now difficult to collect due to unexploded ordinance and location within a U. S. Army facility. Precise locality information and a recently measured section were given by Frest *et al.* (1977: 88-91).
- (6) Paul (1971) Indiana locality 6. Unnamed tributary to W fork, Indian Kentuck Creek, where it crosses under county road S1/2 SE1/4 SE1/4 sec. 7, T5N R11E, Rexville 7½' quadrangle, Jefferson County. Collected by Paul (1971).
- (7) Foerste (1897) locality 58. Unnamed tributary to W fork, Indian Kentuck Creek, from point where it parallels county road and 30 m upstream. SW1/4 NE1/4 SW1/4 sec. 6, T5N R11E, Rexville 7½' quadrangle, Jefferson County. Still collectable in 1985.
- (8) Foerste (1897) locality 77. Banks of Big Creek where it flows under the old Michigan Road and upstream for 20 m, SW1/4 NE1/4 SW1/4 sec. 25, T6N R10E, Rexville 7½'quadrangle, Ripley County. Adjacent to Jefferson Proving Grounds. Still accessible, but poorly exposed in 1975.
- (9) Foerste (1897) locality 81. Banks of Vestal Branch just upstream of the point where it crosses county road 225, SW1/4 NE1/4 sec. 21, T6N R11E, Rexville 7½ quadrangle, Ripley County. Still collectable in 1987.
- (10) New Marion, Foerste (1897) locality 131. Roadcut on old Michigan Road above Big Graham Creek 0.2 mi N of crossroads in New Marion. SW1/4 NE1/4 sec. 36, T7N R10E, Versailles 7½' quadrangle, Ripley County. Still collectable in 1987.
- (11) Osgood quarry. Strippings from sump pit in Ripley County Construction quarry on SW edge of Osgood, NW1/4 SW1/4 sec. 22, T8N R10E, Versailles 7½' quadrangle, Ripley County. The main quarry is now completely water-filled, but collecting is still possible from dump pile on W edge of quarry adjacent to Osgood municipal water facility (1987).
- (12a) Napoleon Quarry. Strippings from drainage ditch on N side of W quarry, Napoleon Limestone Company, 1.7 km (0.8 mi) W of intersection of U.S. Hwy 421 and Indiana Hwy 229 in Napoleon, NW1/4 NE1/4 sec. 29, T9N R10E,

Table 20. Diploporite fauna and stratigraphy of known *Holocystites* fauna localities.

Locality	Stratigraphy	Fauna
ILLINOIS	0 1 7	
(1) Joliet	Markgraf & Romeoville Members, Joliet Dolomite	Holocystites (Holocystites, Megacystites, Sepulticystis) Triamara, Gomphocystites
(2) Romeo	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Holocystites (Holocystites, Megacystites, Sepulticystis) Triamara, Gomphocystites
(3) Lemont	Markgraf & Romeoville Members, Joliet Dolomite	Holocystites (Holocystites)
(4) Bridgeport Reef	Racine Dolomite	Holocystites (Holocystites)
INDIANA		
(1) Marble Hill	Lower Osgood Shales	Trematocystis
(2) North Madison	Osgood (? full section)	Holocystites (Holocystites, Megacystites, Sepulticystis), Triamara, Gomphocystites, Pentacystis Trematocystis, Pustulocystis
(3-5) Big Creek	Osgood (full section)	Holocystites (Holocystites, Megacystites), Triamara, Gomphocystites, Pentacystis Trematocystis, Pustulocystis
(6) Paul (1971) locality 6	Middle Osgood Limestone	Holocystites (Holocystites, Megacystites), Triamara
(7) Foerste (1897) locality 58	Lower Osgood Shales, Middle Osgood Limestone	Trematocystis
(8) Foerste (1897) locality 77	Lower Osgood Shales, Middle Osgood Limestone	Trematocystis, Pustulocystis
(9) Foerste (1897) locality 81	Lower Osgood Shales, Middle Osgood Limestone	Trematocystis, Pustulocystis
(10) New Marion	Osgood	Trematocystis, Holocystites (Holocystites, Megacystites) Pentacystis
(11) Osgood quarry	Upper Osgood Shales	Holocystites (Holocystites, Megacystites), Triamara
(12a) Napoleon Limestone Company	Upper Osgood Shales	Holocystites (Holocystites, Megacystites), Triamara
(12b) New Point Stone Company	Osgood, Laurel	Holocystites (Holocystites, Megacystites), Triamara, Paulicystis, Osgoodicystis, Pentacystis
(13) Vail quarry	Laurel	Holocystites (Holocystites)
(14) Adams quarry	Laurel	Holocystites (Holocystites)
(15) St. Paul Stone Company quarry	Laurel	Holocystites (Holocystites), Triamara
(16) Ryker's Ridge	Osgood	Trematocystis, Pentacystis, Holocystites (Holocystites, Megacystites)
KENTUCKY		
(1) Jefferson County	Lower Osgood Shales	Triamara
OHIO		
(1) Brierly quarry	Cedarville	Holocystites (Megacystites)
(2) Rockford quarry	Huntington	Holocystites (Megacystites)
TENNESSEE		
(1) Newsom	Upper Osgood Shales	Pustulocystis
(2) Pegram	Upper Osgood Shales	Holocystites (Holocystites), Pustulocystis
(3) Clifton	Upper Osgood Shales	Holocystites (Holocystites)

Table 20 (continued).

Locality	Stratigraphy	Fauna
WISCONSIN		
(1) Horlick Reef complex	Racine Dolomite (lower)	Holocystites (Holocystites, Megacystites,
_		Sepulticystis), Triamara,
(2) Ives Reef complex	Racine Dolomite (lower)	Holocystites (Holocystites, Megacystites,
_		Sepulticystis), Triamara, Gomphocystites
(3) Franklin Reef	Racine Dolomite (lower)	Holocystites (Holocystites)
(4) Trimbone Reef complex	Racine Dolomite (lower)	Holocystites (Holocystites), Gomphocystites
(5) Schoonmaker Reef	Racine Dolomite	Holocystites (Holocystites)
(6) Menomonee Falls Reef	Racine Dolomite	Holocystites (Holocystites, Megacystites)
(7) Cedarburg Reef	Racine Dolomite (upper)	Holocystites (Holocystites), Gomphocystites
(8) Cook's quarry	Manistique Formation	Holocystites (Holocystites, Megacystites), Triamara
(9) Halquist quarry	Waukesha Dolomite	Holocystites (Holocystites)
(10) Genessee quarry	Waukesha Dolomite	Holocystites (Holocystites)
(11) Waukesha quarries	Manistique Formation	Holocystites (Holocystites, Megacystites), Triamara,
		Gomphocystites

Osgood 7½' quadrangle. Although now long abandoned, still collectable in 1981.

