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Early Silurian Camerate Crinoids of Eastern Iowa

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Large and diverse Lower Silurian (late Llandoverian) camerate crinoid faunas from the Hopkinton Dolomite of eastern Iowa form the basis of the present study and partially fill the long gap between previously known Late Ordovician and Middle Silurian (Wenlockian) faunas. Taxa are considered in detail up to and including superfamilial level.

Several superfamilies and 12 families are recognized covering 20 genera, of which 8 are new. Three subgenera are recognized, one of which *(Eucrinus)* was originally described as a discrete genus. Thirty-eight species are recognized, 17 of which are described as new taxa, but 15 are relegated to an informal (unnamed) status due to preservational difficulties. New genera are *Luxocrinus, Allozygocrinus, Pregazacrinus, Bolicrinus, Thomasocrinus, Krinocrinus, Archaeocalyptocrinus,* and *Theleproktocrinus*. New species are *Luxocrinus simplex, Dimerocrinites (Dimerocrinites) sculptus, D. (D.) hopkintonensis, Allozygocrinus dubuquensis, Pregazacrinus hemisphericus, Carpocrinus bodei, Bolicrinus globosus, B. deflatus, Thomasocrinus cylindrica, Krinocrinus inflatus, Macrostylocrinus compressus, M. vermiculatus, Allocrinus ornatus, Marsupiocrinus (Amarsupiocrinus) primaevus, Archaeocalyptocrinus nodosus, A. iowensus,* and *Theleproktocrinus davidsoni*.

Stratigraphy of the Hopkinton Dolomite has been summarized elsewhere and is not extensively discussed. New information on the phylogeny of the Silurian camerate crinoids, as interpreted from the Hopkinton collections, has modified and expanded the understanding of an Early Silurian evolutionary radiation.

INDEX DESCRIPTORS: Paleontology, Silurian, Llandoverian, Hopkinton Dolomite; eastern Iowa; Crinoidea, Camerata; new genera *Luxocrinus, Allozygocrinus, Pregazacrinus, Bolicrinus, Thomasocrinus, Krinocrinus, Archaeocalyptocrinus,* and *Theleproktocrinus;* new species *Luxocrinus simplex, Dimerocrinites (Dimerocrinites) sculptus, D. (D.) hopkintonensis, Allozygocrinus dubuquensis, Pregazacrinus hemisphericus, Carpocrinus bodei, Bolicrinus globosus, B. deflatus, Thomasocrinus cylindrica, Krinocrinus inflatus, Macrostylocrinus compressus, M. vermiculatus, Allocrinus ornatus, Marsupiocrinus (Amarsupiocrinus) primaevus, Archaeocalyptocrinus nodosus, A. iowensis,* and *Theleproktocrinus davidsoni*.

INTRODUCTION

Significant advances in camerate crinoid evolution occurred during the interval separating known Late Ordovician and Middle Silurian (Wenlockian) echinoderm faunas. The discovery of diverse Early Silurian (late Llandoverian) crinoid faunas in the Hopkinton Dolomite of eastern Iowa partially fills this long gap in the geologic record. Of the more than 2700 generically identifiable echinoderm fossils examined from the Hopkinton Dolomite during the course of this study, more than 75% of the individuals are camerate crinoids. Additionally, specimens of inadunate and flexible crinoids, rhombiferan and diploporan cystoids, blastoids, eocrinoids, and paracrinoids are also noted (Witzke, 1976; Witzke, Frest and Strimple, 1979; Frest, Strimple and Witzke, 1980). Preservation of the Hopkinton crinoids as internal and external molds is generally poor, although the critical plating arrangement of the dorsal cups is preserved on many of the specimens.

The stratigraphy of the Hopkinton Dolomite is summarized in reports by Johnson (1975, 1977) and Witzke (1978, 1980) whose stratigraphic nomenclature largely follows Calvin and Bain (1900). Echinoderm debris is scattered to abundant throughout most of the Hopkinton Dolomite, most commonly as molds of disarticulated plates and columnals or dolomitized echinoderm wackestone to packstone textures. However, articulated camerate crinoid cups have been noted in only two stratigraphic intervals within the formation. The stratigraphically lower interval, the "*Cyclocrinites* beds" of Johnson (1975), has produced a variety of patelliocrinid and patelliocrinid-derived taxa and the oldest representatives of several camerate crinoid families. The "*Cyclocrinites* beds" are considered by Johnson (1975, 1977) to be of mid Late Llandoverian age (C_3-C_4). Identifiable echinoderm remains are scattered to abundant in this stratigraphic interval, and brachiopods (especially globular *Pentamerus* and *Stricklandia),* molluscan fossils (gastropods, nautiloids), and *Cyclocrinites* (a green alga) are especially prominent.

The "*Cyrtia* beds" have yielded the greatest abundance and diversity of crinoids in the Hopkinton, and this interval is probably C_5-C_6 late Llandoverian in age (Johnson, 1975, 1977; Witzke, 1978). The "*Cyrtia* beds" include dense, micritic, fossiliferous dolomites with scattered to abundant echinoderm, brachiopod, and bryozoan fossils and porous very crinoidal dolomites. A zone of biohermal (reef) buildups and flat-lying inter-reef rocks occurs beneath the "*Cyrtia* beds," and coarse crinoidal packstones may bury these bioherms (Philcox, 1970) in a stratigraphic position equivalent to the lower "*Cyrtia* beds." The "*Cyrtia* beds" are separated from the overlying "*Pentameroides* beds" primarily on the basis of fossils, and together the "*Cyrtia-Pentameroides* beds" form a single rock-stratigraphic unit (Witzke, 1978, 1980). Disarticulated echinoderm debris is volumetrically more important than the articulated crinoid cups which are scattered to abundant throughout much of the interval.

EVOLUTION OF THE SILURIAN CAMERATE CRINOIDS

An explosive evolutionary radiation within the camerate crinoid groups, coinciding with the spread of extensive intracontinental carbonate shelf environments during a generally transgressive marine sequence, occurred during the Llandoverian (Early Silurian) in North America (Witzke, Frest, and Strimple, 1979). Many camerate crinoid genera and families first appeared at that time, and these new taxa formed the root stocks from which many characteristic Wenlockian-Ludlovian (late Silurian) taxa, both endemic and cosmopolitan forms, arose. The Hopkinton crinoid faunas fill a critical gap in the evolutionary history of the camerates, and little supplemental information of Llandoverian crinoid evolution is currently available (*ibid.;* Brower, 1975). A study of the Early Silurian camerate crinoids from Iowa has necessitated several revisions in the proposed camerate phylogenies of Moore and Laudon (1943) and Ubaghs (1978).

Primitive dimerocrinitids, patelliocrinids, melocrinitids, rhodocrinitids, and tanaocrinids formed the primary stocks from which most Silurian camerate crinoids were originally derived. These camerate stocks are represented in Late Ordovician faunas of the North American continental interior. Latest Ordovician carbonate units in Missouri (Girardeau, Noix, Cyrene) are among the best sources of these ancestral camerates (e.g. Brower, 1973).

The camerate crinoids are divisible into monocyclic forms with only a single circlet of plates (the basals) below the radials and dicyclic forms with two circlets of plates (basals, infrabasals) below the radials. The monocyclic—dicyclic schism arose early in the evolution of the camerates and, in most cases, remains of primary phylogenic significance (Warn, 1975). The Hopkinton fauna includes several dicyclic camerate crinoid groups (Rhodocrinitidae, Dimerocrinitidae, Lampterocrinidae, Gazacrinidae). Two rhodocrinitid taxa are meagerly represented in the Hopkinton collections, and both of these taxa represent extremes in dorsal cup simplification for the family. An unnamed rhodocrinitid, apparently derived from a form like *Atactocrinus* (Late Ordovician, Illinois), is characterized by the complete expulsion of the interbrachs in one or more interrays allowing some of the radials and primibrachs to join. This extreme condition is never again repeated in the long history of the dicyclic camerates. *Luxocrinus* has a dorsal cup with one fixed primibrach per ray and a single interbrach per interray producing the simplest plate configuration of any known rhodocrinitacean. No additional rhodocrinitacean taxa are currently known from the Hopkinton Dolomite, and the origins of later Silurian rhodocrinitids and archaeocrinid-derived taxa remains poorly understood. However, the ultra-simplified cup configuration of the known Hopkinton rhodocrinitids suggests that major and apparently rapid evolutionary modifications arose within the Early Silurian rhodocrinitid groups at a time when other camerate groups were also undergoing evolutionary radiation.

Several primitive dimerocrinitid stocks (3 species of *Ptychocrinus)* are known from Late Ordovician faunas of North America, and these forms provided the ancestral stock from which several major crinoid groups radiated in the Llandoverian seas of North America. The development of biserial arms from the *Ptychocrinus* stocks would produce forms assignable to *Dimerocrinites,* a cosmopolitan genus throughout much of the Silurian, or *Eudimerocrinus*. *Dimerocrinites* forms the central stock from which three short-lived North American endemic crinoid families evolved. The development of an anal tube, as in *D. hopkintonensis,* along with the posterior bulging of the calyx produced the highly successful endemic Lampterocrinidae. The expulsion of distal interbrachs and compression of the fixed brachials in a dimerocrinitid stock produced the North American endemic Gazacrinidae. The radiation of the gazacrinids and lampterocrinids probably occurred in the late Llandoverian (about C_5). In clastic deposits of similar age in Scotland and New York (Brower, 1975; Brett, 1978) the still persistent, though archaic, ptychocrinid lines are noted. Another group, the nyctocrinids, has been noted only in Ludlovian deposits of Tennessee and was probably derived from the gazacrinids by expulsion of the interbrachs and fixed brachials allowing the radials to come in contact all around (Moore and Laudon, 1943, p. 84). An unusual additional form in the Hopkinton, *Allozygocrinus,* may be related to the dimerocrinitids and is comparable to probable dimerocrinitids in Scotland (Brower, 1975).

Abundant monocyclic camerate crinoids are noted in the Hopkinton Dolomite (Periechocrinidae, Carpocrinidae, Patelliocrinidae, Marsupiocrinidae, Eucalyptocrinitidae, Hapalocrinidae, and Himeacrinidae), and, excluding the patelliocrinids and possibly the periechocrinids, include the oldest and most primitive members of the included families. The tanaocrinid stock, as represented by *Compsocrinus,* is present in the Late Ordovician faunas of North America, and the periechocrinids were probably derived from this stock (Moore and Laudon, 1943, p. 87). The chief structural character separating the periechocrinids from the carpocrinids is a hexagonal vs. a quadrangular primibrach 1 (IBr 1)(ibid., p. 92). An ancestral carpocrinid is noted in the Hopkinton fauna with variably pentagonal or hexagonal IBr l; it is included in the Carpocrinidae because of its low cup shape and general plate configuration. The proximal flattening of a primitive periechocrinid dorsal cup would result in modification of the IBr 1, and the derivation of the carpocrinids from the periechocrinids is implied to have occurred in such a manner during the Llandoverian. Glyptocrinid stocks produced the divergent Silurian families Melocrinitidae and Scyphocrinitidae. The melocrinids, present in Late Ordovician faunas of North America, were cosmopolitan in the Wenlockian. Unfortunately, no Early Silurian melocrinitids have yet been described; evolutionary trends in the family are summarized by Brower (1976). The scyphocrinitids were not present in North American faunas until the Pridolian, and the family was probably derived in southeast Asia in the early Llandoverian (Witzke, Frest, and Strimple, 1979).

The evolutionary radiation of the Early and mid-Silurian is the most pronounced and dramatic radiation of higher crinoid taxa noted in the Paleozoic. This is particularly evident for the Patelliocrinacea. Only a few taxa of primitive patelliocrinids are present in the Late Ordovician faunas of North America and England. The Hopkinton Dolomite faunas include a diverse array of patelliocrinid and patelliocrinid-derived taxa, and these faunas may help clarify the phylogenic relationships of several camerate groups. The diverging groups of the Silurian patelliocrinid radiation produced a number of recognizable dorsal cup modifications in the basic patelliocrinid plan. Some of the diverging groups became the root stocks of successful and long-lived taxonomic groups (conventionally given family and superfamily rank), while others of these groups were unable to compete in the changing paleocommunities and became extinct. The basic patelliocrinid stocks as represented by *Macrostylocrinus* (a broadly defined genus), are well represented in the Late Ordovician and Llandoverian faunas in North America. Nine species, all lumped under *Macrostylocrinus*, are noted in the Hopkinton Dolomite, some of which represent major evolutionary advances. The archaic *M. cirrifer-M. silurocirrifer* lineage of western Europe probably terminated in the Llandoverian, and all Wenlockian *Macrostylocrinus*, related patelliocrinids, and most patelliocrinid-derived taxa probably originated from North American stocks (Brower, 1975, p. 638). Additionally, *Krinocrinus, Bolicrinus,* and *Thomasocrinus* represent unsuccessful modifications of the basic patelliocrinid plan in the Llandoverian of North America. *Krinocrinus* differs from primitive *Macrostylocrinus* primarily in the posterior interray, while the *Bolicrinus-Thomasocrinus* lineage is characterized by the development of a rigid tegmen and the loss of lateral interbrachs. *Allocrinus* is derived from a *Macrostylocrinus* stock by the expulsion of the distal interbrachs and proximal compression of the fixed brachials.

Primitive marsupiocrinids noted in the late Llandoverian deposits of Iowa are the oldest known representatives of the family. The flattening of the dorsal cup and expulsion of the distal interbrachs in a primitive patelliocrinid stock would produce the characteristic marsupiocrinid cup. Ubaghs (1978) derived the marsupiocrinids from a hapalocrinid (?) stock, although Frest (1975) included the marsupiocrinids within the Patelliocrinacea and derived the family directly from the patelliocrinids. Expulsion of the interbrachs in linear fashion from the cup onto the interambulacral areas apparently produced the rigid tegmen noted in the primitive Hopkinton marsupiocrinids, and these features seem more characteristic of a patelliocrinid ancestry and do not seem closely allied to the hapalocrinids or the Platycrinitacea in general. The group of 10-armed *Marsupiocrinus* remained endemic to North America throughout the Silurian, while the 20-armed forms remained endemic to Europe during the Silurian and may have been derived from a separate, perhaps European, patelliocrinid stock.

The eucalyptocrinitids, previously thought to have been derived from a clonocrinid-like ancestor (Moore and Laudon, 1943, p. 99; Ubaghs, 1978, p. 286) are believed, instead, to have been derived directly from a patelliocrinid stock. Ancestral eucalyptocrinitids (*Archaeocalyptocrinus*) are noted in mid late Llandoverian strata in Iowa, and the conical base of the dorsal cup is most reminiscent of the patelliocrinids. The invagination of the base and the development of tegmen partitions accompanied the C_5-C_6 Late Llandoverian evolution of two highly successful cosmopolitan (Wenlockian, Ludlovian) genera, *Eucalyptocrinites* and *Calliocrinus*. Ray simplification of *Calliocrinus* produced *Chicagocrinus* in the Wenlockian. The Clonocrinidae was probably derived directly from a patelliocrinid stock (Moore and Laudon, 1943, p. 98), although the evolution was apparently independent of the eucalyptocrinitids. A European endemic family, the Stelidiocrinidae, was probably derived from a European patelliocrinid stock sometime in the late Llandoverian or Wenlockian.

The Hopkinton Dolomite has produced the oldest known hapalocrinid, *Theleproktocrinus*. This ancestral hapalocrinid appears to have been derived from a patelliocrinid stock by enlargement of the radials, expulsion of the interbrachs onto the tegmen, and expulsion of the fixed secundibrachs from the cup. Further expulsion of the primibrachs and the development of large oral plates distinguishes most younger hapalocrinids from *Theleproktocrinus*. A North American endemic group, the himeacrinids, were derived from primitive hapalocrinids before the end of the Llandoverian. The platycrinitids appeared later in the Silurian, and were probably derived from a modified hapalocrinid.

The late Llandoverian was a time of unprecedented experimentation among many known camerate crinoid groups, and extremes in camerate dorsal cup simplification and tegmen specialization are noted. The evolutionary relationships among the camerate crinoid groups inferred by Moore and Laudon (1943) and modified or confirmed in this and other studies are summarized in Figure 1. As interpreted by Ubaghs (1978, p. 286), his illustrated evolutionary trends in the Camerata are decidedly gradualistic in the derivation of most higher taxa. Ubaghs derives most Silurian families from remote and unknown ancestors in the Lower, Middle and Upper Ordovician as suggested by his illustration. In light of changing ideas about evolutionary theory and the possibility of geologically rapid evolutionary events (considered viable by many paleontologists), gradualistic inferences imposed upon phylogenies may conceal evolutionary events such as radiations. For example, Ubaghs (ibid.) infers the derivation of the carpocrinids from an unknown tanaocrinid in the Lower Ordovician, whereas this study derives the carpocrinids, based on transitional features exhibited on Hopkinton specimens, directly from the morphologically similar periechocrinids.

The dramatic evolutionary expansion among many of the camerate crinoid groups that occurred during the late Llandoverian seems to coincide with the expansion of carbonate environments as seas inundated the North American continental interior. Differentiation of the existing Late Ordovician carbonate-dwelling crinoids occurred as new niches for benthic suspension-feeding groups were realized in the expanding carbonate environments. Some of the groups, possibly due to restricted larval dispersal potentials, remained endemic to a given carbonate shelf throughout the Silurian (Witzke, Frest and Strimple, 1979). The maximum diversification of these echinoderm groups was reached in the Wenlockian. The Silurian suspension-feeding echinoderm groups became well adapted, not only in many level-bottom paleocommunities, but also as dominant elements of many reef and reef-associated paleocommunities. A general marine regression, apparently beginning in the late Wenlockian and continuing through the remainder of the Silurian, marked a time of crisis among many of the suspension-feeding echinoderm groups. The surviving echinoderm groups show little further diversification until the Devonian.

Unlike the replacement of North American endemic brachiopods by

Old World groups at the beginning of the Silurian (Sheehan, 1975, p. 206), "the Silurian echinoderm radiation has one of its major focal points in the Ordovician faunas of North America" (Witzke, Frest, and Strimple, 1979, p. 127). Speciation in the diversifying benthic echinoderm groups probably occurred within the confines of the epicontinental seas. Many of the echinoderm faunal elements characteristic of the continental interior are notably lacking from continental margin ("onshore") deposits and the preserved lineages of most Silurian echinoderm groups are noted only in carbonate deposits of the continental interior (e.g., Hopkinton Dolomite). The contention that "the opportunities for speciation appear to have been in the onshore areas" (Eldredge, 1974, p. 544) may be an incorrect generalization for benthic invertebrate groups. During transgressive marine sequences many opportunities for speciation and migration should be available within the confines of the epicontinental seas, especially as "endemic" reef and level-bottom environments are created. Marine regressions, on the other hand, would be times of crisis among specialized benthic invertebrate groups restricted to niches on the retreating carbonate shelf.

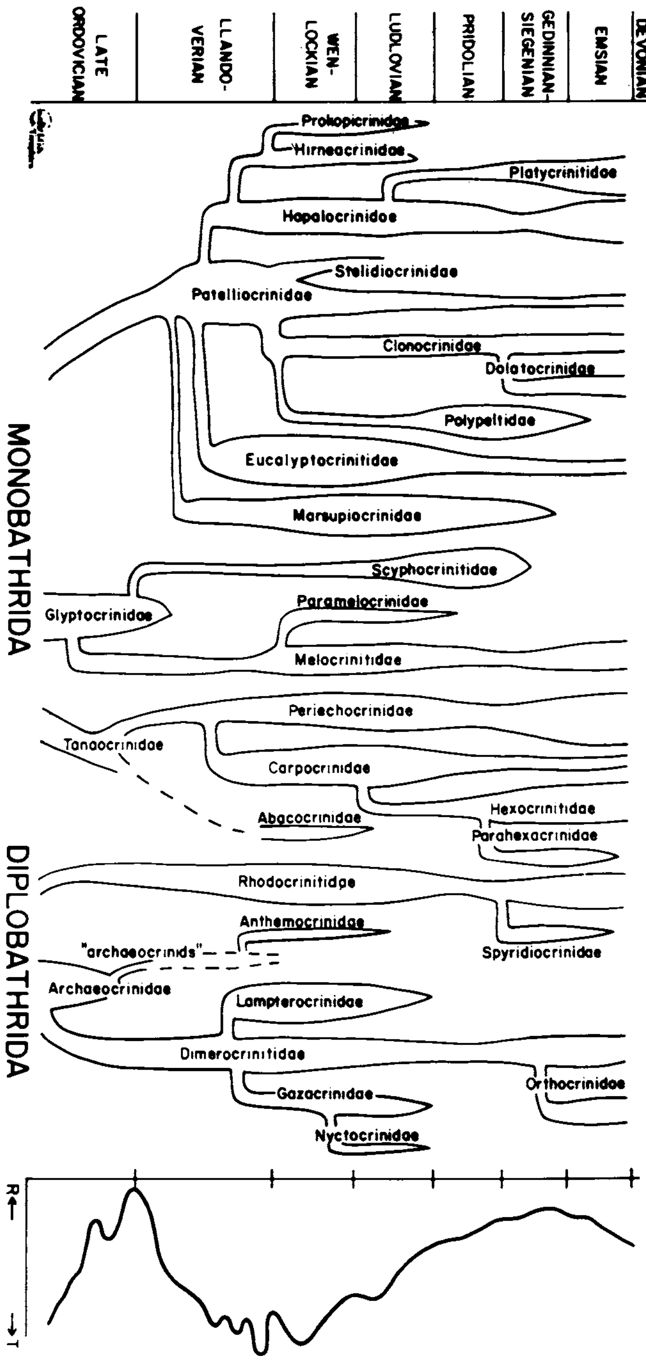

Fig. 1. *Inferred phylogeny of the Late Ordovician through Lower Devonian camerate crinoid families. Width of branches reflects relative abundance or diversity of each family in known collections. Time scale on left side; Llandoverian through Pridolian represents the Silurian. Right side shows probable eustatic sea level curve (R - regressive or shallowing trend, T - transgressive or deepening trend).*

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TERMINOLOGY

The terminology, nomenclature, and diagnoses of taxa above the generic rank utilized in this study are from the *Treatise on Invertebrate Paleontology,* Part T (Univ. Kansas Press), unless otherwise noted.

REPOSITORIES

All specimens examined during the course of this study are reposited in the University of Iowa, Iowa City, Department of Geology collections (SUI) or the Field Museum, Chicago, Walker Museum and other University of Chicago collections (UC). Locality numbers are listed in the Appendix.

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA Miller, 1821
Subclass CAMERATA Wachsmuth & Springer, 1885
Order DIPLOBATHRIDA Moore & Laudon, 1943
Suborder EUDIPLOBATHRINA Ubaghs, 1953
Superfamily RHODOCRINITACEA Roemer, 1855

Diagnosis: Radials generally separated from each other by interbrachs which adjoin basals, although radial circlet may be partly adjoined.
Discussion: The superfamilial diagnosis has been emended from Ubaghs (1978, p. 4-14) to include forms that may have the radial circlet partly adjoined. *Atactocrinus,* some *Lyriocrinus,* and an undetermined rhodocrinitid from the Hopkinton Dolomite are known to possess adjoined radial plates. The trend toward closure of the radial circlet in certain rhodocrinitaceans led to the development of the dimerocrinitaceans.

Family RHODOCRINITIDAE Bassler, 1938

Discussion: Ubaghs' (1978) familial diagnosis should be modified to include forms with partly adjoined radial circlets.