(12b) New Point Stone Company. Napoleon quarry, adjacent to old Napoleon Limestone Company pits, SW1/4 sec. 21 and NW1/4 sec. 28. T9N R11E, Osgood 7½' quadrangle, Ripley County. Not producing diploporites in workings in 1987, but diploporites were still available in place and in dump piles.

- (13) Vail quarry. Old abandoned quarry approximately 0.8 km (0.5 mi) E of Sandusky, SE1/4 SW1/4 sec. 12, T11N R9E, Milroy 7½' quadrangle, Decatur County. Still collectable (1987); the diploporites are from the lower (Laurel) part of the section. Stratigraphic sections and descriptions of this locality were given by Frest & Paul (1971) and Frest (1977).
- (14) Adams quarry. Long-abandoned quarry 0.32 km (0.2 mi) SE of St. Paul, SW1/4 SW1/4 SW1/4 SW1/4 sec. 3, T11N R8E, Waldron 7½ quadrangle, Decatur County. A section and discussion of this locality were given by Frest (1975). The diploporites at this and the succeeding locality are from the upper Laurel (unit 1 of Frest, 1975). The locality was last collected in 1983; it was then a partly developed campground.
- (15) St. Paul Stone Company quarry. Upper Laurel in recently abandoned quarry 1.0 km (0.6 mi) SW of St. Paul, center NE1/4 sec. 9, T11N R8E, St. Paul 7½' quadrangle, Shelby County. For discussion, see Frest (1975) and Frest *et al.* (1977). Still accessible in 1983, when quarry had been pumped.
- (16) Ryker's Ridge (probably Foerste [1897], locality 49). Outcrop on Wolf Run below S side of road 0.32 km (0.2 mi) E of Ryker's Ridge church, NW1/4 SW1/4 sec. 20, T4N R11E, Carrolton 7½' quadrangle, Jefferson County. For discussion

see Frest et al. (1977). Still partly exposed, but no specimens collected recently.

KENTUCKY

(1) Jefferson County. Butts (1915) included diploporites in his faunal lists from the top of the Lower Osgood Shales, Jefferson County. No further information has come to light. A brief search along the Ohio River border of this county in 1975 produced no specimens.

Оню

- (1) Brierly quarry. The type locality of *Holocystites green-villensis* is the banks of Greenville Creek near Brierly quarry, 7.2 km (4.5 mi) E of Greenville (Foerste, 1917: 260). SW1/4 SW1/4 sec. 27, T10N R3E. Greenville East 7½' quadrangle, Darke County. Not recollected recently.
- (2) Rockford quarry. Diploporites have been collected (Busch, 1943) from the Rockford Stone Company quarry, 2.4. km (1.5 mi) NW of Rockford and 0.5 km (0.3 mi) N of U. S. Hwy 33, Rockford 7½' quadrangle, Mercer County. Not recollected recently.

TENNESSEE

- (1) Newsom quarry. Newsom Station, Davidson County, old abandoned quarry near railroad track. Belleview 7½ quadrangle. The recently inactive quarry to the N does not currently (1983) expose the Osgood, but the old quarry did expose the Upper Shales. No longer collectable.
- (2) Pegram. Abandoned quarry 1.6 km (1 mi) E of Pegram, Kingston Springs 7½ quadrangle, Cheatum County. The Osgood is no longer exposed at this locality.

(3) Clifton. Very little available information on this locality. Clifton, Wayne County (Clifton 7½' quadrangle).

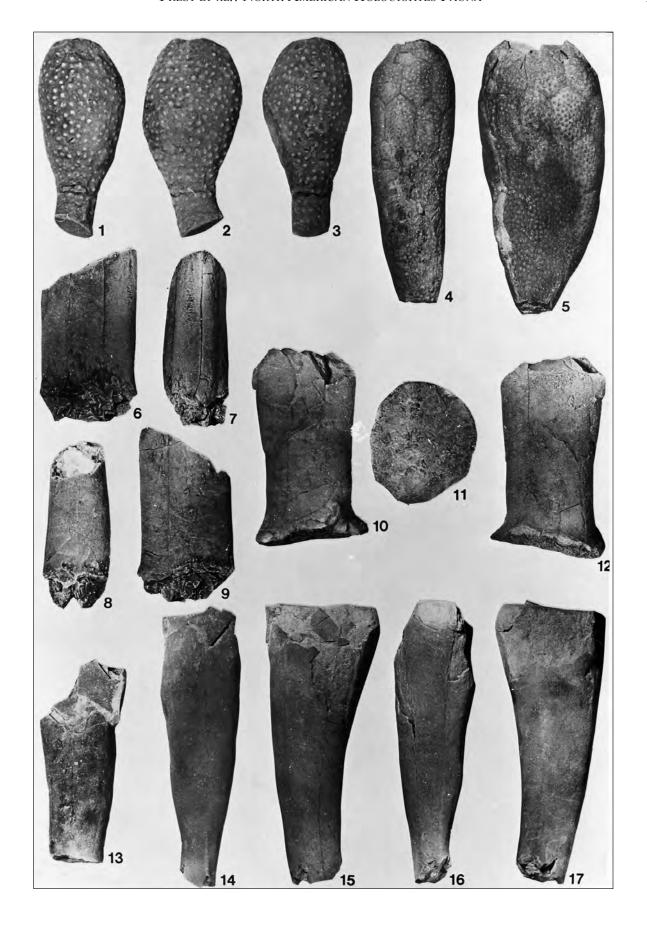
Wisconsin

For further discussion of many of these localities, see Frest et al. (1977: 91-105).