Rhodocrinitid sp.
Plate 1, Fig. 1; Text-fig. 2

Description: Dorsal cup subglobose, wider than high. Infrabasal circlet pentagonal; basals large, adjoining all around; larger BB hexagonal; smaller BB pentagonal, aligned with adjoining RR plate sutures. Radial circlet partly adjoined, partly separated; RR wider than high, pentagonal or hexagonal. Single large primibrach per ray bears arm facets; primibrachs adjoin in those rays in which RR adjoin, otherwise separated by interbrach. Interbrachs present only above hexagonal BB; first interbrach large, heptagonal, bearing two plates in next range that are largely incorporated into tegmen. Two arms per ray. SUI 42278 measures 8 mm high × 10 mm wide.

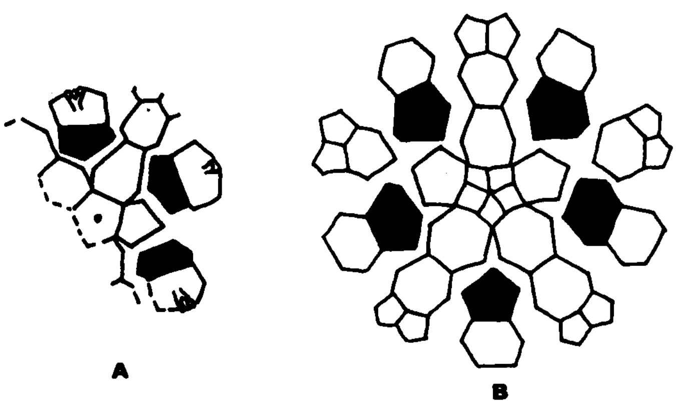


Fig. 2. *Rhodocrinitid plate diagrams (RR black). A) Early Silurian rhodocrinitid, Hopkinton Dolo., Iowa. B) Late Ordovician* Atactocrinus, *Illinois (from Weller, 1916).*

Discussion: A single specimen of a very unusual rhodocrinitid from the "*Cyclocrinites* beds" reveals the radials partly adjoined and partly separated. The specimen may be an abnormal representative of an undetermined rhodocrinitid, although its close resemblance to the Late Ordovician (Illinois) *Atactocrinus* would tend to preclude such an interpretation. Exclusion of the distal cup plates, particularly the interbrachs above the adjoined RR, in *Atactocrinus* (Weller, 1916) would produce a form like SUI 42278. The exclusion of the interbrachs above the pentagonal BB would also allow the primibrachs to adjoin in that position. No other camerate crinoid is known in which the primibrachs from adjacent rays adjoin, and when more material becomes available a new genus will probably be warranted for this unusual rhodocrinitid. Alternatively, the form may represent an abnormally developed rhodocrinitid.
Material: SUI 42278
Horizon and Locality: "*Cyclocrinites* beds;" Locality 28.

Genus LUXOCRINUS n. gen.

Type species: Luxocrinus simplex n. sp.

Diagnosis: Calyx low, bowl-shaped; infrabasals small, in basal concavity, restricted to area of column facet; single large interbrach present above each basal; arms branch from first primibrach; ambulacra form star-like shape internally.
Discussion: Luxocrinus represents the extreme in dorsal cup simplification noted in the superfamily. Although the type species is represented by poorly preserved material, available specimens sufficiently illustrate the simplified dorsal cup plate arrangement. The presence of a single interbrach per interray and a single primibrach per ray readily distinguishes *Luxocrinus* from all other rhodocrinitaceans. Springer (1926, p. 24) discussed the proximal portion of the cup of an indeterminate rhodocrinitid from the Laurel Limestone (Wenlockian); it differs from *Luxocrinus* in lacking a basal concavity and in having large iBB. *Emperocrinus* (Laurel Ls.) resembles *Luxocrinus* in possessing a single interbrach per interray and small iBB but differs in having depressed interrays and well-developed rays (2 IBrr and IIBrr). *Luxocrinus* most closely resembles the Middle Ordovician (Newfoundland) *Trichinocrinus* in possessing small iBB at the bottom of a basal concavity and a single large iBr per interray (Moore & Laudon, 1943a), but *Trichinocrinus* differs primarily in having two fixed primibrachs per ray and in general cup shape and ornamentation.
Derivation of name: Lux, the quarry from which the type species was collected.

Luxocrinus simplex n. sp.
Plate 1, Figs. 2-5; Text-fig. 3

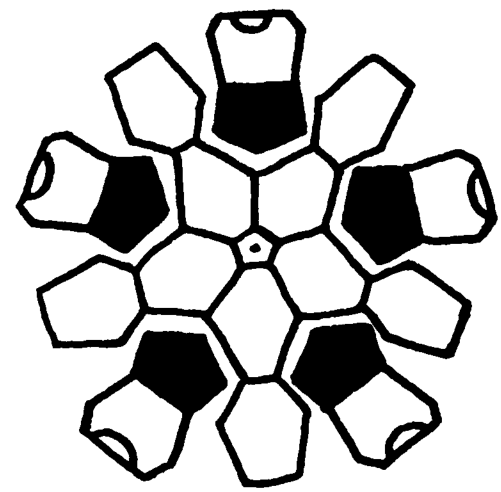


Fig. 3. *Plate diagram of* Luxocrinus simplex. *RR black.*

Description: Dorsal cup low, bowl-shaped, infrabasals small, restricted to column facet at bottom of basal concavity. Basal concavity incorporates proximal portion of BB; basals large, hexagonal. Radials pentagonal, similar in size to BB; single primibrach per ray, hexagonal, distal margin curved onto tegmen. Proximal margin of BB in contact with single hexagonal interbrach, the largest plate in cup; iBr in contact with large plate at lateral margin of tegmen. Tegmen plate structure unknown; five ambulacral tracts preserved internally (and externally?) forming star-like shape. Column and arms unknown. Holotype measure 6 mm high × 10 mm wide; largest paratype measures 7 mm high × 12 mm wide.
Derivation of name: Simplex refers to the greatly simplified cup plate

configuration.
Holotype: SUI 42283.
Material: Four paratypes are designated SUI 42284; 7 additional specimens, SUI 42285.
Horizon and Locality: "*Cyrtia* beds;" Locality 15.

Superfamily DIMEROCRINITACEA Zittel, 1879

Diagnosis: Radials generally adjoining except on posterior side; intraspecific variation is occasionally noted in which the radials may be separated or adjoining.
Discussion: Ubaghs (1978) divided the Eudiplobathrina into two superfamilial groupings, the Rhodocrinitacea and Dimerocrinitacea, based on whether or not the radials are separated from each other by interposing interbrachs (interradials), although variation in this criterion was noted (ibid., p. 287). Moore and Laudon (1943, p. 82) monophyletically derived all dicyclic camerates with adjoining radials from *Ptychocrinus*. However, the shifting of the iBrl higher in the cup allowing the RR to come in lateral contact could have arisen in several independent lineages, and this general trend is evident in three apparently separate ptychocrinid lines. Several dimerocrinitacean taxa can exhibit a radial plate configuration like the rhodocrinitaceans, and these forms are discussed below.

One species included in the Lampterocrinidae, *Siphonocrinus nobilis*, can exhibit features characteristic of both superfamilies; some *S. nobilis* have the RR in lateral contact, others reveal the RR separated by the first interbrachs. Weller (1900, p. 88) recognized the problem and questioned whether the "Thysanocrinidae [=Dimerocrinitacea] and Rhodocrinidae [=Rhodocrinitacea] should be considered as distinct." Specimens of *Dimerocrinites icosidactylus* (Wenlock, England) are also known in which the RR may be separated (Brower, 1973, pp. 446, 451). Likewise, *Griphocrinus*, a genus included in the Dimerocrinitidae, may have all or a variable number of radials separated by interposing interbrachs (Kirk, 1945, p. 350; Breimer, 1962, p. 18). The separation of the radial plates in these mentioned taxa is probably a resultant feature related to the evolution of a widening dorsal cup. Alternatively, these forms may indicate a polyphyletic origin of the Dimerocrinitacea from several nonptychocrinid stocks, although this remains to be seen. Two genera included in the Rhodocrinitacea, *Atactocrinus* and *Lyriocrinus*, may also have partly separated, partly adjoined RR circlets (Breimer, 1962, p. 18). The possible polyphyletic origins of the Dimerocrinitacea is further discussed under the Dimerocrinitidae and Lampterocrinidae.

Although confusing variation in the radial circlet of *Siphonocrinus nobilis, Dimerocrinites icosidactylus* and *Griphocrinus* places the distinction of the Dimerocrinitacea from the Rhodocrinitacea in doubt, Ubaghs' (1978) superfamilial distinction is readily usable for most dicyclic camerate groups. Since forms assignable to the Rhodocrinitacea gave rise to forms assignable to the Dimerocrinitacea, it should not be surprising to find a few "problem" species exhibiting characteristics of both superfamilies. Classification problems of this type are not unusual in the crinoids as Wachsmuth and Springer (1897, p. 262) noted in the Rhodocrinitidae: "Departures . . . within a genus in respect to characters which have always been regarded as of the utmost significance for distinguishing families and genera show how idle it is to expect absolute accuracy in the separation even of very important groups."

Family DIMEROCRINITIDAE Bassler, 1938

Diagnosis: Median ray ridges present in primitive members; radials generally adjoining except on posterior side, although RR may be separated in lateral interrays; interbrachs well developed, regular, may be depressed, connecting with tegmen, iBrl typically followed by two plates; primanal supports 3 plates in next range, often with sagittal series of extra plates leading to anus; arms simple or branching, uniserial, biserial, or compound; stem round to substellate.
Discussion: Ptychocrinus was not regarded by Moore and Laudon (1943, p. 83) as a dimerocrinitid because of its uniserial arms and was classified in a separate family, the Ptychocrinidae. Ubaghs (1978) and Brower (1973) regard *Ptychorinus* as the oldest genus included in the Dimerocrinitidae and modified the familial diagnosis to include both uniserially and biserially armed forms. *Ptychocrinus*, a genus endemic to North America in the Late Ordovician, includes three "highly divergent" species. "By the standards applied to other Ordovician camerate families, the three crinoids would be placed within different genera" (Brower, 1973, p. 445). By the development of biserial arms and a competent tegmen in these three ptychocrinid lines most, if not all, of the typical biserially-armed dimerocrinitids arose. *Ptychocrinus* probably arose from uniserially armed "archaeocrinids" as the distal movement of the iBrl allowed the RR to adjoin. It is the closing of the RR circlet that distinguishes *Ptychocrinus* from similar "archaeocrinids," although the ptychocrinid dorsal cup plate configuration may actually have arisen independently in two or more converging lineages. The three Ordovician species of *Ptychocrinus* do not differ dramatically from each other in general cup characteristics, although the three different arm types are fundamentally different; 10-armed unbranched forms (*P. fimbriatus*), 20-armed unbranched forms (*P. parvus*), and branching forms in which the rays are fixed only up through part of the IIBrr series, (*P. splendens*). *P. fimbriatus* probably arose directly from an "archaeocrinid" like *Rhaphanocrinus subnodosus*.

The Dimerocrinitidae can be conveniently grouped into three different categories based on the nature of the arms, a feature of primary significance for most genera contained in the family. Group 1, typified by *Eudimerocrinus*, is characterized by forms with biserial branching arms (may branch 1, 2, or 3 times). Three genera are included in this group: *Eudimerocrinus, Ambicocrinus*, and *Griphocrinus*. Group 1 may be polyphyletic; several possible origins are proposed. First, it may have arisen directly from an archaeocrinid with biserial branching arms. Alternatively the development of biserial arms from the uniserial branching arms of the *Ptychocrinus splendens* stock would have produced Group 1 characteristics. The development of branching arms from the Group 2 stock is a third possibility. Lastly, the lateral adjoining of the RR from a biserially-armed rhodocrinitacean stock would also have achieved Group 1 characteristics; *Griphocrinus*, with its variably separated or adjoined RR, may have arisen in this manner. The discovery of the archaic line of Group 1 ptychocrinids in Llandoverian clastic environments of New York (*P. medinensis* Brett, 1978) contrasts with the interior carbonate platform where a greater diversity of more advanced Group 1 dimerocrinitids are noted.

Anthemocrinus, placed in the Anthemocrinidae of the Rhodocrinitacea, closely resembles Group 1 dimerocrinitids except that only one primibrach per ray and 4 BB are present. *Macarocrinus*, a Lower Devonian form with branching uniserial arms, is included in the Dimerocrinitidae; a distant but plausible ancestor of *Macarocrinus* would be uniserially-armed forms such as the Lower Silurian *Ptychocrinus medinensis*. *Nyctocrinus*, a Silurian form with a completely closed RR circlet and branching biserial arms, probably arose from a form like *Gazacrinus* (derived from Group 2 dimerocrinitids).

Group 2, characterized by ten simple biserial arms, includes a number of *Dimerocrinites*, herein called *D. (Dimerocrinites)*, and possibly *Cyphocrinus*. Ten-armed *Dimerocrinites (Dimerocrinites)* include *D. decadactylus* (Wenlock Ls., Eng.), *D. brachiatus* (Lockport Ls., N.Y.), *D. liliformis (ibid.)*, *D. occidentalis* (Waldron Sh., Ind.), *D. inornatus (ibid.)*, *D. planus* (Brownsport Fm., Tenn.), *D. milliganae (ibid.)*, *D. roemeri (ibid.)*, *D. elegans* (Jupiter Fm., Anticosti), *D. longimanus* (Silurian, Gotland), *D. hopkintonensis* (Hopkinton

Dolo., Iowa), *D. sculptus (ibid.), D. eugenius* (Ridgely Ss., Md.); questionably included are *D. campanulatus* (Silurian, Ill.), *D. egani* (Racine Dolo., Ill.), and *D. pentangularis* (Racine Dolo., Ill., Wisc.). The most probable origin of Group 2 dimerocrinitids is by development of biserial arms in the uniserially-armed *Ptychocrinus fimbriatus* stock. Alternatively, some of the Group 2 dimerocrinitids could have been derived from the Group 3 stock by loss of some arms. A third possibility was proposed by Moore and Laudon (1943, p. 84) for the origin of *Cyphocrinus*, a broad-cupped form, from the Group 1 dimerocrinitid stock; the loss of arm-branching in the *Eudimerocrinus* stock could have derived some *Dimerocrinites (Dimerocrinites)* in a similar manner. *Lyriocrinus*, a member of the Rhodocrinitidae with ten simple biserial arms, could conceivably be related to Group 2 dimerocrinitids if the RR circlet in the two families can be variably open or closed. The archaic 10-armed ptychocrinid stock persisted into the late Llandoverian as evidenced by the discovery of *Ptychocrinus longibrachialis* in clastic deposits of Scotland (Brower, 1975).

Group 3 dimerocrinitids are represented by *Dimerocrinites* with twenty biserial arms branching on the IIBrr2 (rarely IIBrr1 or IIBrr3) herein termed *D. (Eucrinus)*. Included are *D. laevis* (Silurian, Gotland), *D. interradialis (ibid.), D. quinquangularis (ibid.), D. speciosus (ibid.), D. nodobasis* (Brownsport Fm., Tenn.), *D. lockportensis* (Lockport Ls., N.Y.), *D. whitfieldi* (M. Dev., N.Y.), and *D.* sp. (Hopkinton Dolo., Iowa). *D. icosidactylus* (Wenlock Ls., Eng.) is an irregular Group 3 dimerocrinitid with three or four arms per ray. *Dimerocrinites (Eucrinus)* most likely originated from the simple uniserial 20-armed *Ptychocrinus parvus* stock, although the insertion of fixed tertibrachs in each ray of a *Dimerocrinites (Dimerocrinites)* would achieve similar results. *Dimerocrinites pentlandicus* from the late Llandoverian of Scotland is questionably assigned to the genus by Brower (1975), and this species was probably derived from earlier 20-armed *Ptychocrinus*. The development of a zygodiplobathrid-like base in *D. pentlandicus* is divergent from the general trend of dimerocrinitid evolution (also see *Allozygocrinus* discussion), and probably represents a fourth group of dimerocrinitids independent of normal 20-armed stocks in the Lower Silurian.

Genus DIMEROCRINITES Phillips, 1839

Type species: Dimerocrinites decadactylus; Roemer, 1855, SD.
Diagnosis: Calyx conical to globose; plates smooth to ornamented; median ray ridges generally present; interray areas depressed; series of smooth or ridged anal plates often present; tegmen commonly but not always lacks anal tube; arms biserial, 2 or 4 per ray (rarely 3), generally free above third through sixth brachial; stem circular to pentangular (Weller, 1900; Ubaghs, 1978).
Discussion: Brower (1973, p. 446) noted that "*Dimerocrinites* is a highly heterogeneous genus in dire need of revision," and an attempt has been made at subdividing the genus into two simpler taxonomic units. Two distinct groups are included in *Dimerocrinites*, 10-armed forms and 20-armed forms. These two groups may each have been derived along independent lines. Most described species of *Dimerocrinites* can easily be assigned to either of the two groups contained in the genus; these two taxonomic units are herein assigned subgeneric rank. However, the subgeneric placement of several species of *Dimerocrinites* remains uncertain: *D. aculeatus, D. canaliculatus* (both known only from isolated arms), and *D.? vagans*. Brower (1973, p. 451) believed that *D.? vagans* was monocyclic; Foerste (1919, p. 13) believed that *D.? vagans* might be a dicyclic form with greatly reduced infrabasals (not preserved) in which case it would probably represent an exceptionally flat-cupped dimerocrinitid (RR still adjoining irregardless of the flattening). Angelin (1878, pl. 6, fig. 7) illustrated both 10- and 20- armed *D. ornatus* from Gotland, and it is not known which of the two forms is diagnostic of the species.

Subgenus DIMEROCRINITES (DIMEROCRINITES) Phillips, 1839

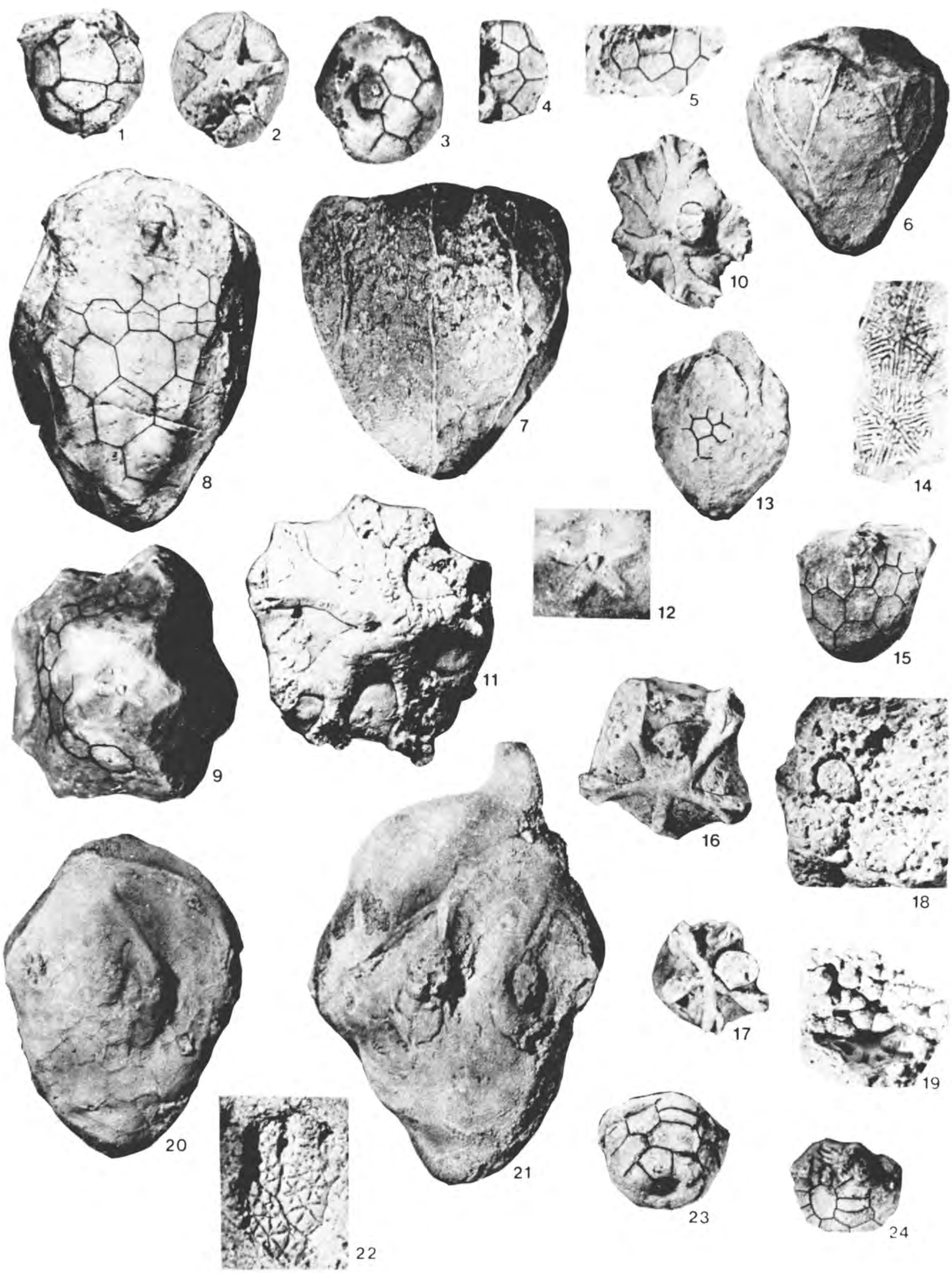
Diagnosis: Dimerocrinites with ten simple biserial arms.
Type species: D. decadactylus.
Included species: D. brachiatus, D. liliformis, D. occidentalis, D. inornatus, D. planus, D. milliganae, D. roemeri, D. elegans, D. hopkintonensis, D. sculptus, D. longimanus, D. eugenius; questionably included *D. campanulatus, D. egani, D. pentangularis.*
Discussion: The type species of *Dimerocrinites (Dimerocrinites)* has quadrangular IBrl and pentagonal or heptagonal IAx. Several other species of the subgenus, *D. planus, D. egani, D. roemeri, D. pentangularis*, have variably shaped (4-, 5-, or 6-sided) IBrl. The remainder of the species included in the subgenus have hexagonal IBrl. Variably shaped IAx (5-, 6-, or 7-sided) are noted in the type species, *D. planus, D. milliganae, D. campanulatus*, and *D. egani*. The remainder of the species in the subgenus have pentagonal IAx. *D. egani* may be a juvenile of *D. pentangularis* (Weller, 1900, p. 75). Hall's (1852) genera, *Thysanocrinus* and *Glyptaster*, are synonymous with *Dimerocrinites (Dimerocrinites)*. Angelin (1878) made a generic distinction between the ten- and twenty-armed dimerocrinitids of Gotland labeling the ten-armed forms *Harmocrinus*, also synonymous with *D.* (*D*). *D.* (*D*). probably originated in North America and spread to Europe (Gotland, England) by Wenlockian time.

Dimerocrinites (Dimerocrinites) sculptus n. sp.
Plate 1, Figs. 8-14

Diagnosis: Calyx obpyramidal, decidedly pentagonal in cross-section;

Note: all specimens on plates 1-5 are internal molds unless otherwise indicated; all specimens are coated with ammonium chloride sublimate; plate sutures are artificially enhanced unless otherwise indicated.

PLATE 1. *1. rhodocrinitid sp.: dorsal cup, side view (SUI 42278). x2. 2-5.* Luxocrinus simplex *n. gen. et sp.: 2. summit view (SUI 42284A), 3. basal view (SUI 24484B), 4. basal view of latex cast (SUI 42283), 5. side view of partial external mold (SUI 42283). All x2. 6,7.* Dimerocrinites (Eucrinus) *sp.: 6. dorsal cup, side view showing median ray ridges (SUI 39811), 7. dorsal cup, side view showing median anal ridge (SUI 39815). x1.5. 8-14.* Dimerocrinites (Dimerocrinites) sculptus *n. sp.: 8,9. dorsal cup, side view and basal view (SUI 31768), 10. summit view with ambulacra and protruberant anus (SUI 31708), 11. summit view illustrating ambulacra (SUI 31766), 12. infrabasal "star" (SUI 31768), 13. side view of calyx with anal tube (SUI 39965), 14. external mold showing ornamentation (SUI 31767). All x 1.5 except 12. x3 and 14. x2. 15-19.* Dimerocrinites (Dimerocrinites) hopkintonensis *n. sp.: 15. dorsal cup, side view (SUI 39870), 16. summit view showing ambulacra (SUI 39962), 17. summit view showing ambulacra and anus (SUI 39976), 18. external mold, nodose tegmen surface (SUI 39969), 19. external mold, dorsal cup plate ornamentation (SUI 39969). All x1.5 except 16. x2. 20-22.* Siphonocrinus nobilis *(Hall): 20. calyx, side view (SUI 39844B), 21. calyx with anal tube, side view (SUI 39844A), 22. external mold showing ornamentation (SUI 39951). All x1.5. 23,24.* Pregazacrinus hemisphericus *n. gen. et sp.: 23. dorsal cup, oblique basal view (SUI 42303), 24. calyx, side view (SUI 31772). x3.*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sutures between infrabasals are elevated into rounded, radiating ridges on internal molds forming a star-shaped calyx base; tegmen flat or nearly so, although anal tube may be developed; surface of plates decorated with a series of parallel ridges adjoining the centers of all plates dividing the surface into concentrically-banded triangular areas.
Description: Calyx obpyramidal, decidedly pentagonal in cross-section. Infrabasals small, triangular, together forming a pentagonal basal disc. Basals pentagonal, except hexagonal posterior basal. Radials large, heptagonal in A, B, E rays, hexagonal in C, D rays, adjoining all around except on posterior side; primibrachs hexagonal; primaxils pentagonal. Secundibrachs hexagonal, 4 IIBr per half ray incorporated into cup. Interrays depressed; first interbrach large, supporting 2 plates in next range, one heptagonal and one hexagonal. Two third range interbrachs developed, one heptagonal and one pentagonal. Interrays probably developed to fifth range, 1:2:2:2:1?. First intersecundibrachs hexagonal, similar in size to secundibrachs, bearing two plates in second range and one in the third range. Primanal hexagonal, resting on posterior basal. Posterior interray differentiated, three hexagonal plates above primanal; sagittal series of unridged anal plates present. Tegmen flat or nearly so; ambulacra branch once, leading to ten arm facets; ambulacrals and interambulacrals developed (SUI 31766, 31708). Anus subcentral, may be elevated (SUI 31708). Sutures between infrabasals are elevated into rounded, radiating ridges on internal molds forming a star-shaped pattern; median ridges bifurcate from basals and adjoin into a single ridge at the radials; median ray ridge bifurcates at primaxil continuing into secundibrach series to arm bases. Surface of plates decorated with a series of distinct parallel ridges adjoining the centers of all cup plates and dividing the surface of the plates into concentrically-banded triangular areas. Calyx measurements (height × width): 8 mm × 9.3 mm to 46 mm × 46 mm. Variation in calyx shape, height/width ratio, 0.85-1.05.
Discussion: D. *(D).* *sculptus* most closely resembles *D. (D.) pentangularis* of the Racine Dolomite but differs in having a generally squatter cup, a distinct star-shaped pattern on internal molds along the infrabasal sutures, and in its ornately sculptured plates (*D. pentangularis* has smooth plates; Weller, 1900, p. 71). One specimen, SUI 39965, differs from all other specimens of *D. (D.) sculptus* in having a high-vaulted tegmen with an anal tube developed; other specimens preserving the oral surface (SUI 31744, 31766) exhibit a nearly flat tegmen with no anal tube. SUI 39965 exhibits a dorsal cup identical with *D. (D.) sculptus;* the development of an anal tube is probably atypical of the species. Some specimens (e.g., SUI 31708) exhibit a slightly protruberant anus somewhat intermediate in form between the flat-tegmened and high-vaulted specimens.
Derivation of name: Sculptus refers to the sculptured ridges on the plate surface (Rowser, 1932, p. 77).
Holotype: SUI 31767 (Locality 2).
Material: Seven paratypes are designated SUI 31768 (4) and 31766 (3). One-hundred seventeen additional specimens are numbered SUI 31701 (2), 31702 (15), 31703 (2, internal, external), 31704 (int., ext.), 31706 (int., ext.), 31707, 31708 (39), 31710 (2), 31715 (3), 31716, 31744 (2), 39963 (10), 39964 (21), 39965 (3), 39966 (2), 39967, 39968 (11).
Horizon and Localities: "*Cyrtia* beds;" Localities 1, 2, 3, 7, 8, 10, 15, 36, 42 (sec. 11).

Dimerocrinites (Dimerocrinites)
hopkintonensis n. sp.
Plate 1, Figs. 15-19

Diagnosis: Calyx subglobose, higher than wide; intersecundibrachs absent; median ray ridges weakly developed internally, nodose at level of RR; tegmen arched, anus elevated; surface of plates decorated with central nodes interconnected between plates by rounded ridges.
Description: Calyx subglobose, higher than wide, roughly circular in cross-section. Radials largest plate in cup, heptagonal in A, B, E rays; primibrachs hexagonal; primaxils pentagonal. One or two secundibrachs per half-ray probably incorporated into cup. Interrays gently depressed only at level of distal interbrachs. First interbrachs hexagonal, followed by 2 plates in the second range. Posterior interray differentiated, wider distally than lateral interrays. Tegmen arched; anus elevated above level of ambulacra. Ambulacra prominent on internal molds; ambulacra do not bifurcate except at lateral margin of tegmen. Two closely-spaced arm facets in five lobed groupings. Plate surfaces decorated with central nodes interconnected between plates by rounded ridges. Tegmen strongly lobate, plates nodose; distinct orals and ambulacrals not evident. Median ray ridges weakly developed internally, forming five broad angular nodes at level of RR. Representative calyx measurements (height × width): 14 mm × 12 mm, 22 mm × 20 mm, 23 mm × 18 mm. Variation in calyx shape, height/width ratio, 1.00-1.35.
Discussion: D. (D.) hopkintonensis differs significantly from all other species of the genus in plate ornamentation, distal ray characteristics, and tegmen development. The paired arms facets are spaced so closely together that the intersecundibrachs are excluded from the cup and some specimens give the general appearance of having only five arm facets (better preserved specimens reveal the presence of ten arm facets). The lack of distinct orals and ambulacrals (see SUI 39969) is not consistent with Ubaghs' (1978) diagnosis of *Dimerocrinites,* and the generic diagnosis is modified to include forms like *D. (D.). hopkintonensis* with tegmens composed of numerous nodose plates and a subcentral elevated anus. *D. (D.) hopkintonensis* exhibits features similar in form to an ancestral five-armed lampterocrinid. The trend toward arm reduction in the ten-armed *D. (D.)* stock is evident in the closely-spaced arm facets, excluded iIIBr, and extreme laterally bifurcating ambulacra of *D. (D.) hopkintonensis.* Enlargement of the basals, development of a more elongate anal tube, loss of arms, and bulging of the posterior interray in a form like *D. (D.) hopkintonensis* would produce forms assignable to *Lampterocrinus.*
Derivation of name: Hopkintonensis refers to the formation in which the species was collected.
Holotype: SUI 39969 (internal, external; Loc. 15)
Material: Paratypes are designated SUI 39970 (6) and 39976 (internal, external). Additional material is numbered SUI 39962 (80).
Horizon and Locality: "*Cyrtia* beds;" Localities 15 and 18.

Subgenus DIMEROCRINITES (EUCRINUS) Angelin, 1878

Diagnosis: Dimerocrinites generally with twenty simple biserial arms; may have 3 to 4 arms per ray.
Type species: Eucrinus laevis Angelin, 1878.
Included species: D. laevis, D. interadialis, D. quinquangularis, D. speciosus, D. lockportensis, D. whitfieldi, D. icosidactylus, D. nodobasis, D. sp.
Discussion: Angelin (1878) made a generic distinction between 10- and 20-armed dimerocrinitids of Gotland, naming the 20-armed form *Eucrinus.* Subsequent workers synonymized *Eucrinus* with *Dimerocrinites* even though the type species of *Dimerocrinites* is a 10-armed form; 20-armed dimerocrinitids *(D. icosidactylus)* were noted from the same locality as the type species (Wenlock Ls., England) and were included along with the 10-armed forms in the same genus, *Dimerocrinites.* In this study, *Eucrinus* will be assigned a subgeneric rank. *D. (E.) laevis* may be synonymous with *D. (E.) interradialis; D. (E.) quinquangularis* may be synonymous with *D. (E.) speciosus. D. (E.) speciosus* exhibits a variably-shaped (4-, 5-, or 6-sided) IBrl. *D. (E.) interradialis, D. (E.) whitfieldi,* and *D. (E.)* sp. may have pentagonal or heptagonal IAx; *D. (E.) lockportensis* may have hexagonal or heptagonal IAx. *D. (E.) icosidactylus* is the most atypical member of the subgenus having 3 or 4 (rarely 2) arms per ray and quadrangular IBrl; it

may variably have separated RR (Brower, 1973, p. 451). *Dimerocrinites (Eucrinus)* first appears in Late Llandoverian strata of North America; it is noted in Wenlockian strata of North America, England, and Gotland; its youngest occurrence is in Middle Devonian strata of New York.

Dimerocrinites (Eucrinus) sp.
Plate 1, Figs. 6,7

Diagnosis: Calyx obpyramidal; radiating pattern on plates; median ray ridge well-developed, bifurcating twice; posterior interray may have median anal ridge.
Description: Calyx obpyramidal, may be large; hexagonal IBrl; pentagonal or heptagonal IAx (see SUI 39820, 39815); hexagonal IIBrl, secundibrachs incorporated into cup to third or fourth level. Interrays gently or not at all depressed; iBrl hexagonal bearing two plates in second range; interrays probably developed to fourth or fifth range. Radiating pattern connecting the centers of cup plates (evident internally on SUI 39958). Median ray ridges well-developed, bifurcating twice, leading to 4 arm facets per ray. Posterior interray may have median anal ridge running the length of the interray leading to the anus (SUI 39815); posterior interray may lack median anal ridge (SUI 39811). Tegmen gently arched (SUI 39815).
Discussion: The poor preservation of the available material does not warrant specific assignment and it is left in open nomenclature. *D. (E.)* sp. is one of the largest crinoids in the "*Cyclocrinites* beds;" the largest dorsal cup (SUI 39958) is at least 43 mm high. Two other specimens measure (height × width) 39 mm × 37 mm and 24 mm × 27 mm. The possibility exists that more than one species may be included under *D. (E.)* sp.; one form may have a lobate calyx with a median anal ridge developed, another form may lack a median anal ridge and have a weakly-lobate calyx.
Material: Twenty specimens are numbered SUI 39807 (2), 39808, 39809, 39810, 39811, 39812, 39813 (2), 39814 (2), 39815, 39819, 39820, 39958, 39971, 39972 (2), 39973 (2).
Horizon and Locality: "*Cyclocrinites* beds;" Localities 9, 17, 18, 19, 21, 22, 23, 27, 31, 35.

Family DIMEROCRINITIDAE (?)
Genus ALLOZYGOCRINUS n. gen.

Type species: Allozygocrinus dubuquensis n. sp.
Diagnosis: Modified zygodiplobathrid-type base, isolated quadrangular BB in contact only with iBB and RR, BB may be absent in at least one interradial position; iBB and RR large, elongate IBrl, possibly the IAx; first three iBrr are diminutive; posterior interray probably differentiated.
Derivation of name: The possible dimerocrinitid origins suggest a different sort of zygodiplobathrid development (allos, Gr., different).

Allozygocrinus dubuquensis n. sp.
Plate 2, Figs. 4,5; Text-fig. 4

Description: Dorsal cup elongate, rounded at base. Angular median ray ridge present. Infrabasals large, irregular in shape; quadrangular basals in contact with iBB below and RR above; suture with RR may be convex. Radials large, irregularly sized, roughly octagonal; first primibrach octagonal, elongate; second primibrach present. Interrays composed of numerous plates; first interbrachs small, pentagonal, flanked by two tiny triangular interbrachs laterally; third range interbrach in contact with all three iBrr proximally, flanked by two quadrangular plates laterally; two interbrachs in next range, probably hexagonal; additional interbrachs in following range. Arms, column, distal portion of cup, and ornamentation are unknown. SUI 42310 preserves a 29 mm portion of the cup, UC 63966 an 18 mm portion.

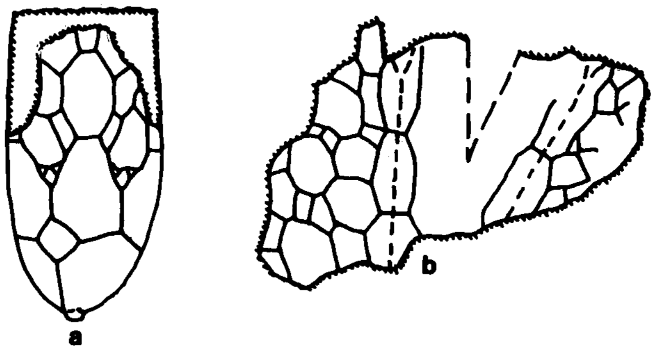


Fig. 4. *A) Lateral view diagram of* Allozygocrinus dubuquensis *holotype (SUI 42310) dorsal cup. B) Plate fold-out diagram of distal portion of a possible* ?A. dubuquensis *(SUI 47222). Hachured edge defines margin of preserved portion of specimens.*

Discussion: The above description is based largely on the holotype, the most complete of the two known specimens (Text-fig. 4a). The second specimen (UC 63966) is more poorly preserved; it reveals 4 adjoining RR, 2 complete and 2 partial. It also reveals two completely isolated basals with convex distal margins; a third isolated basal may be present in the interradial position between the two preserved BB, although preservation is too poor to be certain. One elongate primibrach is preserved, and the median ray ridge is observed to branch at the distal end. This suggests that the rays branch from the IBrl, i.e. IBrl is probably the IAx on this specimen. The interrays of UC 63966 are poorly preserved, although the proximal portions seem to bear several dimunitive plates.

An additional specimen (SUI 47222) from Locality 15 preserves part of the distal portion of a camerate dorsal cup and is tentatively assigned to *A. dubuquensis* (Text-fig. 4b). The elongate primibrachs, angular median ray ridges, and many-plated interrays of the specimen are reminiscent of features noted in *A. dubuquensis,* although the holotype and paratype preserve the proximal portions of the cup. SUI 47222 reveals branching of the median ray ridge from the elongate IBr2 (IBr3?), which contrasts with the condition noted in UC 63966. Additionally, the best preserved interray is wider and has a different plating arrangement than that noted on SUI 42310 and UC 63966; if SUI 47222 is correctly identified with *Allozygocrinus,* then the preserved interray probably occupies the posterior position. The other interray positions on the cup do not satisfactorily preserve the plating arrangement for comparison to *Allozygocrinus,* although the general interradial width is consistent.

The presence of a modified zygodiplobathrid-type of cup base and the complex interradial areas indicate that this taxon is a highly irregular camerate crinoid and may be an aberrant form. The occurrence of two specimens of nearly identical morphology, each in separate collections, increases the likelihood that the form represents a normally-developed and distinctive taxon. The elongate RR and IBrr are reminiscent of the ray structure noted in *Periechocrinus,* and the form could conceivably be an unusual periechocrinid.

Although the relationships of *Allozygocrinus* are certainly obscure, the form reveals features closely similar to an unusual dimerocrinitid (*Dimerocrinites pentlandicus*) noted in late Llandoverian deposits of Scotland by Brower (1975). These features include the isolated quadrangular basal plate, multiple levels of iBrr, elongate RR, and elongate octagonal IBrl. *Allozygocrinus* differs in the greater development of the iBB, by the possible loss of at least one basal, and in the greatly reduced proximal interbrachs. The similarities with the Scottish dimerocrinitid of the same age suggest the tentative dimerocrinitid relationship of *Allozygocrinus*. Brower (1975, p. 641) suggested that *D. pentlandicus* "is different enough from normal dimerocrinitids for a new genus to be proposed." With this in mind, and considering the even more divergent and unique plating arrangement of the Hopkinton taxon, a new genus seems warranted. The Hopkinton specimens, although certainly not ideally preserved, sufficiently illustrate the unique character of the genus. The diagnosis of *Allozygocrinus* conld reasonably be modified to include forms like *D. pentlandicus* (primarily by making interray diagnosis less restrictive), although such an assignment is relegated to later taxonomic studies.

The possible loss of at least one basal in *Allozygocrinus*, a genus probably derived from a form like *D. pentlandicus*, raises some intriguing possibilities concerning the hypothetical origins of certain monocyclic camerates from a divergent dicyclic camerate stock in the Silurian. Although speculative, the continued loss of basals in a form like *Allozygocrinus* would produce a monocyclic (pseudomonocyclic) base. However, the dicyclic-monocyclic schism within the crinoids will probably continue to be of fundamental phylogenic significance in relating most dicyclic and monocyclic forms into more or less "natural" groupings at the order level (Warn, 1975).

Derivation of name: The occurrence in Dubuque County suggests the name.

Holotype: SUI 42310

Additional material: UC 63966 serves as paratype; SUI 47222 tentatively included.

Horiaon and Locality: "*Cyrtia* beds," Locality 15.

Family LAMPTEROCRINIDAE Bather, 1899

Diagnosis: IBB, BB, and RR large; RR generally in contact except on posterior side, although RR may be separated; calyx asymmetrical, extra plates in posterior interray create a bulge that extends onto tegmen; tegmen rigid, strongly arched; anus opens through tube (modified from Moore & Laudon, 1943; Ubaghs, 1978).

Discussion: The diagnosis of the Lampterocrinidae given above was modified to include forms (i.e., *Siphonocrinus nobilis*) with separated radial circlets. The Lampterocrinidae was apparently derived from the Dimerocrinitidae via two independent lineages. The bulging of the posterior interray and tegmen along with the development of an anal tube in both Group 2 and Group 3 dimerocrinitids gave rise to two known lampterocrinid genera, *Lampterocrinus* and *Siphonocrinus*, respectively. *Lampterocrinus* and *Siphonocrinus*, both highly successful forms on the North American Silurian carbonate platform, remained endemic to North America throughout their history (Witzke *et al.*, 1979). The oldest known lamprerocrinids are from the late Llandoverian, Hopkinton Dolomite of Iowa where both genera appear simultaneously; *Lampterocrinus* does not seem to be an offshoot of *Siphonocrinus* but probably arose independently from 10-armed dimerocrinitids. The youngest lampterocrinids are from Ludlovian rocks of Oklahoma and Tennessee.

Genus SIPHONOCRINUS S. A. Miller, 1888

Type species: Glyptocrinus nobilis Hall, 1861; OD

Diagnosis: Calyx very asymmetrical, depressed interradially and lobed at arm level; posterior side of calyx greatly inflated; tegmen high, long anal tube developed; subtegminal ambulacra in grooves on interior surface of plates; 20 arms, grouped; column circular.

Discussion: Strimple (1963) erected a new lampterocrinid genus, *Ochlerocrinus*, to include two species with adjoining RR formerly included in *Siphonocrinus (S. armosus, S. pentagonus)*; *Siphonocrinus* was retained as a genus for those forms *(S. nobilis)* with separated RR and was transferred from the Lampterocrinidae to the Archaeocrinidae. However, *Siphonocrinus nobilis* does not consistently have separated RR (Weller, 1900, p. 87); the RR are generally separated only in larger specimens of the species (Rowser, 1932, p. 83). The radial circlet of *S. nobilis* varies between forms referrable to Strimple's (1963) two genera, *Ochlerocrinus* and *Siphonocrinus;* and Ubaghs' (1978) two superfamilies, Dimerocrinitacea and Rhodocrinitacea; *Ochlerocrinus* is herein regarded as a junior synonym of *Siphonocrinus*. *S. dignis* (Strimple, 1963, p. 73) has separated RR and should probably be assigned to the Rhodocrinitidae.

Wachsmuth and Springer (1897, p. 213) erected a new species of *Siphonocrinus*, *S. pentagonus*, for forms "having but two arms to the ray" (*ibid.*, p. 214). *S. pentagonus* is regarded herein as a junior synonym of *S. nobilis;* the type of *S. pentagonus* is an internal mold which superficially appears to have only 10 arm facets but is like *S. nobilis* in all other respects. However, many internal molds of *S. nobilis* from the Hopkinton Dolomite of Iowa and the Racine Dolomite of Wisconsin also appear to have only 10 arm facets even though external molds of the same species clearly have 20 arm facets. The paired arm facets of *S. nobilis* are spaced very close together, and on internal molds these closely-spaced facets are often indistinguishable as pairs. *S. armosus*, a 20-armed form that also may appear to have only 10 arm facets on internal molds, is readily distinguished from *S. nobilis* by its long anal tube that lies flush along the tegmen surface and opens at the side of the calyx. *Siphonocrinus* probably originated from a 20-armed dimerocrinitid during the Late Llandoverian; the oldest known representatives of the genus are from the Hopkinton Dolomite ("*Cyrtia* beds") of Iowa. *Dimerocrinites (Eucrinus)* sp. from the "*Cyclocrinites* beds" (Hopkinton Dolo.) is a possible ancestor of *Siphonocrinus*.

Siphonocrinus nobilis (Hall, 1861)
Plate 1, Figs. 20-22

Diagnosis; Anal tube directed upward; RR may be separated in large individuals; interrays developed beyond third or fourth range connected in uninterrupted succession with numerous plates on tegmen; arched tegmen about one-half total calyx height; external of plates ornamented with radiating stellate ridges; 4 arms per ray, grouped in closely-spaced pairs.

Discussion; Siphonocrinus nobilis is one of the dominant echinoderm elements noted in the "*Crytia* beds" at several Iowa localities. Several specimens of this species are the largest echinoderms noted from the entire Hopkinton Dolomite. Preserved RR circlets on five specimens (SUI 39844) reveal the RR in lateral contact; on one specimen (SUI 39847) the RR are separated. Calyx size and shape, development of the anal tube, variation in the RR circlet, and external plate ornamentation revealed in the Hopkinton Dolomite sample are identical with that noted in collections of *S. nobilis* from the younger Racine Dolomite (Wisc., Ill.), and the Hopkinton specimens are assigned without reservation to the species. Representative measurements of calyx size variation (height exclusive of anal tube × maximum width) from the Hopkinton sample are: 15 mm × 14 mm, 34 mm × 29 mm, 40 mm × 34 mm, 58 mm × 50 mm, 68 mm × 51 mm, 68 mm × 58 mm, 69 mm × 49 mm.