- (1) Horlick Reef complex. Horlick's quarry and Beswick's quarry, SW1/4 NE1/4 sec. 6, T3N R23E, South Milwaukee and Racine 7½' quadrangles, Racine County. The bioherm at Horlick's quarry (now a public park) is still accessible. Both quarries are long abandoned. For detailed information, see Frest *et al.* (1977: 92).
- (2) Ives Reef complex. Vulcan Materials Company quarry, SE1/4 sec. 29, T4N R23E, South Milwaukee 7½' quadrangle, Racine County. This quarry is still active. A section of the site was figured by Frest *et al.* (1977: fig. 4).
- (3) Franklin Reef. Franklin Stone Products quarry and Vulcan Materials Company quarry, SE1/4 NE1/4 sec. 10 and SW1/4 NW1/4 sec. 11, T5N R21E, Franklin, South Milwaukee 7½ quadrangle, Milwaukee County. These operations were active in 1976 and might still be accessible.
- (4) Trembone Reef complex. Abandoned quarry. SW1/4 sec. 28, T6N R21E, Hale's Corner 7½' quadrangle, Milwaukee County. Partly accessible currently.
- (5) Schoomaker Reef. Francy Quarry, SW1/4 SE1/4 sec. 22, T7N R21E, Milwaukee 7½' quadrangle, Milwaukee County. This site has been filled.
- (6) Menomonee Falls Reef. Road excavation, NE1/4 NW1/4 sec. 10, T8N R20E, Waukesha 7½' quadrangle,

- Waukesha County. Presently poorly exposed and not collectable. [CP: Note that Sec. 10 is not on the Waukesha 7½ quadrangle.]
- (7) Cedarburg Reef. Groth's quarry, center W1/2 sec. 35, T10N R21E, Port Washington 7½' quadrangle, Washington County. The quarry is water-filled, but a portion of a large bioherm, possibly younger than those in the Racine area, is still accessible in the N corner of the quarry.
- (8) Cook's quarry. Campus of Carroll College (on the athletic field) SE1/4 sec, 3, T6N R19E, Waukesha 7½' quadrangle, Waukesha County. Very poorly exposed at present.
- (9) Halquist quarry. Active quarry at Halquist Lannon Stone Company at Sussex, E1/2 NW1/4 sec. 35, T8N R19E, Waukesha 7½' quadrangle, Waukesha County. A few *Holocystites (Holocystites)* have been collected sporadically at this locality.
- (10) Genessee quarry. Active quarry in SW1/4 sec. 24, T6N R18E, Eagle 7½' quadrangle, Waukesha County.
- (11) Waukesha quarries. Old abandoned small quarries (including Hadfield's, now incorporated into two large quarries of the Waukesha Lime and Stone Company, along both sides of the Fox River in N Waukesha, center S1/2 sec. 26, T7N R19E, Waukesha 7½' quadrangle, Waukesha County. Formerly very productive localities, but presently diploporite occurrences are rare.

Figure		Page
Holocyst	itidae and Sphaeronitidae from the Osgood. All specimens coated with ammonium chloride sublimate.	
1-3.	Holocystites (Holocystites) alternatus (Hall, 1861). Three lateral views of a young specimen with a large base of attachment, three plate generations, and pyriform-globular theca; SUI 48176, maximum dimension = ca. 24 mm	. 72
4.	Holocystites (Holocystites) clavus Frest & Strimple, n. sp. Lateral view of large paratype, SUI 48165, maximum dimension = 62 mm.	. 73
5.	Holocystites (Holocystites) cylindricus (Hall, 1861). Lateral view of small specimen, SUI 48177, maximum dimension = 67 mm	. 72
6-17.	Finitiporus boardmani Frest & Strimple, n. gen., n. sp. Attachment bases and distalmost thecal plate circlet	. 64
	13. Lateral view of small specimen with 6 plates and possible traces of diplopores, SUI 48180, maximum dimension = 32.7 mm.	
	14-17. Lateral views of largest specimen found; note very thin adoral plates, unequal widths of 7 plates in this circlet; SUI 48181, maximum dimension = <i>ca.</i> 70 mm.	



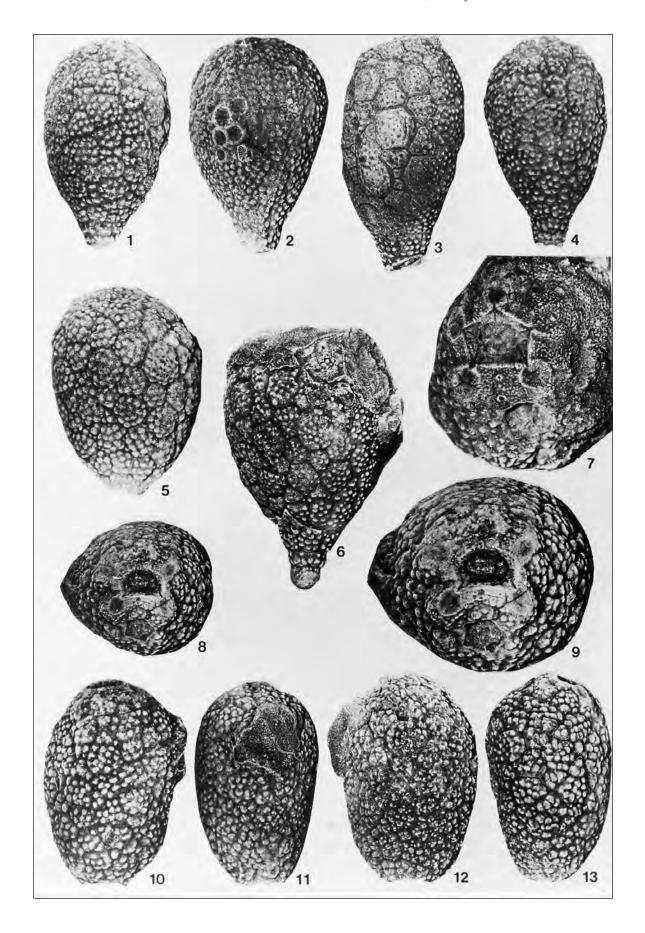
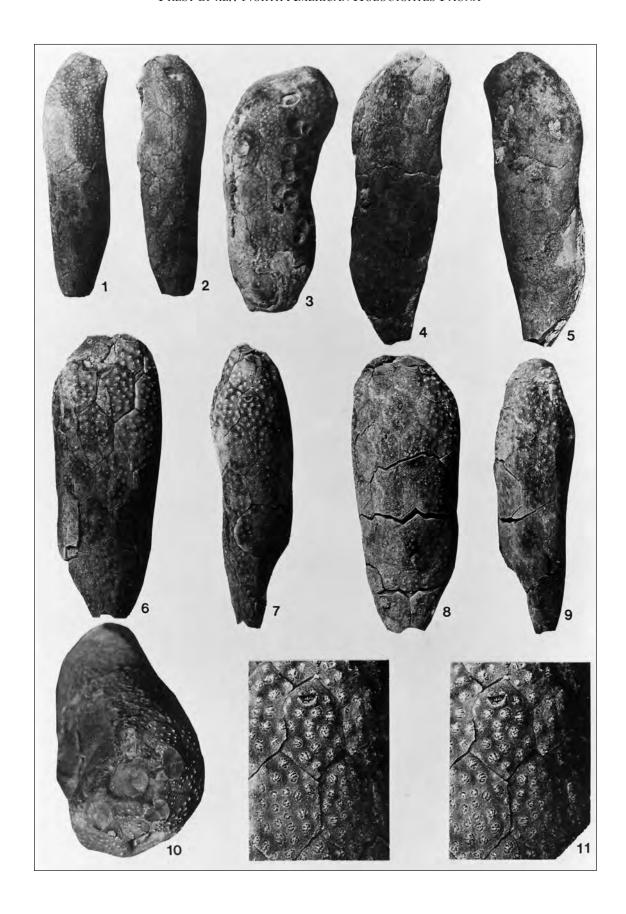


Figure		Page
Holocystii	tes (Holocystites) scutellatus Hall, 1864. All specimens coated with ammonium chloride sublimate.	. 74
1-2, 4.	Most common morph, with pyriform theca, moderately coarse pustulate ornament, and narrow base. 1. SUI 48182, maximum dimension = 35.7 mm. 2. SUI 42735, maximum dimension = 37.1 mm. 4. SUI 48183, maximum dimension = 35.7 mm.	
3.	Rare wide-based subcylindrical form, SUI 48169, maximum dimension = 41.4 mm.	
5.	Uncommon pyriform-globular form with narrow base (note rounded aboral termination), SUI 42734, maximum dimension = 46.4 mm.	
6.	[Ed.: no description or scale for this image was available.]	
7, 9.	 Enlarged peristomial views to show extremes of variation. 7. Common morph with numerous small pustules, wide peristomial border, circular facets, and round hydropore, SUI 48185, height of field of view = 17.3 mm. 9. Rare coarsely pustulate ovate-pyriform form with narrow peristomial border, oval facets, and elongate hydropore, SUI 48186, maximum dimension = 22 mm. 	
8, 10-13.	. Rare, coarsely pustulate, ovate-pyriform morph, SUI 48186. 8. Oral view, maximum dimension = 26.4 mm.	

Figure		Page
Holocyst	cites (Holocystites) clavus Frest & Strimple, n. sp. All specimens coated with ammonium chloride sublimate	. 73
1-2, 10.	Paratype SUI 48165, showing thecal shape (1-2) and peristomial morphology (10). 1. Anterior lateral view, maximum dimension = 62 mm. 2. Posterior lateral view, maximum dimension = 62 mm. 10. Enlarged oral view, note position of gonopore, maximum dimension = 29.7 mm.	
3.	Large paratype SUI 46318, with protruded peristome and borings concentrated on presumed "up" side, maximum dimension = 64 mm.	
4-5.	Large paratype SUI 46319, two lateral views showing three plate generations, maximum dimension = <i>ca.</i> 75 mm.	
6-9, 11.	 Holotype SUI 46317, a small specimen with two plate generations. 6-9. Four lateral views showing thecal morphology and pustular (raised three-dimensional) humatipores, maximum dimension = <i>ca.</i> 48 mm. 11. Stereoscopic pair detailing humatipore morphology on slightly weathered surface, height of field of view = 12.6 mm. 	



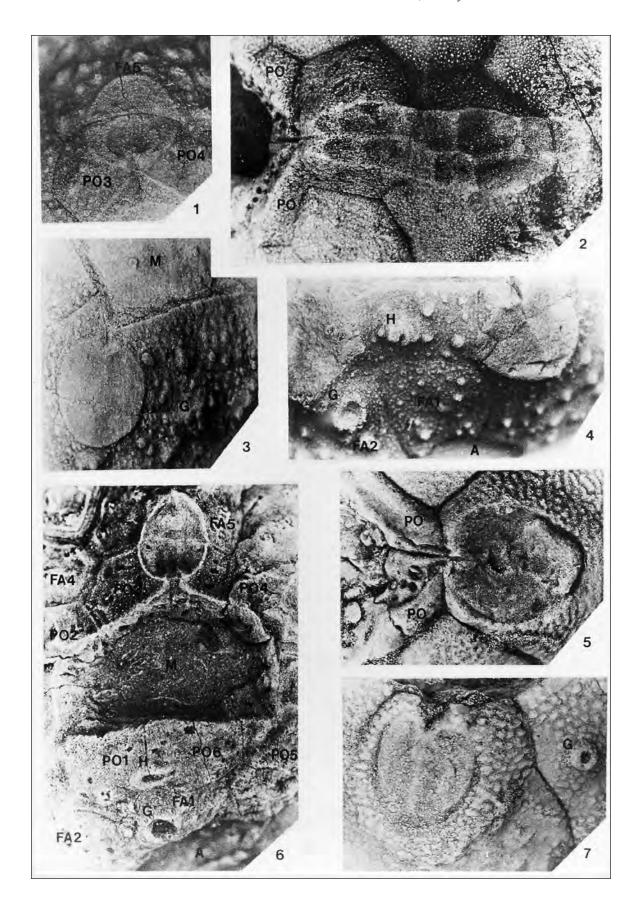
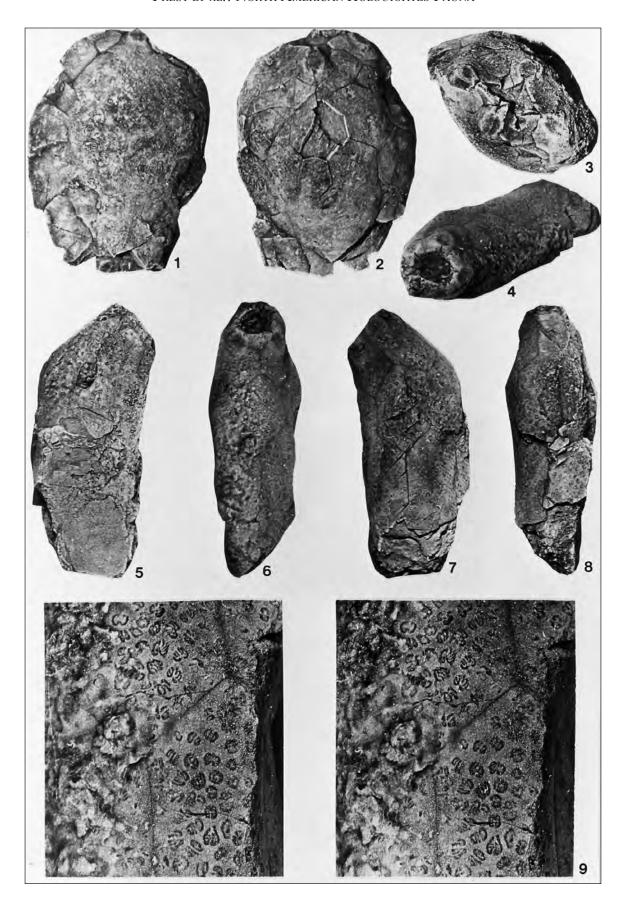