Material: One-hundred seventy-two specimens are numbered SUI 543, 31788 (9), 39844 (7), 39845 (70), 39846 (4), 39853 (12), 39854 (slab, 3), 39855, 39856 (2), 39857 (3), 39858 (4), 39859 (40), 39951, 39980 (7) and 39981 (8).

Horizon and Locality: "*Cyrtia* beds;" Localities 1, 2, 3, 7. Bioherms; Localities 4, 43.

Genus LAMPTEROCRINUS Roemer, 1860

Type species; Lampterocrinus tennesseensis; M.

Lampterocrinus sp.
Plate 2, Figs. 1-3; Text-fig. 5

Diagnosis; Calyx elongate, decidedly pentagonal in cross-section; median ray ridges developed on internal molds; coarse stellate ribbing developed on plate exteriors; IBr2 quandrangular.
Description: Calyx elongate, pentagonal in cross-section, constricted at level of infrabasals, expanding upward to arm bases. Five basals, 4 equal, 1 slightly larger (see SUI 39954). Infrabasals hexagonal, large, similar in size to RR. Observed radials heptagonal, in contact all around except possibly on posterior side. First primibrachs hexagonal; second primibrachs quadrangular; third primibrachs bear arm facets. Median ray ridges evident on internal molds. First interbrachs hexagonal, similar in size to IBr1, bearing two interbrachs in next range. Third range interbrachs pass uninterruptedly from dorsal cup onto tegmen. Posterior interray not preserved on any specimens. Tegmen gently arched, gently bulged on posterior side (SUI 39953). Five arm bases. Exterior of plates decorated with coarse stellate ribbing (SUI 39955). Largest specimen 31 mm long; SUI 39953 measures 28 mm long × 17 mm wide.
Discussion: Although the available material from the Hopkinton Dolomite is poorly preserved and specific assignment is not attempted, the noted features are diagnostic of *Lampterocrinus*. *Lampterocrinus* sp. from the Hopkinton Dolomite exhibits a gently bulged posterior side of the tegmen although the condition represented is primitive compared to the extreme interray and tegmen bulging exhibited in *L. inflatus* (Racine Dolomite). The ornamentation, plate arrangement, and general calyx shape of *L.* sp. is most closely comparable with *L. tennesseensis* from the Ludlovian Brownsport Formation. *Lamptero-crinus* was probably derived from a 10-armed dimerocrinitid during the late Llandoverian (see discussion under *Dimerocrinites (Dimerocrinites) hopkintonensis)*.
Material; Thirty-six specimens include the primary reference specimens SUI 39952, 39953 (2), 39954 (4), and 39955 and additional material SUI 39956 (7) and 39957 (21).
Horizon and Locality: ''Cyrtia beds;'' Locality 15.

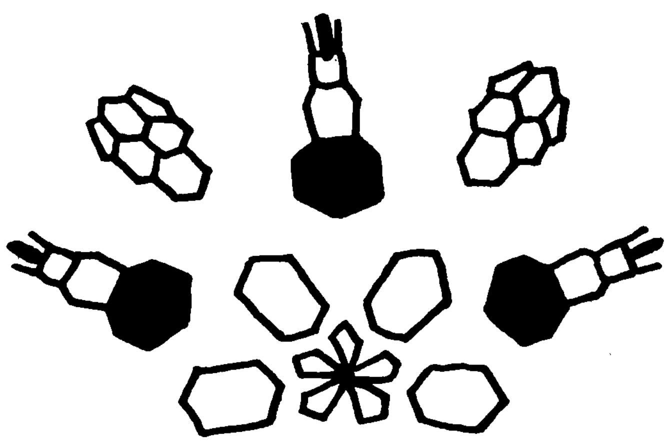


Fig. 5. *Plate diagram of* Lampterocrinus *sp., Hopkinton Dolo., Iowa. Posterior side not shown; RR black.*

Family GAZACRINIDAE S.A. Miller, 1892

Diagnosis (emended): Infrabasals confined to basal concavity; a single large interbrach generally present in each interray although one or two small interbrachs may follow in the next range (3 small plates may follow primanal). Tegmen may have central, vertically-grooved ''pyramid'' or a short subcentral anal tube. Arms 10, simple, biserial; column round in cross section.
Discussion: The familial diagnosis of the Gazacrinidae utilized by Ubaghs (1978) is so restrictive as to include only a single genus, *Gazacrinus*. A new genus discovered in the Hopkinton Dolomite that is closely related, if not ancestral, to *Gazacrinus* could not be placed within the Gazacrinidae without emending the existing familial diagnosis. This new genus *(Pregazacrinus)*, although derived from a dimerocrinitid stock (Moore & Laudon, 1943, p. 84), differs markedly in dorsal cup structure from most genera presently included in the Dimerocrinitidae in having the interbrachs developed to only the second range (large iBrl, small iBrr2) and in having a simplified brachial series. *Pregazacrinus* is more easily grouped with *Gazacrinus* than with any other genus in the Dimerocrinitacea, and the diagnosis of the Gazacrinidae is emended to include both genera. The gazacrinids represent a grade of dorsal cup evolution derived from a dimerocrinitid stock by the development of a basal concavity and by the elimination of the distal secundibrachs plus all interbrachs beyond the first or second ranges. *Pregazacrinus* apparently lacks a specialized tegmen, although an anal tube is present; *Gazacrinus* possesses a specialized tegmen with few interambulacrals and a central, vertically-grooved ''pyramid'' (possibly for the retractile reception of arms as in *Eucalyptocrinites)*. *Gazacrinus* can easily be derived from *Pregazacrinus* by the elimination of the small second range interbrachs from the cup and by the development of the ''pyramid.'' The Gazacrinidae was apparently derived from a dimerocrinitid stock sometime in the late Llandoverian; it persisted into the Pridolian (Strimple, 1963, p. 88). The immediately ancestral dimerocrinitid stock is expected to display a slightly flattened dorsal cup, few fixed brachials, interrays developed to only the second or third range, ten arms, and a short anal tube; *Dimerocrinites decadactylus* is a good example of such a grade of dimerocrinitid development (J. Brower, 1980, pers. comm.). The Gazacrinidae remained endemic to North America throughout the Silurian (Witzke *et al.*, 1979).

Genus PREGAZACRINUS n. gen.

Type species: Pregazacrinus hemisphericus n. sp.
Diagnosis: First interbrachs followed in next range by 2 small plates; primanal followed by 3 small plates. Tegmen lacks pyramid; anus subcentral, at end of short tube.
Discussion: Pregazacrinus resembles *Gazacrinus* in many respects: the iBB are restricted to a basal concavity; the basals, radials, primibrachs, and secundibrachs are identical in general configuration; dorsal cup is subglobose. *Pregazacrinus* differs from *Gazacrinus* in lacking a central ''pyramid'' on the tegmen (it is not known if all species of *Gazacrinus* possess this feature) and in having second range interbrachs present. *Gazacrinus major* from the Racine Dolomite (Weller, 1900, p. 79) has a single second range interbrach per interray, a condition alligning it closely to *Pregazacrinus* (also with second range iBrr). Rowser (1932, p. 85) first noted the similarity of the Iowa form to *Gazacrinus* .
Derivation of name: ''Preceding *Gazacrinus*.''

Pregazacrinus hemisphericus n. sp.
Plate 1, Figs. 23, 24; Text-fig. 6

Description: Calyx small, subglobose; basal concavity incorporates iBB and proximal portion of BB. Infrabasals 5, small, quadrangular.

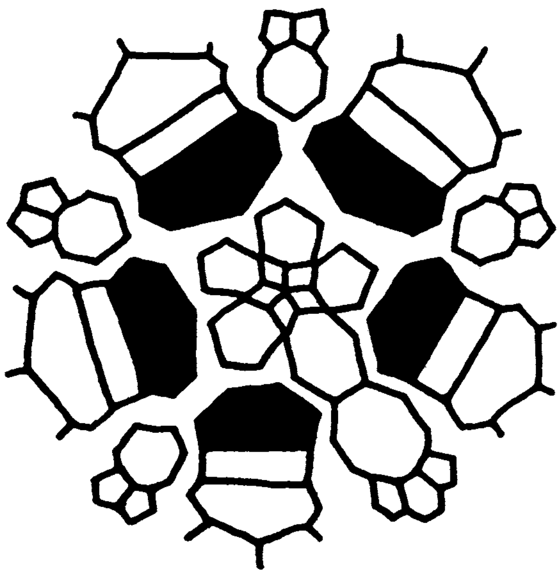


Fig. 6. *Plate diagram of* Pregazacrinus; *RR black.*

Lateral basals pentagonal to hexagonal, similar in size to iBrl; posterior basal in contact distally with primanal. Radials large, in contact except on posterior side; RR hexagonal in C and D rays, heptagonal in remaining rays, twice as wide as high. First primibrach rectangular, twice as wide as high; primaxil larger than iBrl; single secundibrachs present per half-ray. Octagonal first interbrachs occupy about two-thirds of each interray, followed in second range by two small interbrachs in contact with tegmen. Primanal bears 3 small interbrachs in second range. Tegmen structure unknown; short anal tube developed in posterior interambulacral area. Plate exteriors unknown; 10 arms. Holotype measures (height × width) 6 mm × 6.5 mm.
Derivation of name: The specific name is retained from Rowser (1932, p. 86), a *nomen nudum;* hemisphericus refers to the globular shape of the cup.
Holotype: SUI 31772 (Locality 2).
Material: Additionally SUI 31773 (5) and 42303 serve as paratypes.
Horizon and Locality: "*Cyrtia* beds;" Localities 2, 15.

Order MONOBATHRIDA Moore & Laudon, 1943
Suborder TANAOCRININA Moore, 1952

Discussion: Moore's (1952) suborder Tanaocrinina should probably be given priority over Ubaghs' (1978) new suborder Compsocrinina. Moore and Laudon (1943) first informally defined this suborder as the "Tanaocrinid stock" to include both the "periechocrinid section" (i.e. Periechocrinacea) and the "desmidocrinid section" (i.e. Carpocrinacea and Hexacrinitacea), and, therefore, it includes exactly the sama taxa included in Ubaghs' Compsocrinina. The diagnosis of the Tanaocrinina given by Moore (1952, p. 614) states that the basal circlet "typically" has three plates, although Moore and Laudon (1943, p. 87) admitted that primitive members of this group may have four basals. Even though *Tanaocrinus* is apparently a junior synonym of *Canistrocrinus,* the Tanaocrinidae and Tanaocrinina should remain valid higher taxonomic names, and the Compsocrinina is herein regarded as a junior synonym of the Tanaocrinina. Ubaghs (1978) did not explain the reasons for rejecting Moore's (1952) suborder.

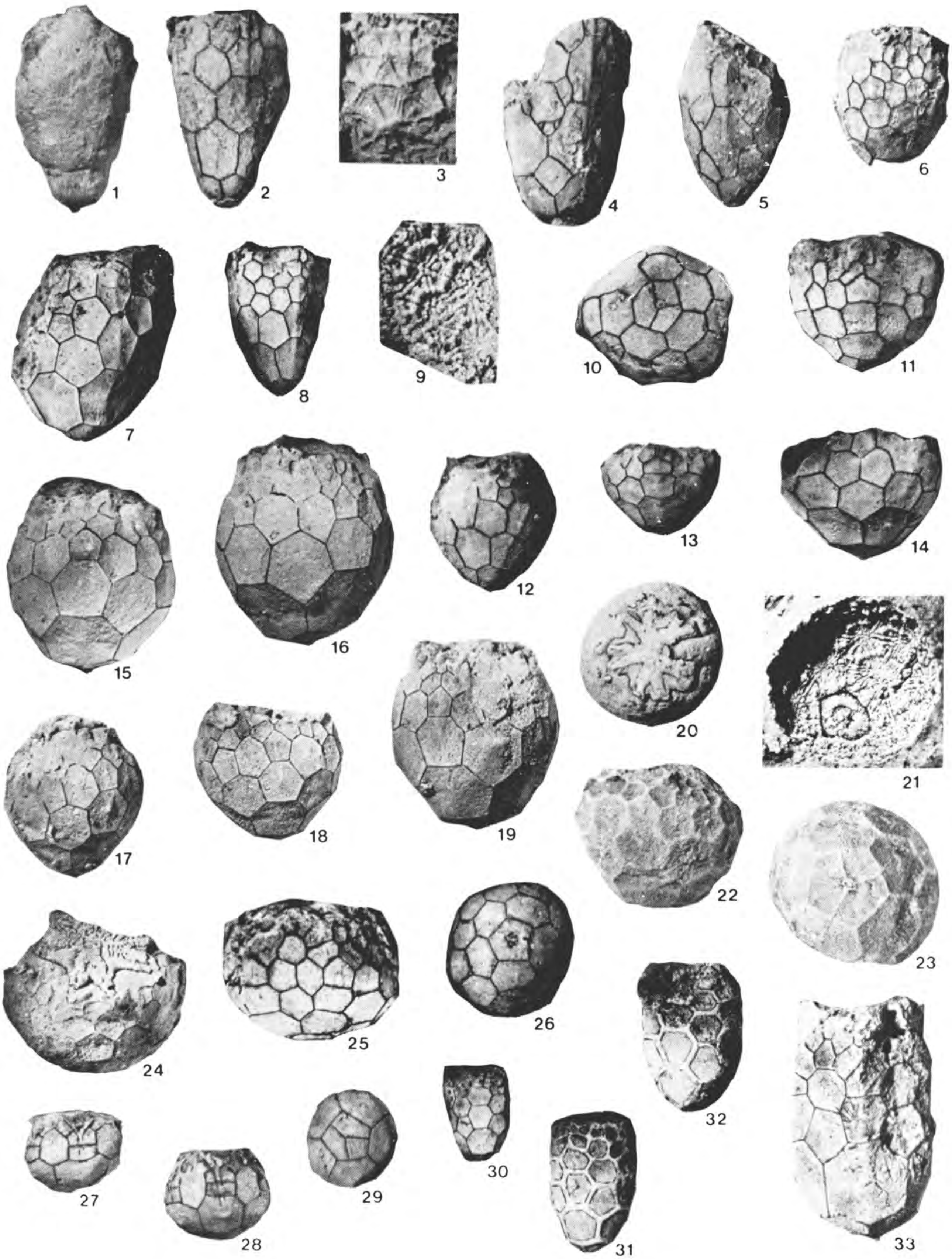
Superfamily PERIECHOCRINACEA Bronn, 1849
Family PERIECHOCRINIDAE Bronn, 1849
Genus PERIECHOCRINUS Morris, 1843

Discussion: The periechocrinids had apparently radiated from the tanaocrinid stock in North America by the latest Ordovician or earliest Silurian; Brower (1973, p. 332) reported a periechocrinid in the Edgewood Fm. of Missouri. The Hopkinton Dolomite specimens (late Llandoverian) are the oldest known representatives of *Periechocrinus*; the genus was cosmopolitan during the remainder of the Silurian.

Periechocrinus sp. A
Plate 2, Fig. 6; Text-fig. 7A

Diagnosis: Cup globose; IBrrl equidimensional; primaxil pentagonal; second range iBrr hexagonal to heptagonal.
Description: Globose cup; radials equidimensional, hexagonal; primibrachs equidimensional, hexagonal, slightly smaller than RR and iBrrl; primaxil pentagonal, smaller than IBrl; first secundibrachs pentagonal to heptagonal; arm facets probably on third IIBrr; iIBrr present. First interbrach hexagonal, bearing two plates in next range, one hexagonal and one heptagonal; interrays probably developed to fifth range; median ray ridge runs the length of each ray; base of cup, posterior interray, and arms not preserved. A single cup measures 19 mm high and 19 mm wide.
Discussion: A single partial specimen of *Periechocrinus* from the "*Cyclocrinites* beds" is, at present, the oldest known representative of the genus. The contemporary *Carpocrinus bodei* resembles *P.* sp. A in general cup characteristics but differs primarily in the shape of the IBrrl.
Material: SUI 45880.

PLATE 2. *1-3.* Lampterocrinus *sp.: 1. calyx with bulged posterior interray, side view (SUI 39953), 2. dorsal cup, side view (SUI 39952), 3. external mold with ornamentation (SUI 39955). All x1.5. 4,5.* Allozygocrinus dubuquensis *n. gen. et sp.: 4. partial dorsal cup, side view (SUI 42310), 5. partial dorsal cup, side view (UC 63966). x1.5. 6.* Periechocrinus *sp. A: dorsal cup, side view (SUI 45880). x1.5. 7,8.* Periechocrinus *sp. B: 7. dorsal cup, side view (SUI 39804), 8. dorsal cup, side view (SUI 39871). x1.5. 9-12.* Carpocrinus bodei *n. sp.: 9. external mold showing plate ornamentation (SUI 42277), 10,11. dorsal cup, basal and side views (SUI 39807), 12. dorsal cup with median ray ridge, side view (SUI 39796). 9. x2, 10-12. x1.5. 13,14.* Carpocrinus *sp.: 13. dorsal cup, side view (SUI 39961), 14. dorsal cup, side view (SUI 39806). x1.5. 15-23.* Bolicrinus globosus *n. gen. et sp.: 15, 19. dorsal cup, side and posterior view (SUI 39362), 16. dorsal cup, side view (SUI 39692), 17. calyx, side view (SUI 39774), 18. dorsal cup, side view (SUI 39768), 20. summit view with ambulacra (SUI 39762), 21. external mold of dorsal cup with plate ornamentation, oblique basal view (UC 63141), 22,23. dorsal cup, unretouched, side and basal views (SUI 46844). All x1.5 except 21 (x2). 24-26.* Bolicrinus deflatus *n. sp.: 24. oblique summit view of calyx and ambulacra (SUI 39793), 25. dorsal cup, side view (SUI 39788), 26. dorsal cup, basal view (SUI 39791). 24,25. x1.5, 26. x2. 27-29.* Allocrinus *cf.* A. subglobosus *(Weller): 27. dorsal cup, side view (SUI 39839A), 28,29. dorsal cup, side and basal views (SUI 39839B). All x2. 30-33.* Thomasocrinus cylindrica *n. gen. et sp.: 30. dorsal cup, side view (SUI 31600), 31. dorsal cup, side view (SUI 31601A), 32. dorsal cup, side view (SUI 31601B), 33. dorsal cup, side view (UC 64720). All x2.*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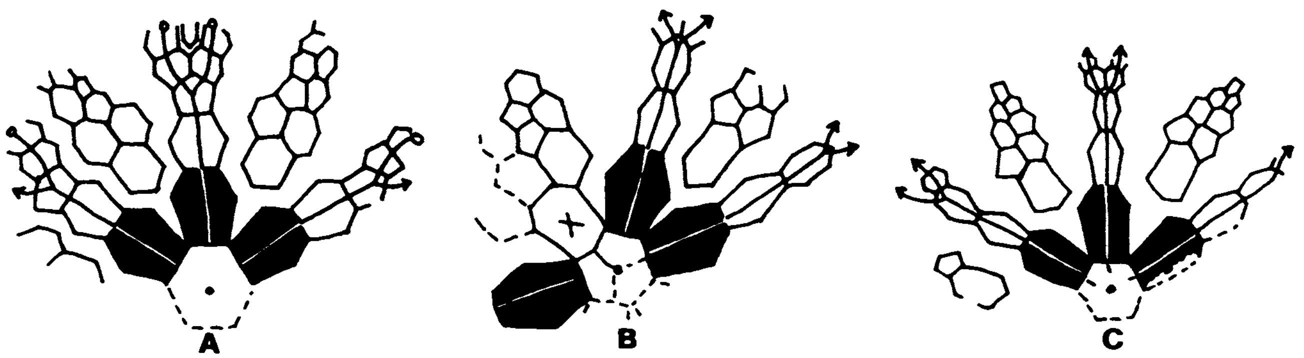


Fig. 7. *Plate diagrams of* Periechocrinus, *Lower Silurian, Iowa. A)* P. *sp. A. (SUI 45880); B, C)* P. *sp. B (SUI 39804, 39871). Median ray ridge shown; RR black; primanal with X.*

Horizon and Locality: "*Cyclocrinites* beds;" Locality 23.

Periechocrinus sp. B
Plate 2, Figs. 7,8; Text-fig. 7A,B

Diagnosis: Cup elongate; IBrrl elongate; primaxil heptagonal; second range iBrr pentagonal to hexagonal.
Description: SUI 39804 and 39871, the primary reference specimens, reveal the following features: elongate cup; base hexagonal; radials elongate, hexagonal, smaller than first iBrr and RR; primaxil heptagonal, smaller than IBrl; first secundibrachs hexagonal; first interbrach hexagonal, bearing two plates in next range, one pentagonal and one hexagonal; interrays arranged in order 1:2:2:2:1; primanal heptagonal, not as high as the adjacent RR, bearing three plates in next range; median ray ridge running the length of each ray. Arms and column unknown.
Discussion: Although the observed features clearly place the "*Cyrtia* beds" specimens within *Periechocrinus*, the features are not sufficient to place it within a described species. The internal molds of *P. infelix* and *P. necis* from the Racine Dolomite are the most similar to the Hopkinton specimens.
Material: SUI 39804, 31755 (6), 39871 (internal, external), 39872 (2).
Horizon and Locality: "*Cyrtia* beds;" Localities 1, 7, 42 (sec. 10).

Superfamily CARPOCRINACEA de Koninck & Le Hon, 1854
Family CARPOCRINIDAE de Koninck & Le Hon, 1854
Genus CARPOCRINUS Muller, 1840

Type species: Actinocrinites simplex Phillips, 1839; Roemer, 1855, SD.
Discussion: The Carpocrinidae and Periechocrinidae were both derived sometime in the latest Ordovician or early Silurian, and confusing similarities are evident in the early history of both families. The superfamilial distinction made between these two groups by Ubaghs (1978) is not directly applicable to many of the known Silurian forms. If the carpocrinids and periechocrinids are to be included within the same superfamily, the Periechocrinacea has priority. The distinctions between *Carpocrinus* and *Periechocrinus*, two genera assigned by Ubaghs (1978) to different superfamilies, are often confusing. *Carpocrinus* differs from *Periechocrinus* in having two rather than four arms per ray and thicker plates with beveled edges (Slocum, 1907, p. 204). Ubaghs (1978), however, also placed some 10-armed forms in *Periechocrinus*. The primaxll is generally heptagonal in *Periechocrinus* and commonly pentagonal in *Carpocrinus; Periechocrinus* also has a more elongate calyx with proportionately longer ray plates. *Periechocrinus* and some *Carpocrinus* have hexagonal IBrl. Kirk (1946) erected the genus *Stiptocrinus* to include forms variously referred to *Saccocrinus, Periechocrinus, Habrocrinus,* and *Aorocrinus* but did not place the genus within a family. The description of *Stiptocrinus* given (Kirk, 1946, p. 33) agrees well with the diagnosis of *Carpocrinus* (Ubaghs, 1978), and *Stiptocrinus* is considered a junior synonym of *Carpocrinus*. Kirk only considered American forms and did not compare *Stiptocrinus* with the known European *Carpocrinus* (=*Habrocrinus, Pionocrinus*). The oldest known *Carpocrinus* are from mid late Llandoverian strata in Iowa; the Carpocrinidae may have been derived from a "periechocrinid" sometime in the Llandoverian of North America (see discussion in Frest and Strimple, 1977, p. 134).