Figure		Page
Peristom	ial and ambulacral morphology of members of Holocystitidae. All specimens coated with ammonium chloride sublimate. Abbreviations: A, anus; FA, facetal plate; G, gonopore; H, hydropore; M, mouth; PO, perioral plate.	
1, 3, 6.	 Holocystites (Holocystites) scutellatus Hall, 1864	. 74
2.	Paulicystis sparsus Frest & Strimple, n. gen., n. sp., ambulacrum IV, SUI 48164, width of field of view = 10.9 mm. Large elongate facet overrunning facetal onto adjoining two thecal plate circlets and divided into biserially arranged muscle and ligament fields (?). The ambulacral groove is short and narrow, and oral pores (on periorals) are prominent	. 85
4.	Holocystites (Holocystites) clavus Frest & Strimple, n. sp., posterior interradius, SUI 48166, width of field of view = 11.4 mm. Hydropore on small, prominent elongate tubercle, almost closed; open gonopore on large, elevated tubercle on FA2. Note divided ambulacral facet (V).	73
5.	Osgoodicystis bissetti Frest & Strimple, n. gen., n. sp., ambulacrum V, SUI 48166, width of field of view = 8.4 mm. This specimen retains portions of two or three large, very thin, uniserial brachials. Note small periorals and oral pores	. 94
7.	Pentacystis gibsoni Frest & Strimple, n. sp., ambulacrum I and part of posterior interradius, SUI 48170, width of field of view = 9.6 mm. This specimen retains single proximalmost uniserial brachial, which still reflects divided ambulacral facet beneath. Periorals absent, gonopore on elevated prominent rounded tubercle, and hydropore not evident	. 92

Figure	P	age
Peristom	nial and thecal morphology of members of Holocystitidae. All specimens coated with ammonium chloride sublimate.	
1-3.	<i>Trematocystis magniporatus</i> Frest & Strimple, n. sp., paratype SUI 48717, showing large, dense humatipores (1-2), divided ambulacral facets and peristomial morphology (3) 1-2. Lateral views, maximum dimension = <i>ca.</i> 30 mm. 3. Oral view, maximum dimension = 23 mm; note apparent lack of a gonopore.	83
4-9.	 Holocystites (Holocystites) ?cylindricus (Hall, 1861), abnormal specimen, SUI 48172. 4. Oral view showing peristome (scale not recorded). 5-8. Lateral views showing six-plate circlets and protruding peristome, maximum dimension = ca. 44 mm. 9. Enlarged (stereoscopic pair) portion of Fig. 6, showing humatipore morphology, height of field of view = 22.3 mm. 	72



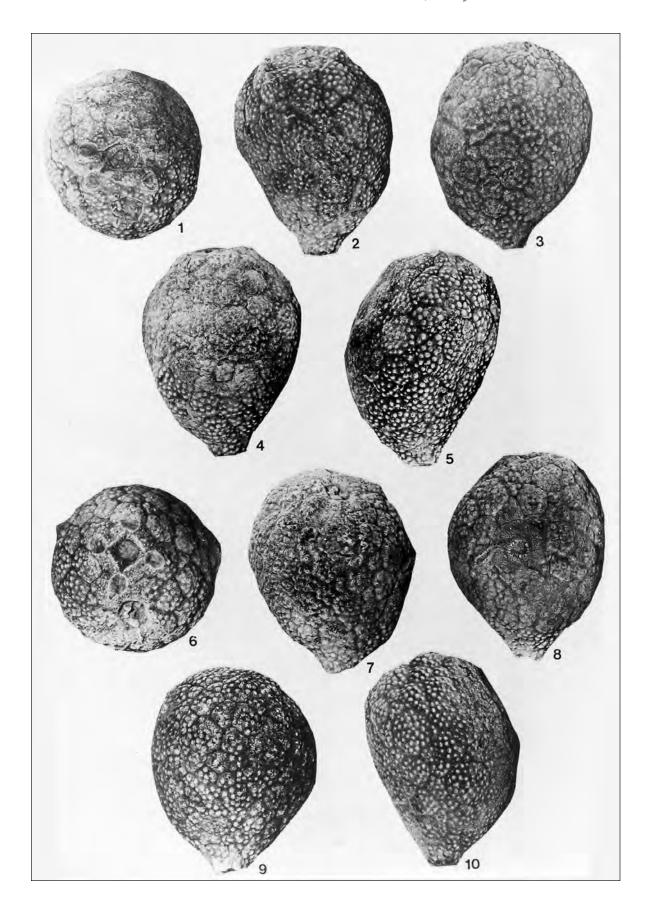
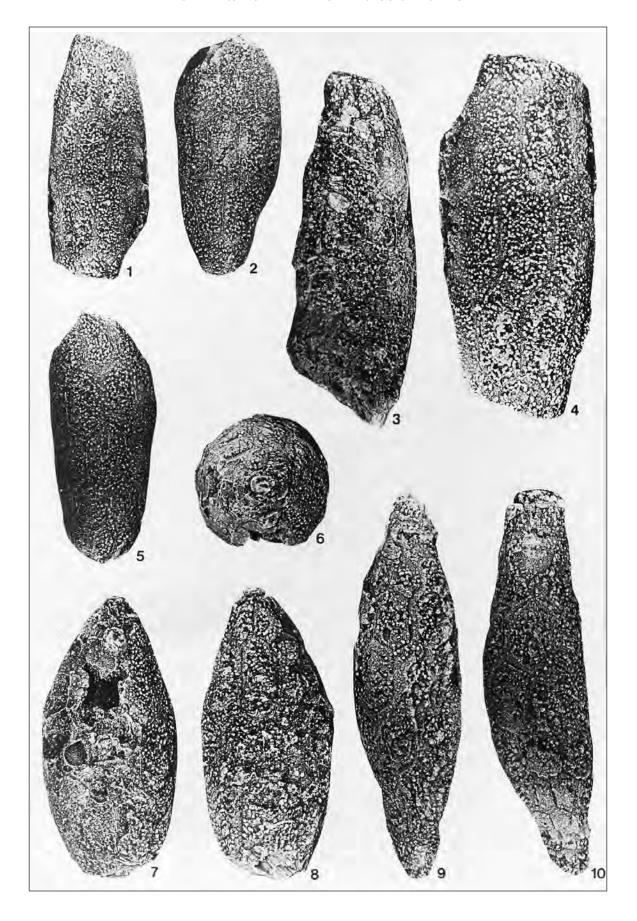