Carpocrinus bodei n. sp.
Plate 2, Figs. 9-12; Text-fig. 8

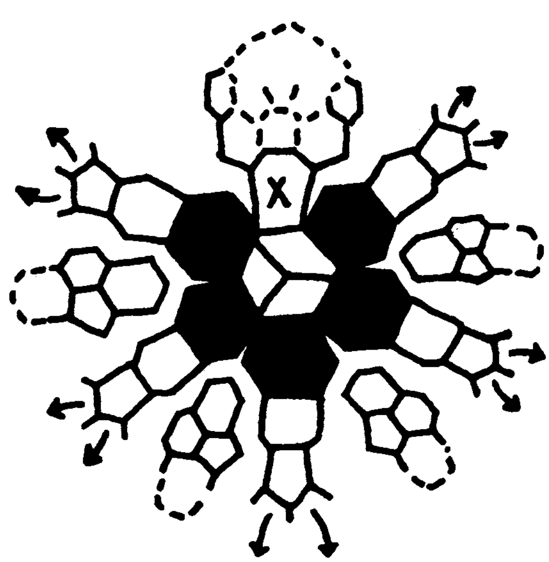


Fig. 8. *Plate diagram of* Carpocrinus bodei. *Distal portions of cup unclear. RR black; primanal with X.*

Diagnosis: Dorsal cup lobate, turbinate to subglobose; 3 basals unequal; first primibrachs hexagonal to irregularly pentagonal; median ray ridge may be developed; plate exteriors decorated with radiating ridges.
Description: Wide variation in dorsal cup shape, turbinate to subglobose, contracting slightly at top. Internal molds of cup gently to strongly lobate. Basal hexagon conical internally, forming steep walls above column facet externally; 3 basals unequal, smallest plate alligned with BC interray. Five hexagonal radials largest plates in cup, approximately equidimensional, in contact all around except on posterior side. First primibrachs hexagonal to irregularly pentagonal, smaller than RR; primaxil pentagonal, slightly smaller than IBrl. Fixed secundibrachs present, probably 2 or 3 per half-ray. Median ray ridges weakly developed on some specimens and visible internally. Interrays slightly depressed between arm bases; first interbrach hexagonal bearing 2 plates in next range; interbrachs probably developed to fourth range. Primanal narrower than the adjacent radials, probably heptagonal; distal region of CD interray up to twice as wide as the lateral interrays. External surface of plates weakly to strongly decorated with radiating ridges (SUI 42276). Ten (?) arm facets. Tegmen, arms, column unknown. Observed size variation: Height, 7.5-22 mm, maximum width, 9-19 mm. Shape variation: height/maximum width, 0.7-1.1.
Discussion: Carpocrinus bodei reveals two primitive features aligning it with a tanaocrinid or periechocrinid ancestry: development of median ray ridges and unequal basals. *Carpocrinus umbonatus* from Gotland (Angelin, 1878) also reveals weakly developed median ray ridges, a feature reminescent of *Periechocrinus*. Other features of *C. bodei* indicate a close relationship with younger members of the genus: reduction in the number of interbrachs and the development of an irregularly pentagonal IBrl in some specimens, a condition approaching the quadrangular IBrl characteristic of the Carpocrinidae as a whole. The Wenlockian *C. comtus* from Gotland (Angelin, 1878) also possesses irregularly pentagonal IBrl. *Carpocrinus bodei* compares most closely with *C. benedicti* and *C. chicagoensis* but differs in general cup shape, width of primanal, size and shape of the IBrl, and surface ornamentation. The species is the most common echinoderm found in the upper level of the "*Cyclocrinites* beds" at Locality 11 where it exhibits a wide variation in cup shape. Some dorsal cups of *C. bodei* are similar in general shape to *Krinocrinus*, although the plating arrangement is completely different.
Derivation of name: Named in honor of the late William C. Bode, Milwaukee, Wisc., collector of the holotype.
Holotype: SUI 39802 (Loc. 28).
Material: Four paratypes are numbered SUI 39794, 39795, 39796, 39799. Additional specimens are numbered SUI 39797, 39798 (3), 39800 (20), 39801 (2), 39803 (4 partial externals), 39842 (internal & external), 42276 (2 externals).
Horizon and Locality: "*Cyclocrinites* beds;" Localities 15, 16, 23, 24, 28.

Carpocrinus sp.
Plate 2, Figs. 13,14

Diagnosis: Dorsal cup lobate, globose; 3 basals equal; first primibrach hexagonal; interbrachs developed to third range.
Description: Dorsal cup lobate, globose. Three basals equal. Radials hexagonal, largest plates in cup. IBrl hexagonal, may be compressed distally, similar in size to iBrl. Primaxil (IBr2) pentagonal; fixed secundibrachs present on lobes. First interbrachs hexagonal, bearing 2 hexagonal interbrachs in second range; third range interbrachs present. Primanal and posterior interray unknown. SUI 39805 measures 19 mm × 25 mm wide.
Discussion: The presence of lobate *Carpocrinus (C. bodei, C.* sp.) in the Hopkinton Dolomite extends the range of the North American "*Stiptocrinus* lineage" into the late Llandoverian (Frest & Strimple, 1977). *C.* sp. differs from other lobate *Carpocrinus* in having a more globose cup; the specimens are left in open nomenclature because the posterior interray remains unknown and a full description is not possible.
Material: Eight specimens are numbered SUI 39805 (5), 39806, 39961 (2).
Horizon and Locality: "*Cyrtia* beds;" Locality 15.

Suborder GLYPTOCRININA Moore, 1952
Superfamily PATELLIOCRINACEA Angelin, 1878

Diagnosis: Glyptocrinina with few fixed Brr in calyx; iBrr composed of a small number of plates, RR large relative to IBrr; arms uniserial, biserial, or compound Brr; column cylindrical.
Remarks: Ubaghs (1978) included in his diagnosis of the Patelliocrinacea, "first primibrachs quadrangular," a feature inconsistent with several patelliocrinacean genera that have hexagonal IBrl including some *Eopatelliocrinus* (Brower, 1973, p. 332) and *Macrostylocrinus* (*ibid.*, p. 363) and all new patelliocrinacean genera described herein. Brower (1973, p. 363) found that in *Macrostylocrinus* "rarely the primanal is followed by two, four, or five plates with or without an anal interray ridge." Other patelliocrinacean genera show little or no differentiation of the CD interray in which the proximal interradials and the primanal are followed by from none to three plates (e.g., *Patelliocrinus, Allocrinus, Laurelocrinus, Thomasocrinus).* In some patelliocrinacean genera the CD interray is differentiated, generally by the inclusion of an extra plate immediately above the primanal (e.g., *Eopatelliocrinus, Stelidocrinus, Bolicrinus).* In *Krinocrinus* the primanal is followed by two plates, a feature identical to the lower iBrr of the lateral interrays, but the wider distal region of the CD interray is differentiated from the narrower distal region of the lateral interrays. Although the Patelliocrinacea "typically" have three plates following the primanal (Ubaghs, 1978), there are known patelliocrinaceans with no, one, two, four, five or six plates following the primanal. The primanal and the plates it supports should not be used in the superfamilial diagnosis although the variability of this region may be of generic significance.

Family PATELLIOCRINIDAE Angelin, 1878

Diagnosis: Patelliocrinacea with BB circlet usually with 3 plates, generally two large, one small (or BB fused); calyx conical to subglobose or subcylindrical; tegmen with numerous plates; uniserial, biserial, or compound Brr arms; arms 2 or 4 per ray.
Remarks: The diagnosis given above is essentially that of Brower (1973, p. 331), although calyx shapes follow Ubaghs (1978). Moore and Laudon (1943, p. 98) noted in their diagnosis of the Patelliocrinidae that the "anal side commonly differentiated by extra plates." Ubaghs (1978) took another view in his diagnosis noting that the "CD interray ordinarily little or not at all differentiated in calyx." Although some patelliocrinid genera do show little or no differentiation of the CD interray, others display differentiation of the CD interray to varying degrees *(Macrostylocrinus, Eopatelliocrinus, Bolicrinus, Krinocrinus).* The differentiation of the CD interray is not a consistent feature in the family and is not included in the diagnosis for this reason. *Bolicrinus* and some *Macrostylocrinus* have a rigid tegmen; the presence of an incomptent tegmen should not be included in the diagnosis of the Patelliocrinidae as Ubaghs (1978) has done.

Genus BOLICRINUS n. gen.

Type species: Bolicrinus globosus n. sp.

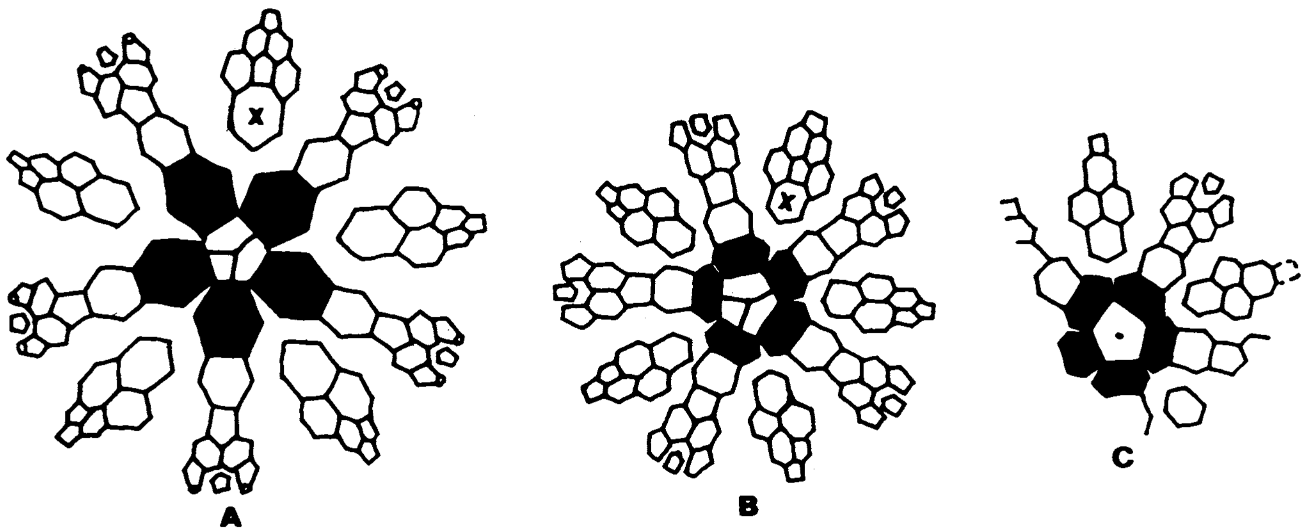


Fig. 9. *Plate diagrams of* Bolicrinus, *Lower Silurian, Iowa. A)* B. globosus, *B)* B. deflatus, *C)* B. deflatus *specimen (SUI 39788) with single third range iBrr. RR black; primanal with X.*

Diagnosis: A genus of the Patelliocrinidae with hexagonal first primibrachs, pentagonal primaxils; 2 fixed secundibrachs in each half-ray; flat to gently convex basal circlet; radials largest plates in cup; first interbrach large, hexagonal, followed by two plates in second range; interrays developed to fourth range; CD interray differentiated, heptagonal primanal bearing 3 plates. Calyx globose to bowl shaped, contracting distally; tegmen flat; 10 arms.

Discussion: The well-developed interrays of *Bolicrinus*, a primitive feature in the Patelliocrinidae, align the genus most closely with some *Macrostylocrinus* and *Eopatelliocrinus*. Upper Ordovician *Eopatelliocrinus* and *Macrostylocrinus* from the Girardeau Limestone of Missouri (Brower, 1973) possess hexagonal primibrachs in some specimens, and interbrachs may be present to the fifth or sixth range in adult forms; this Upper Ordovician grade of patelliocrinid evolution is reminiscent of (and probably ancestral to) that noted in *Bolicrinus*. *Bolicrinus* differs from *Eopatelliocrinus* in its globular to bowl-shaped cup, competent tegmen, and slightly reduced interray development (although iBrr are proportionately larger). Forms here assigned to *Bolicrinus* could be lumped within a broadly defined *Macrostylocrinus*, although the distinctive bowl-shaped to globular cup shape, hexagonal primibrachs, and well-developed interrays readily distinguishes *Bolicrinus* from most species included in *Macrostylocrinus*. *Macrostylocrinus* is a broadly defined genus including a confusing array of patelliocrinid forms. Patelliocrinid forms with hexagonal primibrachs and globular cup shapes are included in the new genus *Bolicrinus*, partly in an effort to avoid burgeoning the genus *Macrostylocrinus* with additional forms and partly to reflect the independent *Bolicrinus-Thomasocrinus* evolutionary line. The reduction in interray width in *Bolicrinus* probably led directly to the subcylindrical form, *Thomasocrinus*. *Bolicrinus globosus* is one of the most common and distinctive crinoids in the "*Cyclocrinites* beds." The group of Iowa Silurian patelliocrinids with hexagonal primibrachs includes *Bolicrinus, Thomasocrinus, Krinocrinus*, and two species included for convenience in *Macrostylocrinus;* these forms represent a grade of patelliocrinid evolution that achieved its greatest degree of diversification and success during the Early Silurian.

Derivation of name: Bol (Greek), rounded mass.

Bolicrinus globosus n. sp.
Plate 2, Figs. 15-23; Text-fig. 9A

Diagnosis: Dorsal cup globular; cup height greater than or equal to maximum cup width; basal circlet width/maximum cup width greater than 0.4.

Description: Dorsal cup globular, constricting towards oral surface, widest at the top level of the proximal interradials. Basal pentagon slightly convex internally; three basals, 2 large, 1 small; smallest B aligned with AE interray. Five hexagonal radials, the largest plates in cup, connected in an uninterrupted circlet. First primibrachs hexagonal, smaller than RR and proximal iRR. Primaxil pentagonal, smaller than second range of iRR. First fixed secundibrach hexagonal; second fixed secundibrach small, bears arm facets. Smallest ray plate is a single fixed intersecundibrach per ray. First interbrachs are second largest plates in cup; hexagonal iBrl bears 2 iBrr on their distal margins, one pentagonal and the other heptagonal (heptagonal plate always adjacent to B or E rays). Primanal heptagonal, bears 3 iBrr on distal margin (2 lateral iBrr hexagonal, central iBr pentagonal). Third level of iBrr with one pentagonal and one hexagonal plate in every lateral interray; in CD interray both plates are hexagonal. One very small fourth level iBr in each interray at distal margin of cup. Lateral interrays arranged in order 1:2:2:1; posterior interray arranged in order 1:3:2:1. Tegmen flat; ambulacra branching outward into 10 arm facets. Anus laterally situated on side of CD interray; anus elevated on internal molds indicating that the anus opened directly through the tegmen. A single specimen (UC 63141) reveals an external plate ornamentation of ridges perpendicular to plate sutures. Structure of column or arms unknown. Observed size variation: height, 10-31 mm, maximum width, 9.5-30.5 mm. Shape variation: height/maximum width, 1.0-1.3.

Derivation of name: Globosus refers to globular shape.

Holotype: SUI 39692 (Loc. 28)

Material: One-hundred specimens include paratypes SUI 39767, 39768, 39769 (2), 39970 (5), 39774 (4), UC 63141 and additional specimens SUI 39771 (12), 39772 (21), 39775 (7), 39776 (2), 39773, 39777 (2), 39778 (2), 39779, 39780, 39781, 39782 (2), 39783 (17), 39784 (2), 39785 (2), 39786 (3), 39787 (11).

Horizon and Locality: "*Cyclocrinites* beds;" Localities 9, 11, 16, 20, 21, 23, 24, 25, 27, 28, 32, 35.

Bolicrinus deflatus n. sp.
Plate 2, Figs. 24-26; Text-fig. 9B,C

Diagnosis: Dorsal cup low, bowl-shaped; cup width greater than cup height; basal circlet width/cup width less than 0.4.
Description: Dorsal cup low, bowl-shaped, gently constricting towards oral surface, widest at level of primaxils. Basal pentagon gently concave to gently convex internally; 3 basals, 2 large, 1 small. Columnar facet occupies half the width of basal pentagon. Radials wider than high. First primibrachs hexagonal but approaching a quadrangular shape in all specimens. All other plate shapes and relations as in *B. globosus*, except in SUI 39788 where the second range of iBrr are all hexagonal and the third range iBrr consists of only one heptagonal plate. All other features of SUI 39788 are consistent with assignment to *B. deflatus*. The lateral interrays of *B. deflatus* are arranged in order 1:2:2:1 or 1:2:1:1. External ornamentation consists of coarse to fine striae alligned perpendicular to the plate sutures (UC 63141). Tegmen flat. Size variation: height, 5-18 mm, width, 7-23 mm. Shape variation: height/width, 0.6-0.8.
Derivation of name: Deflatus, deflated bowl-shaped cup.
Holotype: SUI 39791 (Loc. 23).
Material: Additional material SUI 39788 (2), 39789, 39790, 39792 (5), 39793, 39959, UC 63141 (int., ext.).
Horizon and Locality: "*Cyclocrinites* beds;" Localities 11, 21, 23, 28.

Genus THOMASOCRINUS n. gen.

Type species: Thomasocrinus cyclindrica n. sp.
Diagnosis: A genus of the Patelliocrinidae with hexagonal first primibrachs, pentagonal to heptagonal primaxils; 2 fixed secundibrachs in each half-ray; gently convex basal circlet; radials largest plates in cup; first interbrach pentagonal; interrays developed to fourth range, only one iBr in each range (1:1:1:1). No differentiation of CD interray. Dorsal cup subcylindrical; tegmen flat; 10 arms.
Discussion: Thomasocrinus is one of the few patelliocrinids to have achieved nearly perfect pentamerous symmetry. The rays of *Thomasocrinus* are very similar to those noted in *Bolicrinus;* the difference between the two genera lies primarily in the interrays. The linear arrangement of four interbrachs per interray in *Thomasocrinus* is markedly different from the more developed interrays of *Bolicrinus*. *Bolicrinus* is the most likely ancestor of *Thomasocrinus*; no descendents from this stock are known in any Wenlockian or younger deposits.
Derivation of name: Rowser (1932) proposed the name *Thomasocrinus*, then a *nomen nudum*, in honor of Prof. A.O. Thomas, University of Iowa, and the proposal is reiterated herein.

Thomasocrinus cylindrica n. sp.
Plate 2, Figs. 30-33; Text-fig. 10

Description: Dorsal cup subcylindrical; basal pentagon gently convex internally; 3 basals, 2 large, 1 small. Radials approximately equidimensional, hexagonal to gently heptagonal, largest plates in cup. First primibrach hexagonal; primaxil pentagonal to heptagonal, if hexagonal or heptagonal in contact with iBr3. First interbrachs pentagonal, supporting one hexagonal to octagonal interbrach in second range (if octagonal, in contact with IIBrl). A single third range iBr per interray, hexagonal; single fourth range iBr per interray. All five interrays arranged in order 1:1:1:1. No apparent differentiation of CD interray; cup achieves apparent pentamerous symmetry. Tegmen flat; 10 arm facets. External surface of plates probably smooth. Structure of column or arms unknown. Observed height variation, 8.5-23.2 mm.

Fig. 10. *Plate diagrams of individual specimens of* Thomasocrinus cylindrica. *1) UC 64720, 2) SUI 31601A, 3) SUI 31601B, 4) SUI 31600, 5) SUI 39870 (approximately to scale). RR with diagonal ruling.*

Height/width ratio, 1.5-1.6.
Discussion: None of the specimens preserves the cup plates in its entirety, although a series of partial specimens outlines the general cup characteristics. The largest specimen (UC 64720) is the only one with octagonal iBr2 and pentagonal IAx; this specimen may represent another species of the genus, although these differences were more likely generated during ontogeny. The smaller specimens of *T. cylindrica* have heptagonal or hexagonal IAx that are in contact with one or both adjacent iBr2 and iBr3, whereas the IAx of UC 64720 does not contact the iBrr3.
Holotype: SUI 31600 (partial internal and external).
Material: Thirteen paratypes numbered SUI 31601 (11), 39870, and UC 64720. Three poorly preserved and slightly larger specimens, SUI 31602, are tentatively included in this species.
Horizon and Locality: "*Cyrtia* beds;" Localities 1, 18, 42 (sec. 10).

Genus KRINOCRINUS n. gen.

Type species: Krinocrinus inflatus n. sp.
Diagnosis: A genus of the Patelliocrinidae with hexagonal first primibrachs, heptagonal primaxils; conical basal pentagon; hexagonal radials largest plates in cup. First interbrachs, including primanal, hexagonal supporting two hexagonal iBrr in second range; interray well developed to fifth or sixth range; CD interray differentiated in its wider distal region. Dorsal cup conical, contracting distally; 10 arm facets.
Discussion: The CD interray of *Krinocrinus* is primarily differentiated in its distal region, a feature that would make it unique among the members of the Patelliocrinidae. The inclusion of *Krinocrinus* in the Patelliocrinidae is based on the large RR, a basal pentagon, and a conical cup. The noted occurrence of the primanal supporting two plates in some *Macrostylocrinus* (Brower, 1973, p. 363) lends further support to the familial assignment of *Krinocrinus*. *Krinocrinus* was apparently derived from a *Macrostylocrinus*-stock, but *Krinocrinus*-like forms are unknown in collections from younger Silurian strata. The development of a distally inflated CD interray is reminiscent of the highly successful but unrelated North American Silurian Lampterocrinidae.
Derivation of name: Krin (Greek, distinguish), the distally inflated CD interray distinguishes the genus.

Krinocrinus inflatus n. sp.
Plate 3, Figs. 1-4; Text-fig. 11

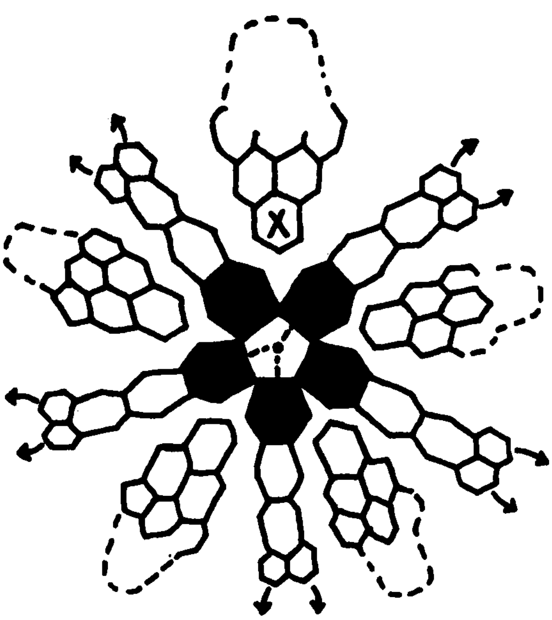


Fig. 11. *Plate diagram of* Krinocrinus inflatus *(distal portion of interrays unclear). RR black; primanal with X.*

Description: Dorsal cup conical, contracting toward oral surface; basal pentagon internally conical, forming steep sides externally; number of BB unknown although collectively SUI 39824 and 39822 externals suggest an arrangement consistent with the patelliocrinids. Five hexagonal radials, the largest plates in cup, connected in an uninterrupted circlet. First primibrachs hexagonal, second largest plates in cup. Primaxil heptagonal, slightly smaller than IBrl. First fixed secundibrachs hexagonal. Distal region of rays indeterminate. Hexagonal first interbrachs support two hexagonal iBrr in second range. Interrays well developed, plates developed to at least the fifth, probably the sixth range. Primanal supports only two plates; CD interray differentiated in distal region being almost twice as wide as in the lateral interrays. Tegmen flat; 10 arm facets. Anus laterally situated above CD interray. External surface of plates smooth. Structure of column or arms unknown. Size variation: height, 10-40 mm, maximum width, 8-30 mm. Shape variation: height/maximum width, 1.2-1.4.
Derivation of name: Inflatus; characteristic feature is distally inflated CD interray.