Figure Page 1-5. Small normal Osgood individual with 5 ambulacral facets (catalog number not recorded), maximum dimenension (2-5) = ca. 35 mm. 1. Oral view, maximum dimension = 28 mm. 2. Posterior view. 3. Right anterior view. 4. Anterior view. 5. Left anterior view. 6-10. Individual with 4 ambulacral facets and abnormal perioral plate arrangement, SUI 48188 (see Text-fig. 22), maximum dimension (7-10) = ca. 34 mm. 6. Oral view, maximum dimension = 28.7 mm. 7. Posterior view. 8. Right anterior view. 9. Anterior view.

10. Left anterior view.

Figure	Y.	'age
Holocyst	ites (Megacystites Frest & Strimple, n. sgen.) greenvillensis Foerste, 1917. All specimens coated with ammonium chloride sublimate.	77
1, 5.	Small specimen showing five ranges of thecal plates, SUI 48192, maximum dimension = <i>ca.</i> 40 mm.	
2.	Small specimen with four thecal plate circlets, SUI 48196, maximum dimension = 39.3 mm.	
3.	Incomplete large specimen with five thecal plate circlets, SUI 48193, maximum dimension = 58.7 mm.	
4.	Largest individual, broken at both ends, with five thecal plate circlets, SUI 48194, maximum dimension = 60 mm.	
6-8.	Large specimen, SUI 48195, maximum dimension = <i>ca.</i> 47 mm. 6. Oral view showing facetal and perioral plates, maximum dimension = 22.3 mm. 7. Posterior lateral view. 8. Anterior lateral view.	
9-10.	Medium-sized complete specimen showing nine circlets of thecal plates and preserving external surfaces of a few thecal plates, SUI 42732, maximum dimension = <i>ca.</i> 63 mm. 9. Left anterior view. 10. Posterior view.	



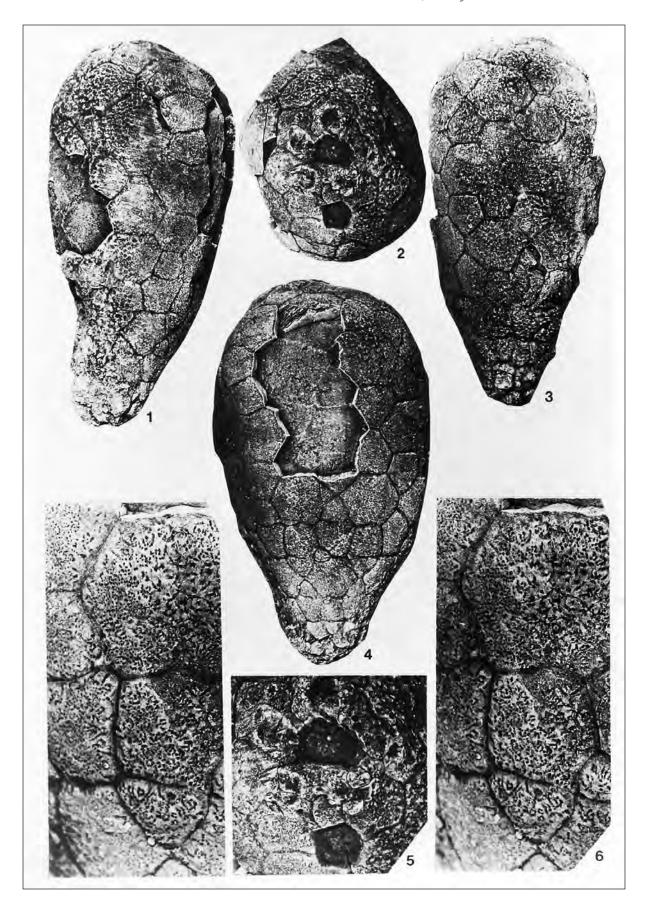
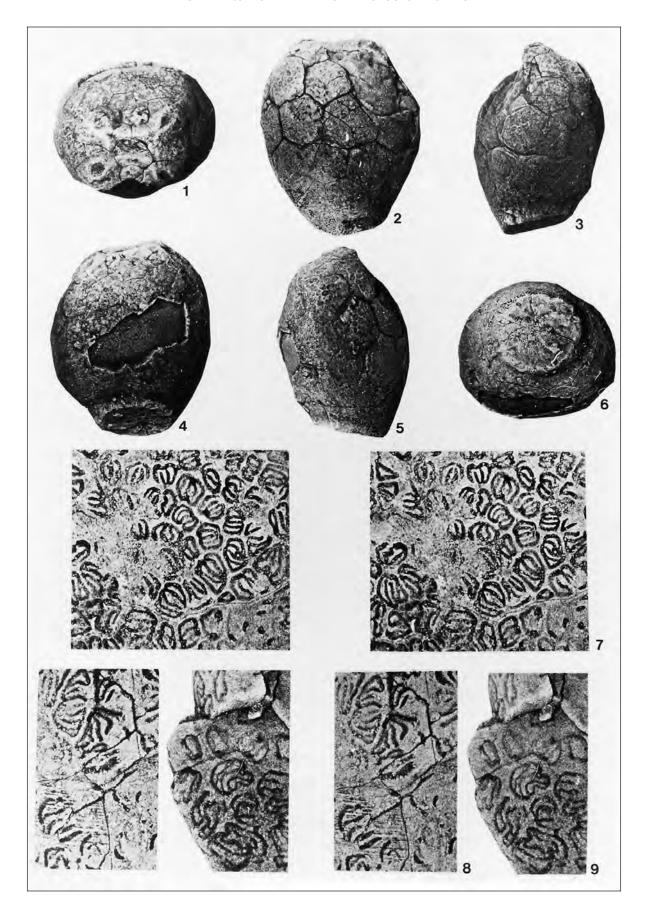


Figure		Page
Holocysti	ites (Sepulticystis Frest & Strimple, n. sgen.) spangleri Miller, 1891, Large specimen, SUI 48197, maximum dimension ca. 96 mm. All specimens coated with ammonium chloride sublimate.	. 79
1.	Anterior view.	
2.	Oral view, maximum dimension = 56 mm.	
3.	Left anterior view.	
4.	Posterior lateral view.	
5.	Enlargement of peristome to show atypical perioral plate arrangement and gonopore in FA2, width of field of view = 32.7 mm.	
6.	Enlargement (stereoscopic pair) of thecal plates to illustrate morphology of humatipores, height of field of view = 31 mm.	

PLATE 9 Figure Page All specimens coated with ammonium chloride sublimate. 1-6. Holotype SUI 48198. 1. Oral view, peristome showing four rounded facets, periorals surrounding peristomial opening, and position of gonopore and hydropore, maximum dimension = 26.7 mm. 2-5. Lateral views showing few plate circlets (one generation), large humatipores, maximum dimension ca. 33 mm. 2. Posterior view. 3. Left anterior view. 4. Anterior view. 5. Right anterior view. 6. Basal view showing circular, flat attachment base, approximately one-half of ambital diameter, maximum dimension = 26 mm. 8-9. Enlarged stereoscopic pairs of portions of a few plates of the two type specimens. Note large, densely packed humatipores with irregular outlines, height of each field of view = 10 mm 8. Holotype SUI 48198. 9. Paratype SUI 48171. 7. Trematocystis rotundus (Miller, 1879). Enlarged stereoscopic pair of portions of several plates of SUI 46309, height of field of view = 10 mm. Small, moderately densely packed humatipores



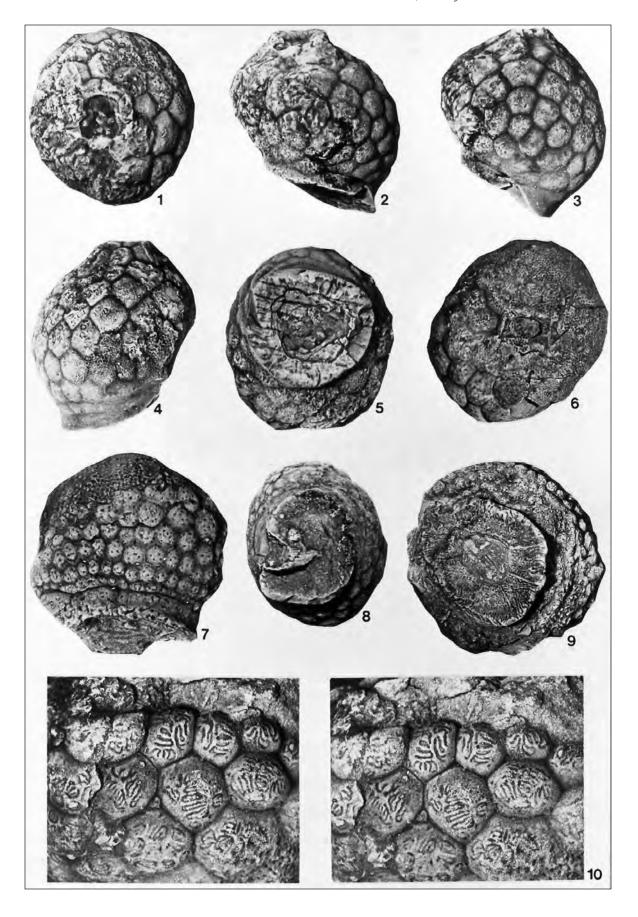
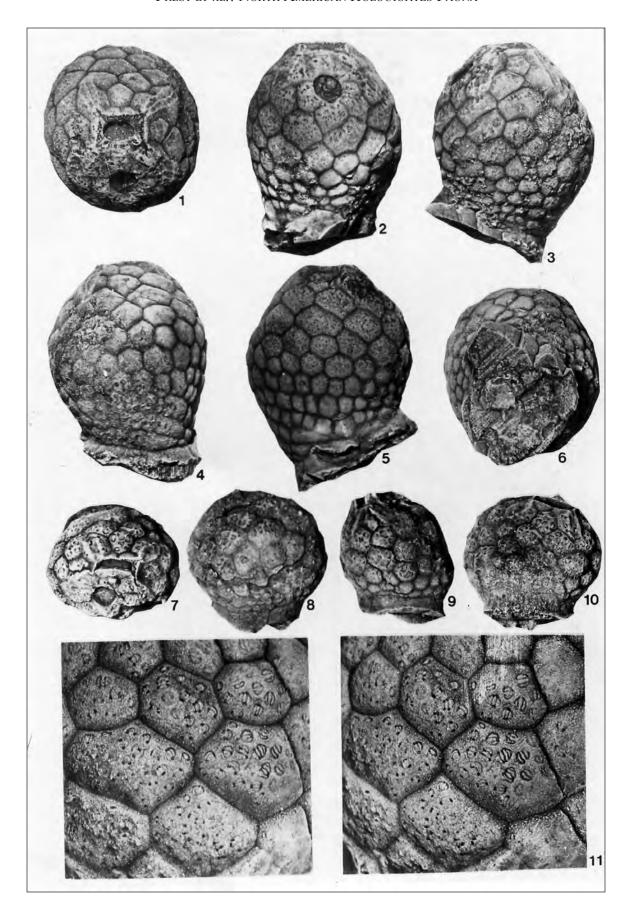