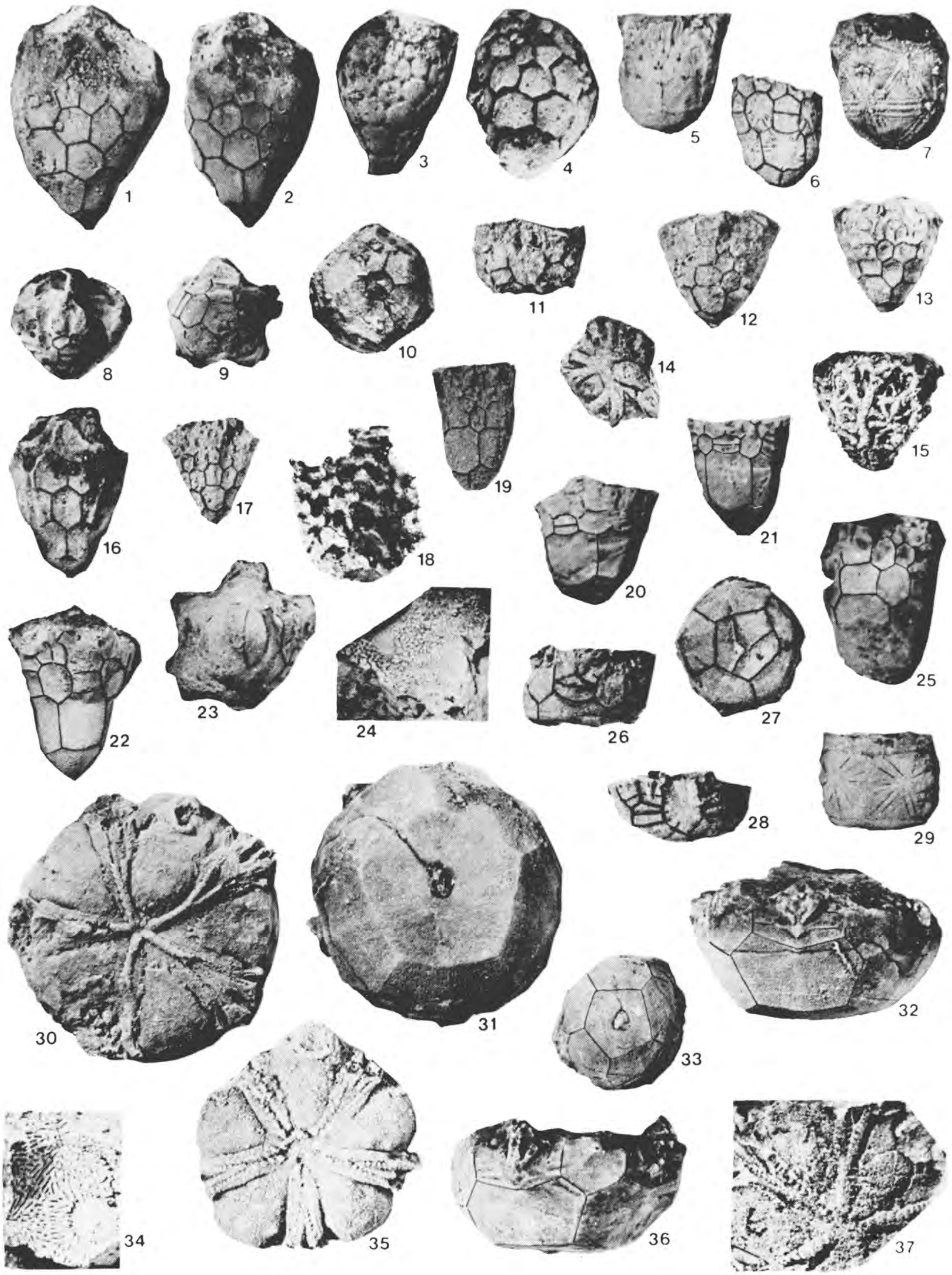
Holotype: SUI 39822 (partial external and internal mold; Loc. 11).
Material: Paratypes are numbered SUI 39823 (internal), 39781 (external), 39821 (internal), and 39824 (internal). Twenty-two additional specimens include SUI 39825 (int. & ext.), and internal molds SUI 39826 (9), 39827 (2), 39828, 39829 (5), 39830 (2), 39831(3).
Horizon and Locality: "*Cyclocrinites* beds;" Localities 9, 11, 16, 23, 28, 35.

Genus MACROSTYLOCRINUS Hall, 1852

Type species: Macrostylocrinus ornatus; M
Discussion: Macrostylocrinus (Late Ordovician-Early Devonian) exhibits a wide range of variation in calyx shape, degree of development of the interrays, and shape and size of the primibrachs in the included species. *Macrostylocrinus* presently includes a diverse group of patelliocrinids; further work will probably necessitate splitting the genus into several taxa with more restricted diagnoses. The dorsal cup shape in *Macrostylocrinus* presently ranges between conical, subglobose, bowl-shaped, and subcylindrical. The radials are consistently large. The first primibrach varies between greatly compressed-rectangular forms and elongate-hexagonal forms; the primaxil varies between compressed pentagonal (approaching obliquely triangular) forms and elongate heptagonal forms in the various species. These variations in the primibrachs are already evident in two upper Ordovician forms, *M. cirrifer* (England) and *M. pristinus* (Missouri). The primanal is generally followed by 3 or 5 plates in the next range, although forms are known in which 2, 4, or 6 plates follow the primanal [Springer (1926, p. 181) illustrated a *M. laevis* in which 6 plates follow the primanal.] The CD interray is always differentiated in *Macrostylocrinus*. Interrays are developed to varying degrees in the different species: development to the second range in some species and to the fifth range and beyond in other species such as *M. fasciatus, M. cirrifer,* and *M. pristinus.* If the lateral interrays are not developed beyond the first range (i.e., only one large iBr per interray) or if the second range consists of 1 or 2 diminutive plates connected with the tegmen, such forms are referred herein to *Allocrinus* (emended). The Late Ordovician *M. cirrifer* to Early Silurian *M. silurocirrifer* lineage (Brower, 1975, p. 638) is probably an independent line of macrostylocrinid evolution that was followed in western Europe. Nine of the patelliocrinid species from the Hopkinton Dolomite are lumped in *Macrostylocrinus*; for the most part these forms are represented by poorly preserved specimens distinguished from each other largely by cup shape and ray structure.

Macrostylocrinus sp. A
Plate 3, Figs. 5-7; Text-figs. 12(1),13(1,2,3)

PLATE 3. *1-4.* Krinocrinus inflatus *n. gen. et sp.: 1,2. dorsal cup, posterior and side views (SUI 39813), 3. dorsal cup, side view, latex cast of external (SUI 39822), 4. dorsal cup, oblique basal view, latex cast of external (SUI 39781). All x1.5. 5-7.* Macrostylocrinus *sp. A: 5. dorsal cup, side view (SUI 39833A), 6. dorsal cup, side view (SUI 39833B), 7. dorsal cup with external ornamentation (SUI 39832). All x1.5. 8,9.* Macrostylocrinus *sp. B: calyx, side and basal views (SUI 39984). x1.5. 10,11.* Macrostylocrinus *sp. C: dorsal cup, basal and side views (SUI 39985). x1.5. 12-15.* Macrostylocrinus *sp. D: 12. calyx, side view (SUI 39818), 13,14. calyx, side and summit views (SUI 39816), 15. calyx, side view, latex cast of external (SUI 39816). All x1.5. 16-18.* Macrostylocrinus *sp. E: 16. dorsal cup, side view (SUI 42281), 17,18. dorsal cup, side view and external mold (SUI 42282). 16,17. x1.5, 18. x2. 19.* Macrostylocrinus *sp. F: dorsal cup, side view (UC 59069). x2. 20,21.* Macrostylocrinus compressus *n. sp.: 20. dorsal cup, side view (SUI 39836), 21. dorsal cup, side view (SUI 39835). x2. 22-24.* Macrostylocrinus vermiculatus *n. sp.: dorsal cup, side view, basal view, and external mold with ornamentation (SUI 31741). 22. x1.5, 23,24. x2. 25.* Macrostylocrinus *cf.* M. striatus *Hall: dorsal cup, side view (SUI 39868). x1.5. 26-29.* Allocrinus ornatus *n. sp.: 26,27. dorsal cup, side and basal views (SUI 39841A), 28. dorsal cup, side view (SUI 39841B), 29. dorsal cup, side view with external plate ornamentation (SUI 39840). 26-28. x2, 29. x1.5. 30-37.* Marsupiocrinus (Amarsupiocrinus) primaevus *n. sp.: 30. summit view, laterally-situated anus and ambulacra visible, unretouched (SUI 39920), 31,32. dorsal cup, basal and side views (SUI 39919A), 33. dorsal cup, basal view, "*Cyclocrinites *beds" (SUI 39911), 34,35,37. external plate ornamentation, dorsal cup, summit view, and external mold, summit view (SUI 39923), 36. dorsal cup, side view (SUI 39919B). All x1.5 except 35,37. x2.*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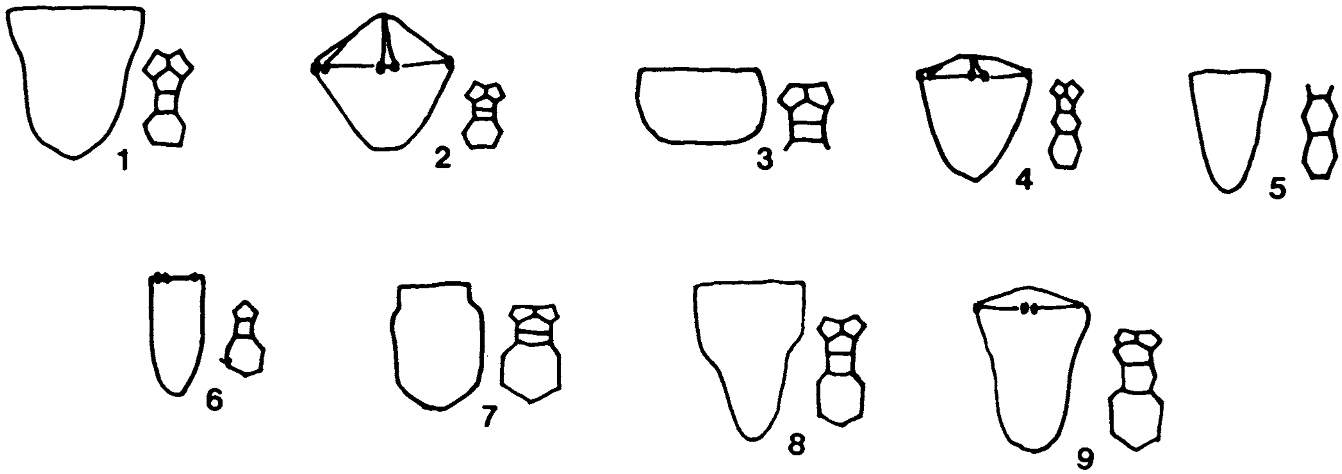


Fig. 12. *Dorsal cup profiles (silhouettes) and ray structures (to IIBrl) of* Macrostylocrinus, *Lower Silurian, Iowa. 1)* M. *sp. A., 2)* M. *sp. B., 3)* M. *sp. C, 4)* M. *sp. D, 5)* M. *sp. E., 6)* M. *sp. F, 7)* M. compressus, *8)* M. vermiculatus, *9)* M. *cf.* M. striatus *(approximately to scale).*

Diagnosis: Dorsal cup rounded at base, gently flaring above; coarse striae transect plate sutures; IBrl quadrangular; 3 fixed IIBrr per half-ray.
Description: Dorsal cup rounded at base, gently flaring above to lobate; subcircular in cross-section proximally, pentangular toward arm bases. RR large, hexagonal; IBrl quadrangular; IBr2 pentagonal; 3 secundibrachs per half-ray. Proximal interbrachs bear 1 or 2 plates in next range. Posterior interray unknown. Coarse striae aligned perpendicular to plate sutures externally.
Discussion: This group of "*Cyrtia* bed" patelliocrinids is difficult to interpret due to poor preservation. Two different species may be lumped here under *M.* sp. A, one with coarse external striae, the other with a more lobate cup and possibly smooth plates. More material is necessary to properly diagnose the species. Any "*Cyrtia* bed" patelliocrinid with a rounded base, large RR, and prominent IIBrr is here informally grouped in *M.* sp. A.
Material: Nineteen specimens available; primary reference specimens SUI 39832 (displays external) and SUI 39833 (2); additional specimens SUI 39834 (15) and 39867.
Horizon and Locality: "*Cyrtia* beds;" Localities 7, 15.

Macrostylocrinus sp. B
Plate 3, Figs. 8,9; Text-figs. 12(2),13(4)

Diagnosis: Dorsal cup subglobose, strongly lobate; tegmen well-developed, arched; basals not visible in lateral view; second range interbrachs partly incorporated in tegmen, third range interbrachs excluded from cup.
Description: Dorsal cup subglobose, strongly lobate; basal pentagon not visible in lateral view. Radials hexagonal; IBrl rectangular; IBr2 pentagonal; two IIBr per half-ray. First interbrachs decagonal, large, bearing one plate in next range, adjacent to arm facets, arching onto tegmen. Primanal bears two plates in next range, adjacent to arm facets, arching onto tegmen. Primanal bears two plates in next range, adjacent to arm facets, with third range interbrach incorporated in the tegmen. Tegmen well-developed, arched, bearing prominent ambulacra. 10 arm bases. Calyx height, 13 mm; width, 14 mm.
Discussion: A single specimen of a patelliocrinid is included in *Macrostylocrinus* based on the plate arrangement. It differs from most other species included in the genus in having a rigid tegmen.
Material: SUI 39984.
Horizon and Locality: "*Cyrtia* beds;" Locality 15.

Macrostylocrinus sp. C
Plate 3, Figs. 10,11; Text-figs. 12(3),13(5)

Diagnosis: Dorsal cup bowl-shaped, excavated at base; basals small; IBrl quadrangular.
Description: Dorsal cup bowl-shaped, excavated at base. Basal pentagon small, in depression on internal molds, 2 BB equal, 1 unequal. Radials visible primarily in basal view, hexagonal. IBrl rectangular, IBr2, pentagonal. First interbrachs large, probably decagonal; second range interbrachs present. Surface of plates probably smooth. Cup height, 9 mm; width, 16 mm.
Discussion: A single specimen from the "*Cyclocrinites* beds" exhibits a plate arrangement consistent with a simplified patelliocrinid form. It differs from other species of the genus in having the base excavated and in general cup shape. This form is tenatively referred to *Macrostylocrinus*, although it may represent an undescribed genus. By further reduction of the interrays, *M.* sp. C may be ancestral to *Allocrinus*.
Material: SUI 39985 (internal, external).
Horizon and Locality: "*Cyclocrinites* beds;" Locality 11.

Macrostylocrinus sp. D
Plate 3, Figs. 12-15; Text-figs. 12(4),13(6)

Diagnosis: Dorsal cup subconical; external ornament of coarse radiating ridges; IBrl hexagonal; tegmen rigid.
Description: Dorsal cup subconical, gently lobed at distal margins. 3 BB, 1 small, 2 large. Radials large, hexagonal to heptagonal. First primibrach hexagonal; primaxil pentagonal, secundibrachs incorporated in cup. Proximal interbrachs hexagonal, bearing 2 plates in next range; lateral interrays arranged 1:2:2:3?, distal portion incorporated into tegmen. Posterior interray differentiated, primanal bearing 3 plates. Tegmen rigid, flat, preserved on all noted specimens; ambulacra lead to 10 arm facets; anus subcentral. External ornament of coarse radiating ridges. SUI 42280 (calyx) measures 16 mm high × 15 mm wide.
Material: 6 specimens are numbered SUI 39816 (external), 39817, 39818 (2), 42279, 42280.
Horizon and Locality: "*Cyclocrinites* beds;" Localities 16, 23, 27, 28.

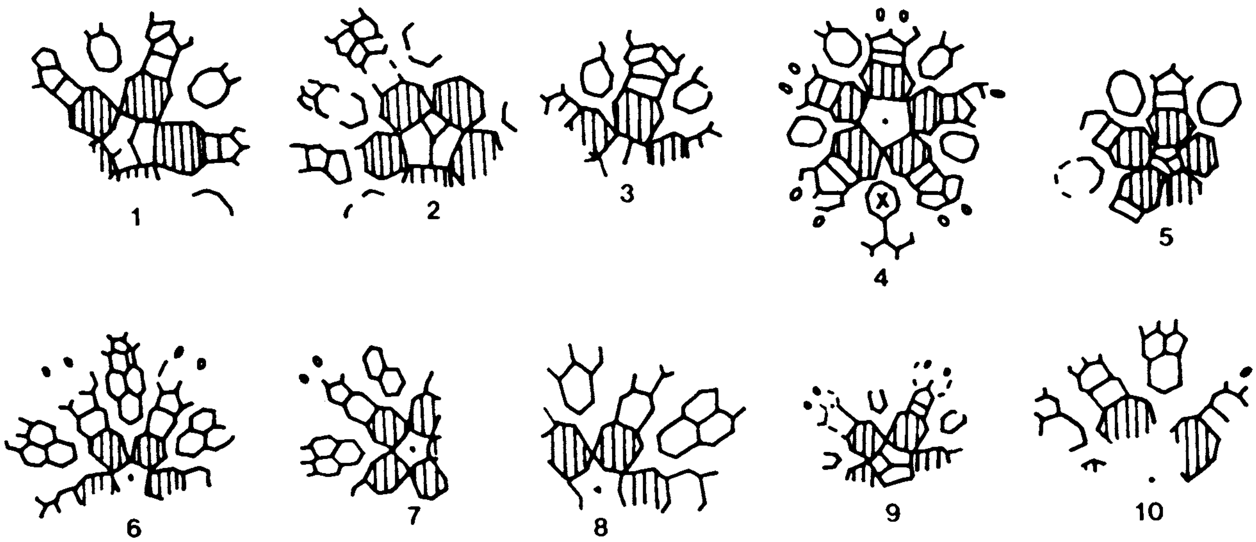


Fig. 13. *Plate diagrams from various specimens of* Macrostylocrinus, *Lower Silurian, Iowa. RR with diagonal ruling; primanal with X. 1)* M. *sp. A (SUI 39833A), 2)* M. *sp. A (SUI 39833B), 3)* M. *sp. A. (SUI 39834), 4)* M. *sp. B (SUI 39984), 5)* M. *sp. C (SUI 39985), 6)* M. *sp. D (SUI 42280), 7)* M. *sp. E (SUI 42282), 8)* M. *sp. E (SUI 42281), 9)* M. *sp. F (UC 59069), 10)* M. *cf.* M. striatus *(SUI 39868). Approximately to scale.*

Macrostylocrinus sp. E
Plate 3, Figs. 16-18; Text-figs. 12(5),13(7,8)

Diagnosis: Dorsal cup subconical; external of plates nodose; IBrl hexagonal.
Description: Dorsal cup subconical, lobed at distal margin. Radials large, hexagonal to heptagonal; IBrl hexagonal; IBr2 pentagonal; IIBrl hexagonal; IIBr2 present; single intersecundibrach present per ray. Proximal interbrachs hexagonal; lateral interrays arranged 1:2:2:2. Posterior interray unknown. External of plates nodose. SUI 42282 (dorsal cup) measures 14 mm high × 11 mm wide.
Discussion: Internal molds of *M.* sp. E are similar to *M.* sp. D except that *M.* sp. E has a more steeply conical cup, more pronounced lobes, and apparently lacks a rigid tegmen. Externally the two species differ dramatically.
Material: Two specimens are numbered SUI 42281 (internal, external) and 42282.
Horizon and Locality: "*Cyclocrinites* beds;" Localities 11, 18.

Macrostylocrinus sp. F
Plate 3, Fig. 19; Text-figs. 12(6),13(9)

Diagnosis: Dorsal cup subcylindrical; IBrl quadrangular.
Description: Dorsal cup subcylindrical, higher than wide. Basal pentagon broadly conical. Radials large, hexagonal. First primibrach quadrangular, wider than high; primaxil pentagonal. Secundibrachs incorporated into cup, probably to second range. First interbrachs small, probably hexagonal; second range interbrachs may be absent, and secundibrachs from adjacent rays may be in contact. 10 arm facets. UC 59069 measures 9.8 mm high × 6.5 mm wide.
Material: UC 59069; tentatively included are two poorly preserved specimens with more distally flaring cups (SUI 39843).
Horizon and Locality: "*Cyclocrinites* beds;" Locality 16 (SUI 39843, Locality 11).

Macrostylocrinus compressus n. sp.
Plate 3, Figs. 20,21; Text-figs. 12(7),14A

Diagnosis: Dorsal cup conical at base, subcylindrical above; pentangular in cross-section at base, subcircular above; broad median ray ridge developed internally from base of cup to top of RR; IBrl distally compressed, subpentagonal.
Description: Dorsal cup obconical; 5 broad ridges present internally beneath level of primibrachs; radials very large, occupying almost one-half of cup height; distal margin of RR concave; first primibrachs distally compressed, subpentagonal, three times wider than high; primaxils about same size as IBrl, pentagonal. First interbrachs heptagonal bearing two plates in second range; primanal unknown. Observed size variation (unbroken specimens); height, 7-14 mm, width 5-11 mm.
Discussion: The cup shape of *M. compressus* closely resembles *M. obconicus*. However, the distally compressed subpentagonal IBrl of *M. compressus* readily distinguishes it from *M. obconicus* with roughly equidimensional hexagonal IBrl. Rowser (1932) described a *Macrostylocrinus* from the "Lower Gower" (=Hopkinton) with hexagonal IBrl that is probably referrable to *M. obconicus;* the specimens have not been located.
Derivation of name: Compressus; compressed IBrrl characterize the species.
Holotype: SUI 39835 (Loc. 15).
Material: Six paratypes with group number SUI 39836 and additional specimens SUI 39837 (16), 31770 (7), 39838, 39866.
Horizon and Locality: "*Cyrtia* beds;" Localities 1, 7, 15. Adjacent to bioherms; Locality 33.

Macrostylocrinus vermiculatus n. sp.
Plate 3, Figs. 22-24; Text-figs. 12(8),14B

Diagnosis: Rays form distinct lobes, interrays depressed (concave); dorsal cup expands broadly to base of arms; base conical; surface of plates with numerous delicate nodes; first primibrachs quadrangular.

Description: Calyx higher than wide, conical at base, subcylindrical at level of radials, rays rapidly expanding to base of arms. Interrays depressed, rays forming distinct lobes. Radials large, almost one-half height of cup; lateral edges of RR parallel; first primibrach much smaller than RR, approximately square; primaxil pentagonal, roughly same size as IBrl. First interbrach probably octagonal, supporting two plates in next range; CD interray over 50% wider than lateral interrays. Surface of plates covered by numerous delicate nodes; rows of nodes between adjacent plates not interconnective. Tegmen, column, arms unknown. Holotype measures 15 mm high, 14 mm wide at arm bases, 7 mm wide at level of RR.
Discussion: Macrostylocrinus vermiculatus most closely resembles *M. striatus,* but differs in being relatively narrower at the level of the RR and by its delicate nodes on the plate surface. *Macrostylocrinus striatus* is ornamented by radiating striations.
Derivation of name: Vermiculatus refers to the ornamented surface of the plates (Rowser, 1932).
Holotype: SUI 31741 (internal and external molds).
Material: Additionally 3 specimens are numbered SUI 31742.
Horizon and Locality: "*Cyrtia* beds;" Locality 1.

Macrostylocrinus cf. *M. striatus* Hall, 1863
Plate 3, Fig. 25; Text-figs. 12(9),13(10)

Discussion: Three poorly preserved internal molds from the "*Cyrtia* beds" at Locality 7, are tentatively assigned to *M. striatus* based on general calyx shape and the presence of three levels of interbrachial plates. The specimens differ from *M. vermiculatus* in being less lobate and in the shape of the IBrr.
Material: SUI 39868 (3).

Genus ALLOCRINUS Wachsmuth & Springer, 1890

Type species: Allocrinus typus; OD.
Diagnosis: Calyx low bowl-shaped, first interbrach large, may or may not be followed in next range by 1 or two small plates connected with tegmen; 1 or 2 small primibrachs and 1 or 2 small fixed secundibrachs per ray. Arms 10, simple. Columnals long with narrow pentangular axial canal.
Discussion: Described species of *Allocrinus* include a greater range of variation than Ubaghs' (1978) diagnosis suggests. Globular-cupped forms could be removed to a new genus with the basally excavated forms kept in *Allocrinus*, although the genus is herein treated in a broadly defined sense. Characteristically, most species of *Allocrinus* show little or no differentiation of the CD interray; however, *A. globulus* has a well differentiated CD interray (Strimple, 1963, p. 108). *Allocrinus* was probably derived directly from *Macrostylocrinus* by a reduction in interray height and distal compression of the fixed primibrachs and secundibrachs as the cup became more globose. These trends are evident in species such as *Macrostylocrinus pustulosus. Allocrinus irroratus* and *A. divergens* are atypical of the genus in displaying branching from the first primibrach (Strimple, 1963, p. 107); the extreme reduction in the height of the fixed brachials apparently resulted in the loss of the second primibrach in these species. Species with only one primibrach per ray are assigned herein to *Allocrinus* and the generic diagnosis revised accordingly; alternatively, forms with one IBr per ray could also be referred to a new genus. *Allocrinus irroratus,* a species that represents an extreme in patelliocrinid dorsal cup simplification, has three basals of equal size, a condition atypical of the family in general. "*Macrostylocrinus*" *subglobosus* has a subglobose cup, compressed primibrachs, and very large first interbrachs filling the interray spaces (Weller, 1900, p. 96); these features align the species with *Allocrinus* (*A. subglobosus* n. comb.). The *Allocrinus* from the Hopkinton Dolomite are the oldest known forms of the genus. *Allocrinus* probably diverged from a *Macrostylocrinus* stock sometime in the Llandoverian.

Allocrinus cf. *A. subglobosus* (Weller, 1900)
Plate 2, Figs. 27-29

Diagnosis: Dorsal cup small, subglobose; basal pentagon gently convex; distal margin of radials concave; first primibrach sublunate; first interbrach large, filling interrays; external of plates with delicate nodes.
Description: Dorsal cup small, subglobose, length and width about equal; three basals unequal forming gently convex pentagon; radials large, distal margin of radials concave; first primibrach small, twice as wide as high, sublunate; primaxil pentagonal, about same size as IBrl. First interbrach large, practically filling the whole interray space; second range interbrachs either absent or very small; CD interray indeterminate in available Hopkinton specimens. External of plates marked by delicate nodes.
Discussion: The lack of distinct second range interbrachs, large first interbrachs, and a subglobose cup align the Hopkinton Dolomite specimens most closely with *Allocrinus subglobosus (Macrostylocrinus subglobosus* Weller, 1900, p. 96) from the Racine Dolomite of Illinois. *Allocrinus subglobosus* differs from the Hopkinton specimens in having a broadly arched tegmen, radials lacking distal concave margin, and first primibrachs perfectly quadrangular.
Material: Seventeen specimens are available numbered SUI 39839 (6), 31771 (10), and 39865.
Horizon and Locality: "*Cyrtia* beds;" Localities 2, 7, 15.

Allocrinus ornatus n. sp.
Plate 3, Figs. 26-29

Diagnosis: Dorsal cup subpentagonal in cross section; base of cup marked by broad, shallow basally excavated region; strongly convex radially ornamented RR.
Description: Dorsal cup subpentagonal in cross section; base of cup marked by broad, shallow basally excavated region; cup wider than high; 3 unequal BB; radial plates large, strongly convex, marked by radiating ornamentation. Primibrachs greatly compressed, over twice as wide as high; IBrl quadrangular with proximal margin commonly convex; IBr2 pentagonal, nearly triangular. Two fixed secundibrachs per half-ray; interrays with single elongate interbrach. Observed cup width: 5-15 mm. Column, arms, and tegmen unknown.
Derivation of name: Ornatus refers to radiating ornamentation.
Holotype: SUI 39890 (Loc. 18).
Material: Ten paratypes are numbered SUI 39840, 39841 (9).
Horizon and Locality: "*Cyrtia* beds;" Localities 15, 18, 34.

Family MARSUPIOCRINIDAE Bronn, 1855

Genus MARSUPIOCRINUS Morris, 1843

Type species: Marsupiocrinites coelatus Phillips, 1839; M

Subgenus MARSUPIOCRINUS (AMARSUPIOCRINUS)
Frest, 1975

Type species: Marsupiocrinus (Amarsupiocrinus) striatissimus Springer, 1926; OD
Discussion: North American species of *Marsupiocrinus* are distinguished largely on the basis of calyx shape, tegminal curvature, size and shape of the basal pentagon, and plate ornamentation. The presence of a basil rim and two arms per ray distinguish *Marsupiocrinus (Amarsupiocrinus)* from *Marsupiocrinus* (*Marsupiocrinus*) with four arms

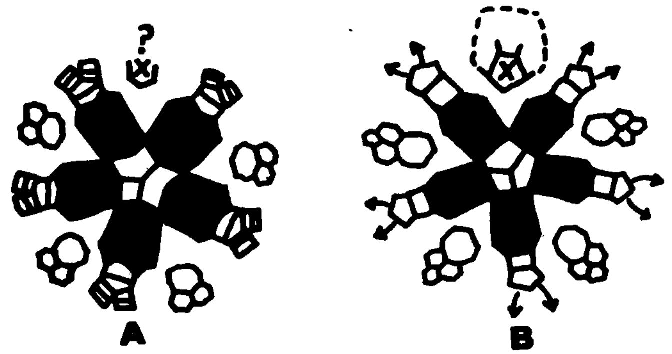


Fig. 14. *Plate diagrams of two new species of* Macrostylocrinus. *A)* M. compressus, *B)* M. vermiculatus *(distal portion of posterior interrays unclear). RR black; primanal with X.*

per ray. The subgenus *Amarsupiocrinus* is exclusively North American whereas all Silurian *Marsupiocrinus* (s.s.) are exclusively European (Frest, 1975, p. 568; Witzke *et al.*, 1979). Frest (1975, p. 567) believed the Patelliocrinidae, a family first noted in the Ordovician of North America and England, to be ancestral to the Marsupiocrinidae. If the Marsupiocrinidae evolved from the Patelliocrinidae, the discovery of well-developed *Marsupiocrinus* in mid-late Llandoverian rocks of Iowa would indicate that the families probably diverged in the early or middle Llandoverian. Internal molds of the genus from the Hopkinton Dolomite of Iowa reveal ray and ambulacral features indicative of *Amarsupiocrinus*. External molds of the Iowa specimens reveal a basal rim surrounding the column facet, another feature consistent with assignment to *Amarsupiocrinus*. Ubaghs' (1978) diagnosis of *Marsupiocrinus* should be modified to include forms such as *M. primaevus* with a laterally situated anus.

The Hopkinton specimens, all late Llandorverian in age, are the oldest known marsupiocrinids. Younger North American occurrences include Wenlockian specimens from the Laurel Ls. (Ind.), Racine Dolo. (Ill., Wisc.), and Cedarville Dolo. (Ohio), Ludlovian specimens from the Brownsport Fm. (Tenn.) and Henryhouse Fm. (Okla.), and Pridolian specimens from the Decatur Ls. (Tenn). The occurrence of *Marsupiocrinus (Marsupiocrinus) tentaculatus* in the Lower Devonian New Scotland Limestone of New York indicates that a migration from Europe of the endemic *Marsupiocrinus* stock with four arms per ray occurred towards the end of the Silurian or the beginning of the Devonian.

Marsupiocrinus (Amarsupiocrinus) primaevus n. sp.
Plate 3, Figs. 30-37; Plate 4, Figs. 1-3; Text-fig. 15

Diagnosis: A species of *Amarsupiocrinus* with a plano-convex calyx; gently convex to gently concave basal pentagon about one-half the width of the dorsal cup; striato-corrugate plate ornamentation; anus laterally located; linear series of iambb flanked by two large iambb.
Description: The calyx is plano-convex (i.e., tegmen flat or gently arched, dorsal cup angular and convex), although one specimen (SUI 39922) tentatively included in the species is biconvex (i.e., tegmen and dorsal cup of equal size and similar shape). The basal pentagon, always about one-half as wide as the dorsal cup, can be gently concave (most extreme in SUI 39919A), flat (e.g., the holotype), or gently convex (e.g., SUI 39911). A raised rim surrounds the column facet externally. The radials suture with the basals forming about a 140° angle. The radials of *M. primaevus* are among the least convex known for the genus and have a width/height ratio of 1.6 to 1.8. The tegmen, characteristically flat or gently convex, has prominent ambulacra bifurcating at about one-half their length. Ambulacra branch several times at lateral margin of tegmen, leading to two arm facets per ray. Numerous compressed interambulacrals (interbrachs) arranged in linear series, flanked by two large interambulacrals adjacent to ambulacra; iambb flat, delicately pustulose externally. Anus situated near lateral margin of tegmen (SUI 39923, 39920); posterior interambulacrals unknown. The lumen, if preserved, is pentalobate. The external plate ornamentation is to varying degrees striato-corrugate (see SUI 31723, 39923, 39924). The corrugated striations are aligned normal to the sutures they transect. Specimens vary in size; dorsal cups from the "*Cyclocrinites* beds" are between 7 and 31 mm wide, those from the "*Cyrtia* beds" are between 7 and 34 mm wide.
Discussion: Marsupiocrinus primaevus most closely resembles *M. striatus* and *M. verneuili* from much younger (Ludlovian) deposits in Tennessee but differs from both by its laterally-placed anus and the plating of the tegmen. The basal pentagon of *M. primaevus* is not broadly excavate nor is it bounded by a conspicuous triangular rim as in *M. verneuili* (Springer, 1926, p. 59). Less prominent ambulacral plates, less convex radials, and a basal pentagon that is commonly flat or convex contrasts *M. primaevus* wtih *M. striatus*.
Derivation of name: Primaevus, the most ancient representative of the Marsupiocrinidae.
Holotype: SUI 39923 (Loc. 15).
Material: Eleven specimens from the "*Cyclocrinites* beds" are numbered SUI 39906 (4), 39907, 39908, 39909, 39911 (2), 39912 (2); three specimens from beds adjacent to bioherms are numbered 39913, 39914 (2); 108 specimens from the "*Cyrtia* beds" include paratype SUI 39920 (5) and 39924 (4) and additional material SUI 31719, 31721, 31722 (2), 31723, 31724 (2), 31725, 31727 (3), 31728, 31729, 31730, 31732 (2), 31769, 39910, 39915 (2), 39916, 39917, 39918 (19), 39919 (40), 39921 (5), 39922 (2), 39925 (10).
Horizon and Locality: "*Cyclocrinites* beds" specimens from Localities 11, 16, 23, 24, 28, 33, 35, 36, 40 (sec. 33); "*Cyrtia* beds" and bioherm associated specimens from Localities 1, 2, 4 (SW sec. 9; sec. 10; c. sec. 25; SE sec. 35), 6, 15, 18, 22, 30, 34, 41 (sec. 19; SW sec. 36).

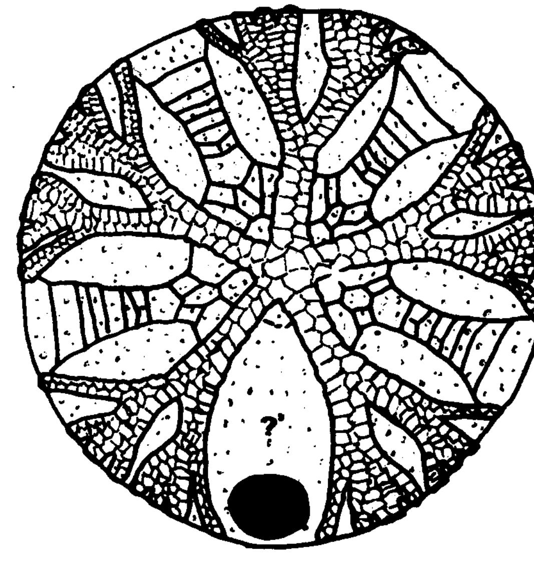


Fig. 15. *Tegmen plating arrangement of* Marsupiocrinus primaevus. *Laterally situated anus colored black. Plating unclear in posterior interambulacral area.*

Superfamily EUCALYPTOCRINITACEA Roemer, 1855

Family EUCALYPTOCRINITIDAE Roemer, 1855

Discussion: The diagnosis of the Eucalyptocrinitidae utilized in this study is from Ubaghs (1978) with some modification: fixed tertibrachs one or two in each quarter-ray, basal concavity may or may not be present. The dorsal cup is commonly wider than high in the superfamily (Ubaghs, 1978), although in *Archaeocalyptocrinus* and some *Eucalyptocrinites* (e.g., *E. proboscidialis)* the reverse is true. Moore and Laudon (1943, p. 99) believed that the Eucalyptocrinitidae was derived from the Clonocrinidae, although the first occurrences of *Archaeocalyptocrinus* and *Eucalyptocrinites* predate the earliest known occurrence of the Clonocrinidae. The presence of a single interbrach in the second range of *Clonocrinus*, the oldest known representative of the Clonocrinidae, contrasts markedly with the two second range interbrachs of the Eucalyptocrinidae and strongly precludes the origin of the Eucalyptocrinidae directly from a form like *Clonocrinus*. Also, the basal invagination of *Clonocrinus* is an advanced feature compared to the more primitive conical base of *Archaeocalyptocrinus*. Both the Clonocrinidae and the Eucalyptocrinitidae were probably derived independently from a similar patelliocrinid stock. *Laurelocrinus* is a good example of a patelliocrinid very close in form to the stock that gave rise to the Clonocrinidae and the Eucalyptocrinitidae; some *Laurelocrinus* even possess four BB (Springer, 1926, p. 186, fig. 13a).

Four genera are included in the Eucalyptocrinitidae: *Eucalyptocrinites, Calliocrinus, Archaeocalyptocrinus,* and *Chicagocrinus.* The first three of these genera are distinguished largely on the following features: size of iIIBr compared to iBr2, presence of a basal concavity, size of BB, extent of tegmen arm partitioning, development of the anal tube and its ornamentation, presence of spinose processes, and general calyx shape. *Chicagocrinus,* although regarded as a synonym of *Calliocrinus* by Ubaghs (1978), is considered herein as a distinctive member of the family typified by a greatly modified primibrach series (the complete loss of the quadrangular IBrl along with reduction of IBr2 to a small triangular plate). Specimens from the Hopkinton Dolomite extend the range of *Eucalyptocrinites* and *Calliocrinus* down into the latest Llandoverian, and the discovery of a new eucalyptocrinitid genus, *Archaeocalyptocrinus*, extends the range of the family down to at least mid Late Llandoverian. The Eucalyptocrinitidae probably diverged in North America from the Patelliocrinidae sometime during the Llandoverian. By the Wenlockain *Eucalyptocrinites* and *Calliocrinus* had become nearly cosmopolitan in their distribution. Text-figure 16 summarizes the interpreted evolutionary changes noted in the family.

Genus ARCHAEOCALYPTOCRINUS n. gen.

Type species: Archaeocalyptocrinus nodosus n. sp.
Included species: A. nodosus n. sp., *A. iowensis* n. sp., *A. obconicus* (Hall), *A. slocumi* (Foerste).
Diagnosis: A genus of the Eucalyptocrinitidae with dorsal cup higher than wide; basals extending up sides of cup, visible in lateral view; basal concavity absent or weakly developed; primaxil pentagonal; adjacent first secundibrachs share common suture; 1 or 2 fixed tertibrachs per quarter-ray; tegmen divided by 10 small vertical partitions; anus elevated into central vertical tube.
Discussion: Archaeocalyptocrinus differs from other members of the family in possessing primitive features such as an elongate calyx, large basals, and weakly developed tegmen partitions (at least in *A. nodosus). Archaeocalyptocrinus* differs from *Eucalyptocrinites* primarily in cup shape, in having the basals extending up the sides of the cup (instead of resting in an inverted basal funnel), and in having the first two secundibrachs in each ray sharing a common suture (i.e., primaxil pentagonal, does not contact intersecundibrach). Rarely, some species of *Eucalyptocrinites* (e.g., *E. crassus)* can have adjacent IIBrl in contact, although this condition is atypical; generally the primaxil contacts the intersecundibrach (Macurda, 1968, p. 102). The only species of *Eucalyptocrinites* that consistently has adjacent IIBrl in lateral contact is *E. proboscidialis* (Foerste, 1920, p. 72). *Calliocrinus* differs in having a broader basal concavity than *Eucalyptocrinites* with

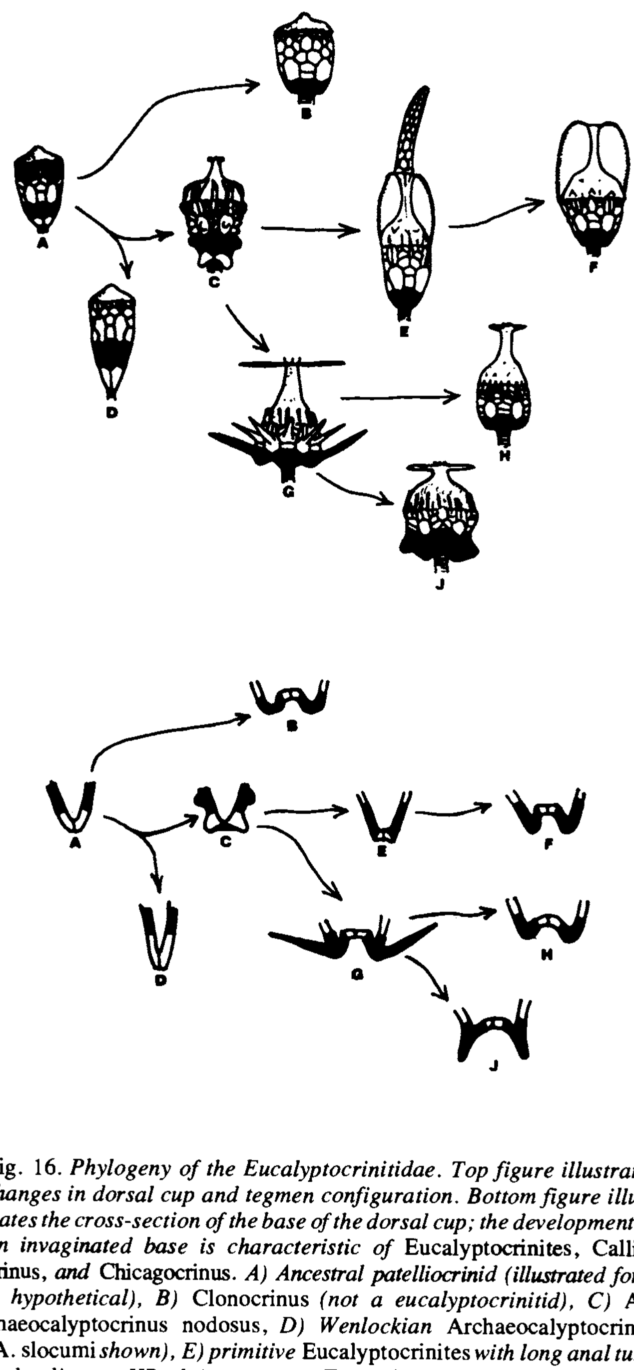


Fig. 16. *Phylogeny of the Eucalyptocrinitidae. Top figure illustrates changes in dorsal cup and tegmen configuration. Bottom figure illustrates the cross-section of the base of the dorsal cup; the development of an invaginated base is characteristic of* Eucalyptocrinites, Calliocrinus, *and* Chicagocrinus. *A) Ancestral patelliocrinid (illustrated form is hypothetical), B)* Clonocrinus *(not a eucalyptocrinitid), C)* Archaeocalyptocrinus nodosus, *D) Wenlockian* Archaeocalyptocrinus (A. slocumi *shown), E) primitive* Eucalyptocrinites *with long anal tube and adjacent IIBrrl in contact (*E. proboscidialis*), F) advanced* Eucalyptocrinites *with invaginated base and loss of anal tube above level of tegmen partitions (e.g.* E. milliganae*), G) spinose* Calliocrinus *(e.g.* C. longispinus, C. murchisonianus*), H) unspined* Calliocrinus *(e.g.* C. costatus*), J)* Chicagocrinus. *All RR are black.*

very small basals restricted to the area of the column facet; some species of *Calliocrinus* have the first secundibrachs in lateral contact. *Archaeocalyptocrinus*, the oldest known member of the Eucalyptocrinitidae, was apparently derived from a patelliocrinid stock with an elongate calyx and a rigid tegmen. Subsequent reduction in calyx height, further specialization of the tegmen partitions, and invagination of the BB in *Archaeocalyptocrinus* would produce forms like *Eucalyptocrinites* and *Calliocrinus*.

Two species, formerly included in *Eucalyptocrinites*, are here transferred to *Archaeocalyptocrinus*: *A. obconicus* (Hall) and *A. slocumi* (Foerste). *Archaeocalyptocrinus obconicus*, known only from internal molds recovered in the Racine Dolomite of Wisconsin and Illinois (probably Wenlockian), has a dorsal cup much higher than wide, basals extending up the sides of the cup in lateral view, pentagonal primaxils, adjacent first secundibrachs sharing a suture; it lacks a basal concavity (Weller, 1900, p. 109). These mentioned features are consistent with assignment to *Archaeocalyptocrinus*, and the species is transferred to the genus (*A. obconicus* n. comb.). Slocum (1907) assigned to "*Eucalyptocrinites*" *obconicus* a specimen from the Chicago Drainage Canal; this specimen served subsequently as the type for a new species, "*E.*" *slocumi* Foerste (1920, p. 72). *Archaeocalyptocrinus slocumi* (n. comb.) is the most steeply conical member of the genus, with extremely elongate basals extending up the sides of the cup to more than one-fifth the total cup height. The tegmen of *A. obconicus* and *A. slocumi* is unknown; the presence of small tegmen partitions given in the generic diagnosis is therefore tentative.