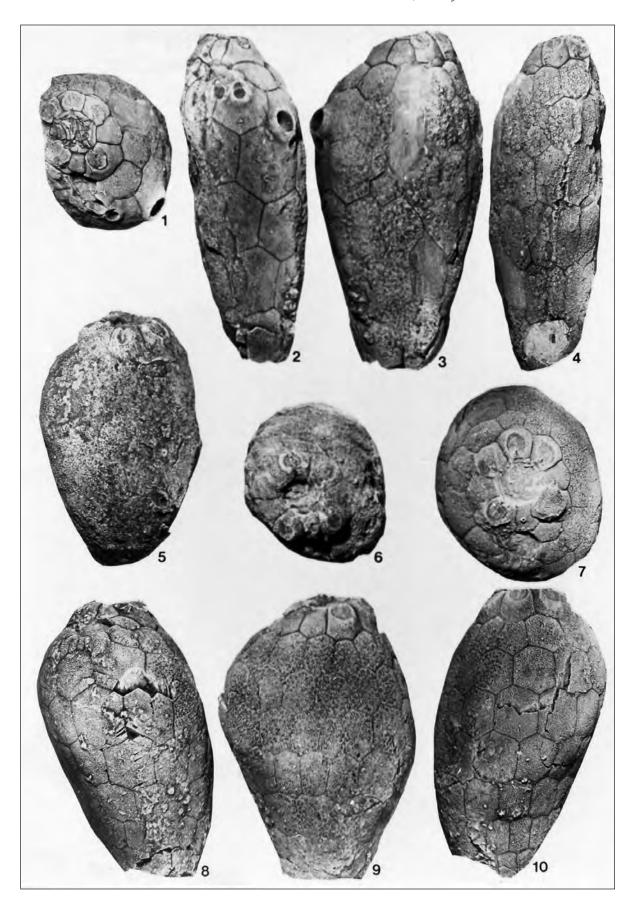
Figure	P	age
Paulicyst	tis Frest & Strimple, n. gen. All specimens coated with ammonium chloride sublimate.	
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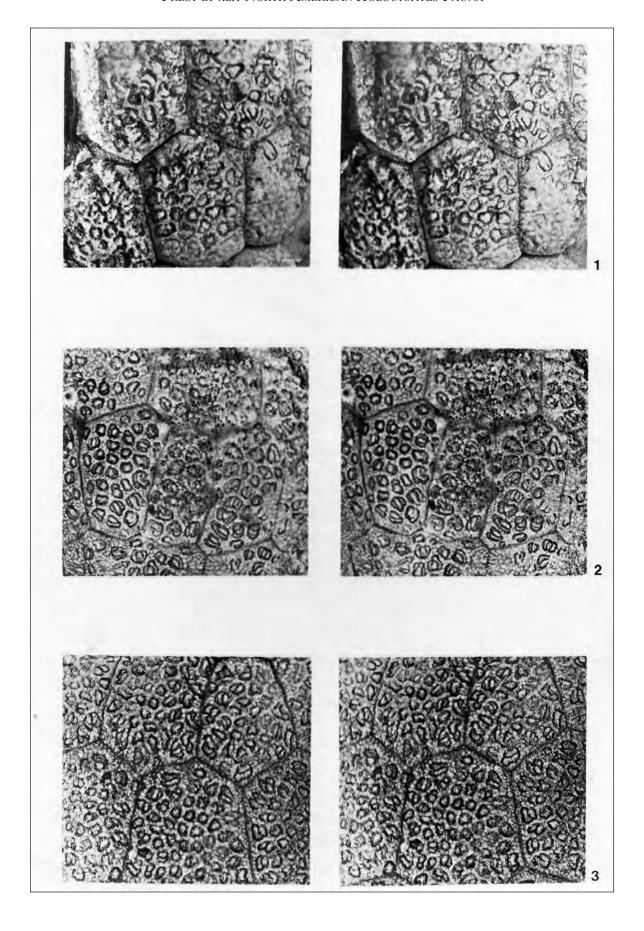
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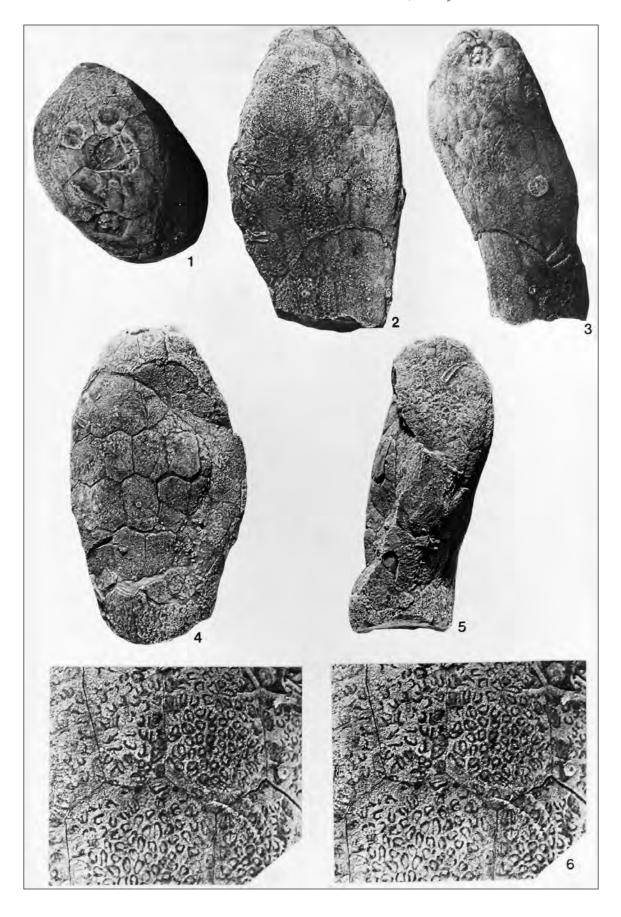


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PREPARATION OF MANUSCRIPTS

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ISSN 0007-5779