Archaeocalyptocrinus nodosus n. sp.
Plate 4, Figs. 4-7; Text-fig. 17

Diagnosis: Dorsal cup obconical, higher than wide; first interbrachs similar in size to radials; 2 fixed tertibrachs per quarter-ray; internal molds of cup strongly lobate; rigid tegmen elevated, divided by 10 small partitions; each cup plate with single large protruberant node.
Description: Dorsal cup obconical, higher than wide; basal concavity developed externally, not evident internally; four basals unequal. Radials hexagonal, approximately equidimensional, in contact all around. First primibrachs quadrangular, smaller than RR; primaxil pentagonal, similar in size to IBrl. Adjacent first secundibrachs in lateral contact; second secundibrach pentagonal. Two fixed tertibrachs present per quarter-ray (see SUI 39860, 39905). Single intersecundibrach per ray above level of IIBrl, smaller than iBr2. First interbrach decagonal, large, similar in size to RR, supporting two elongate interbrachs in second range. No differentiation of CD interray. Rigid tegmen elevated, externally bearing 10 small vertical partitions (SUI 39849); anal tube centrally located. Twenty arm facets project on lobes on internal molds. Externally, each plate of dorsal cup bears a single protruberant node (SUI 39850, 39860, 39905). Column and arms unknown. Size variation: calyx height (including tegmen), 6-15 mm (partial specimen to 19 mm); width, 4.5-18 mm.
Disucssion; Internal molds of *A. nodosus* bear a superficial resemblance to *Siphonocrinus;* 20 arm facets on lobes, elevated rigid tegmen, development of an anal tube. However, *Siphonocrinus* is a dicyclic many-plated form with pronounced asymmetry as opposed to *Archaeocalyptocrinus*, a monocyclic form exhibiting nearly perfect pentamerous symmetry. *A. nodosus* differs from *A. iowensis* primarily in calyx shape and external plate ornamentation.
Derivation of name: Nodosus, protruberant nodes on cup plates.
Holotype: SUI 39848 (Loc. 28).
Material: Four paratypes are designated SUI 39849 (internal, external), 39850 (internal, external), 39860 (internal, external), and 39905 (external). Nine additional specimens are numbered SUI 39851 (2), 39852 (2), 39847 (4), 39960.
Horizon and Locality: "*Cyclocrinites* beds;" Localities 11, 17, 21, 23, 28.

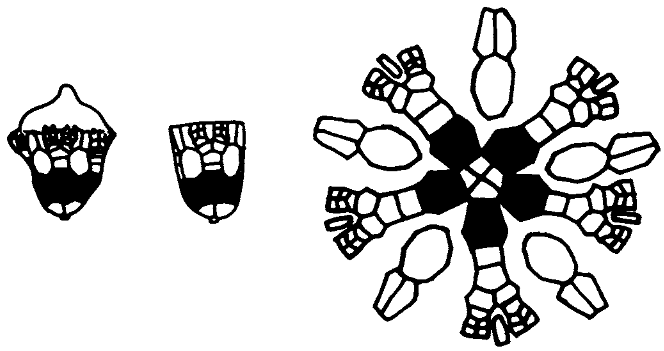


Fig. 17. *Plating arrangement of* Archaeocalyptocrinus, *Lower Silurian, Iowa. Left – cup profile and plates of* A. nodosus *internal mold. Center – cup profile and plates of* A. iowensis *internal mold. Right – Plate diagram (fold-out) of* Archaeocalyptocrinus. *All RR black.*

Archaeocalyptocrinus iowensis n. sp.
Plate 4, Figs. 8-11; Text-fig. 17

Diagnosis: Dorsal cup elongate, gently expanding upward, higher than wide; first interbrachs larger than radials; single (?) fixed tertibrach per quarter-ray; cup not strongly lobate; surface of plates probably smooth.
Description: Dorsal cup elongate, contracted at level of radials, gently expanding upward, higher than wide; external basal concavity unknown; on internal molds, base gently conical. Radials hexagonal, slightly wider than high, internal molds of radials concave. Rays as in *A. nodosus* except a single (?) fixed tertibrach per quarter-ray (see SUI 39862). First interbrach decagonal, larger than radials. Tegmen not preserved on any specimens. Arm facets approximately flush with cup on internal molds; cup is not strongly lobate. Exterior of plates apparently unornamented (lacking large nodes as in *A. nodosus*). Observed dorsal cup dimensions (height × width): 9 mm × 7 mm; 11.5 × 10 mm (holotype); 13 mm × 10.5 mm; 20 mm × 14 mm.
Derivation of name: Iowensis, all specimens are from Iowa.
Holotype: SUI 39864 (Loc. 35).
Material: Two paratypes are numbered SUI 39861, 39862; 4 additional specimens are numbered 39863 (2), 39869 (2).
Horizon and Locality: "*Cyclocrinites* beds;" Localities 11, 16, 23, 32, 35.

Genus EUCALYPTOCRINITES Goldfuss, 1831

Type species: Eucalyptocrinites rosaceus; M
Diagnosis: A genus of the Eucalyptocrinitidae with one or two primibrachs per ray; 4 small basals not visible in lateral view; base of dorsal cup generally invaginated (may have flat base); intersecundibrachs similar in size and shape to paired distal interbrachs; 10 riblike vertical partition plates on elevated tegmen forming alcoves for complete enclosure of the 20 arms (partition plates aligned with intersecundibrachs and paired distal interbrachs); central anal tube developed entire length of vertical tegmen partitions, in some species elongate plated anal tube developed well beyond distal margin of tegmen partitions.
Discussion: The great profusion of species included in *Eucalyptocrinites* (over 50 species described in the literature and 13 additional species in Rowser's unpublished 1932 dissertation) has not been adequately re-examined. Macurda (1968) and Kesling *et al.* (1973) measured plate proportions in collections of *Eucalyptocrinites crassus* from the Waldron Shale in order to define the observed ontogenetic changes. Macurda (1968) also included information on several other

species, particularly *E. tuberculatus*. A somewhat confusing array of variation was discovered; dorsal cup shape, individual plate shape, degree of basal invagination, and plate junctions all were found to be highly variable within collections of *E. crassus*, particularly those from Tennessee. Kesling *et al.* (1973, p. 46) noted a wide range of variation in dorsal cup shape in collections from Tennessee:

> Adults vary more in shape than young crinoids. All small cups are conical. Some large cups are also conical, only slightly modified from the small ones, but more are markedly flattened. And among the cups that are flattened, there is a variety of profiles.

Variation in individual plates is significant, not only in general proportions, but also in shape (e.g., most IBr2 hexagonal, some pentagonal). Some specimens are missing the quadrangular IBr1 in one or more rays. The degree of basal invagination varies (p. 49) and plate junctions are not consistent within collections of *E. crassus;* "some plates change their junctions during ontogeny" (p. 11).

These comparisons of Waldron Shale collections from Indiana and Tennessee reveals a broad range of variation in calyx shape, plate proportions, and basal invagination that includes forms previously described under five different specific names; *E. crassus* was demonstrated by Macurda (1968) to be the senior synonym of *E. constrictus, E. ellipticus, E. ovalis,* and *E. subglobosus*. *E. tuberculatus*, also from the Waldron Shale, based on similarities in plate ornamentation was believed to be the senior synonym of *E. elrodi* although no intermediate forms actually link the high-cupped *E. tuberculatus* forms with the broad-cupped *E. elrodi* forms. The high-cupped *E. tuberculatus* forms are closer to *E. crassus* in general calyx proportions than to *E. elrodi;* the synonomy of *E. tuberculatus* and *E. elrodi* is regarded herein as tentative.

Rowser (1932, pp. 102-134) recognized 19 species of *Eucalyptocrinites* from the Silurian rocks of Iowa, 11 of which are from the "*Cyrtia* beds," Hopkinton Dolomite. Over 500 specimens of *Eucalyptocrinites* from the "*Cyrtia* beds," including Rowser's original material, were examined in this study in order to define the range of variation exhibited within the sample. Based on criteria exclusive of ornamentation the "*Cyrtia* bed" sample was closely comparable to many specimens described from the Racine Dolomite (Wisconsin, Illinois). Thirteen species of *Eucalyptocrinites* from the Racine Dolomite were recognized (Hall, 1861; Weller, 1900) based largely on isolated specimens with little or no consideration given to the range of variation within the collections. However, transitional forms are noted that link together several of the Racine "species" into a continuous series. Weller (1900, p. 113) recognized a gradational series connecting *E. depressus, E. ornatus,* and *E. asper;* "the internal casts of all three of these species show considerable variation, and in a large collection of specimens almost a complete series, with all intermediate forms, may be selected." The separation of such a sample exhibiting a complete range of variation into several distinct "species" is an arbitrary procedure, and serious taxonomic problems can arise when dealing with the intermediate forms of the series. For the purposes of this report a sample that reveals a continuous range of variation for all features that vary within the sample will be regarded as a single species.

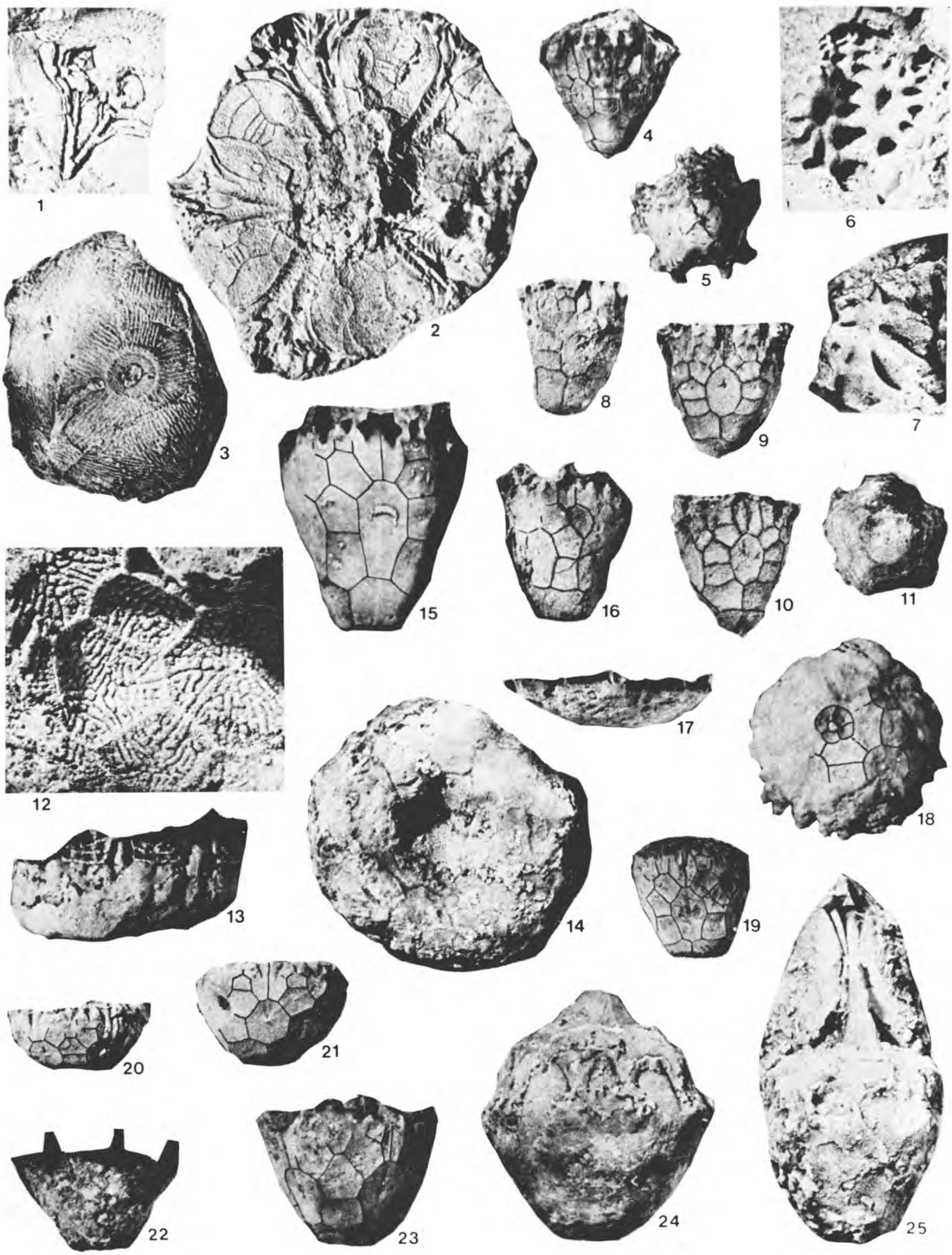
The preservation of the Hopkinton Dolomite material is generally poor, although variation in dorsal cup shape and the degree of basal invagination is observable on about half of the 500 specimens. Based on qualitative comparisons, a complete range of variation in the degree of basal invagination is noted for all specimens with the exception of 15 specimens with a broad base excavated to a depth equal to the entire height of the dorsal cup and with the RR completely invaginated; this group of specimens is referred to *E. depressus*. The gradation of *E. depressus* into *E. ornatus* noted in the Racine Dolomite by Weller (ibid.) is not observable in the Hopkinton Dolomite sample, and *E. depressus* is recognized as a distinct species in the Hopkinton until transitional forms are found from the same horizon.

The variation in cup shape is observable on 222 of the remaining specimens; the dorsal cup shape varies between conical, subglobose, subturbinate, turbinate, subhemispherical, and low saucer-shaped (see Text-fig. 18). A quantitative measure of the dorsal cup shape is approximated by measurements of the cup's height and width. A bivariate plot of these measurements is shown in Text-fig. 19; a wide range of variation is noted. The plots are clustered around two regression lines with significantly different slopes. A histogram plot of cup shape vs. frequency (cup shape is expressed as the ratio of height/width) reveals complete gradation of cup shape between 0.36 and 0.98 for the majortiy of the specimens. The lack of a natural break within this series and the bell-shaped frequency distribution is interpreted as representing the total range of dorsal cup variation exhibited within a single species; this abundant species is regarded as *E.* sp. (cf. *E. ornatus*). Rowser (1932) using size, dorsal cup shape, and degree of basal invagination erected seven new specieswithout considering the range of variation of the diagnostic features within his Iowa collections. These seven "species" all fall within the range of variation that we are considering to be a single species.

Eucalyptocrinites from the Racine Dolomite are closely comparable to the Hopkinton specimens in their range of variation; *E. egani, E. crassus (sensu* Weller, 1900), *E. turbinatus,* and *E. ornatus* all fall within the range of variation noted for the single Hopkinton species, *E.* sp., as indicated in Text-fig. 19. A number of low saucer-shaped dorsal cups of *Eucalyptocrinites* plot as a distinct group on both the bivariate plot and the histogram; these forms are recognized as a distinct species conspecific with the Racine Dolomite form, *E. inornatus*. Weller (1900, p. 116) believed *E. inornatus* to be readily separable from all other species in the Racine.

Collections of *Eucalyptocrinites* from the Racine Dolomite (Wisc.,

PLATE 4. *1-3.* Marsupiocrinus (Amarsupiocrinus) primaevus *n. sp.: 1. oblique summit view of external mold with ambulacra and two arm facets (SUI 39924B), 2. summit view, external mold (SUI 39924A), 3. dorsal cup, basal view of latex cast showing external ornamentation (SUI 39924C). 1,3. x1.5, 2. x2. 4-7.* Archaeocalyptocrinus nodosus *n. gen. et sp.: 4,5. dorsal cup, side and basal views (SUI 39850), 6. dorsal cup, external mold with nodose ornamentation (SUI 39905), 7. summit view, external mold with small tegmen partitions (SUI 39849). 4,5. x1.5, 6,7. x2. 8-11.* Archaeocalyptocrinus iowensis *n. sp.: 8. dorsal cup, side view (SUI 39864), 9,11. dorsal cup, side and basal views (SUI 39861), 10. dorsal cup, side view (SUI 39864). All x1.5. 12-14.* Eucalyptocrinites depressus *Miller: 12. external mold illustrating plate ornamentation (SUI 31670), 13. dorsal cup with arm bases, side view (SUI 39891), 14. dorsal cup, basal view (SUI 31668). 12. x2, 13,14. x1.5. 15,16.* Eucalyptocrinites proboscidialis *Miller: 15. dorsal cup, side view, Racine Dolomite, Wisc. (SUI 39903), 16. dorsal cup, side view (SUI 31655). x1.5. 17,18.* Eucalyptocrinites inornatus *Weller: 17. dorsal cup, side view (SUI 39898), 18. dorsal cup, basal view (SUI 39894). x1.5. 19-25.* Eucalyptocrinites *sp. cf.* E. ornatus *Hall: 19. dorsal cup, side view (SUI 31666A), 20. dorsal cup, side view (SUI 39882), 21. dorsal cup, side view illustrating two rays with single primibrachs (SUI 39878), 22. dorsal cup, side view (SUI 39877), 23. dorsal cup, side view (SUI 39874C), 24. dorsal cup, side view with tegmen exclusive of partitions (SUI 39874B), 25. calyx, side view, preserving anal tube and tegmen partitions (SUI 39874A). All x1.5.*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Ill.), the Brownsport Formation (Tenn.), and from Gotland (Sweden) have not been defined in terms of the total range of variation noted, and the validity of many of the defined species must remain in question until such comparisons are made. Known collections of *Eucalyptocrinites* (Hopkinton Dolomite, Waldron Shale) show features that vary within a continuous series. Variable features such as size, cup shape, degree of basal invagination, ornamentation, loss of one or more IBr, and IIBr1 in lateral contact should not be used to diagnose a species unless such features can be demonstrated to vary within a definable range of values distinct from that noted in other species of the genus.

Eucalyptocrinites first appears in four late Llandoverian formations in North America: the Jupiter Formation (Anticosti Island), the Brassfield Limestone (Ohio), the Joliet Dolomite (Illinois), and the Hopkinton Dolomite (Iowa)(Witzke *et al.*, 1979). *Eucalyptocrinites* probably arose directly from *Archaeocalyptocrinus* during the late Llandoverian. The development of an invaginated base accompanied by rapid expansion of the tegmen partitions and anal tube in *Archaeocalyptocrinus* would produce forms assignable to *Eucalyptocrinites.* The separation of adjacent IIBr1 and the development of an elongate anal tube above the platform of the tegmen were achieved early in the evolution of *Eucalyptocrinites*. The loss of one primibrach in one or more rays is a feature common in many species of *Eucalyptocrinites*, a characteristic already evident in some Hopkinton specimens but more common in Devonian collections (Ubaghs, 1978). Geologically younger *Eucalyptocrinites* generally exhibit a loss of the elongate anal tube above the tegmen platform and the development of more massive tegmen partitions (e.g., *E. milliganae, E. rosaceus*). *Eucalyptocrinites* is among the most widespread, long-ranging, and abundant of all Paleozoic crinoids. Its known geologic range is from Late Llandoverian (L. Silurian) to Eifelian (M. Devonian). The unique partitioning of the tegmen allowed for the complete retraction of the arms into alcoves, an adaptation that may have served to protect the delicate interior of the arms from predators and/or currents.

Eucalyptocrinites proboscidialis Miller, 1882
Plate 4, Figs. 15, 16

Diagnosis: Calyx obconical; dorsal cup slightly higher than wide; base small, flat, consists only of basals; adjacent first secundibrachs share common suture; elongate anal tube rising well above the distal margin of the tegmen partition plates.
Description: Two dorsal cups from Iowa exhibit features consistent with assignment to *E. proboscidialis:* dorsal cup higher than wide; small flattened base consists only of basals; first primibrachs taper gently toward distal margin; adjacent first secundibrachs hexagonal, share common suture; primaxil and intersecundibrach do not touch. The elevated partitioned tegmen and elongate anal tube characteristic of the species are not preserved on the Iowa specimens. Dorsal cup dimensions (height × width): 16.5 × 15.7 mm and 9.0 × 8.6 mm.
Discussion: The dorsal cup of *Eucalyptocrinites proboscidialis* exhibits primitive features aligning it with *Archaeocalyptocrinus*: height of dorsal cup greater than width, BB not invaginated, IIBr1 share common suture, iIIBr small. *E. proboscidialis* is the only species of the genus that consistently has the IIBr1 sharing a common suture and that lacks a basal invagination; it is not included in *Archaeocalyptocrinus* because the basals are not visible in lateral view (base is not conical) and because the tegmen is partitioned all the way to the top of the arms. The development of an elongate anal tube (*''Crinocystites''*) extending above the platform of the tegmen is seen in several species of *Eucalyptocrinites* including *E. proboscidialis* (Foerste, 1920, p. 69). *E. proboscidialis* is the most primitive species of the genus; it was probably derived from *Archaeocalyptocrinus* by reduction of the base, enlargement of tegmen partitions, and elongation of the anal tube. The other species of *Eucalyptocrinites* could have been derived from a form like *E. proboscidialis* by a broadening of the dorsal cup with subsequent separation of adjacent IIBr1 (primaxil comes in contact with iIIBr) and by invagination of the flat base. *E. proboscidialis* is noted herein for the first time from the Racine Dolomite of Racine, Wisconsin.
Material: The holotype is numbered 13867 (Ohio State Univ. Orton Museum). The Iowa specimens are numbered SUI 31655, 31656. Three Racine Dolomite specimens are numbered SUI 39903.
Horizon and Locality: The holotype is from the Cedarville Dolomite (probably Wenlockian) at Pontiac, Ohio. The Iowa specimens are from the ''*Cyrtia* beds'' at Loc. 10. The Wisconsin specimens are from Racine Dolomite (Wenlockian) at ''Racine.''

Eucalyptocrinites depressus S. A. Miller, 1880
Plate 4, Figs. 12-14

Diagnosis: Calyx subcylindrical; dorsal cup twice as wide as high; basal concavity deeply and broadly funnel-shaped; basals and radials completely invaginated at base, IBr1 and iBr1 may be slightly invaginated; plates convex, their surface ornamented with rugose markings.
Discussion: E. depressus represents the extreme in basal invagination noted for the genus. Weller (1900, p. 113) noted gradation between *E. depressus* and *E. ornatus* in the Racine Dolomite, although this gradation has not yet been observed in the Hopkinton collections. Three specimens (SUI 39892) are not as deeply excavated as the others; with further material the transition observed by Weller may also be observed in the Hopkinton Dolomite. Until the transition is demonstrated, *E. depressus* will be regarded as a distinct species in the Hopkinton. SUI 31670 clearly reveals that the plates of *E. depressus* are ornamented with coarse rugose markings, a feature that remained indeterminate in the Racine specimens (Weller, 1900, p. 114, ''surface apparently rugose'').
Material: Fifteen specimens are numbered SUI 31642, 31668, 31669 (5), 31670, 39891, 39892 (3), 39893, 39899 (2).
Horizon and Locality: ''*Cyrtia* beds;'' Localities 1, 2, 3, 7, 42 (SE sec. 35), 43.

Eucalyptocrinites inornatus Weller, 1900
Plate 4, Figs. 17, 18; Text-fig. 19

Diagnosis; Dorsal cup greatly depressed, low saucer-shaped, more than twice as wide as high; basal concavity small and shallow; plates flat, unornamented.
Discussion; Hopkinton *Eucalyptocrinites* with greatly depressed cups plot as a distinct group of specimens on the bivariate plot with no overlap for those specimens with a cup width greater than 17 mm. These specimens are assigned to *E. inornatus*. Smaller specimens on the bivariate plot (less than 17 mm width) are more tightly spaced, and separation into two distinct groupings (*E. inornatus, E.* sp.) is more difficult. The histogram shows three specimens that appear to grade dorsal cup shape between *E.* sp. and *E. inornatus*. Some specimens included in *E. inornatus* (SUI 39896, 39898) are reminiscent of low-cupped *E.* sp. (e.g., SUI 31625), and a transition may exist between the two forms. However, the rise in frequency on the histogram between 0.31 and 0.35 may suggest that there is a distinct but smaller population present. The smaller population clustered around 0.33 on the histogram is assigned to *E. inornatus*. Weller (1900, p. 116) regarded *E. inornatus* as a distinct group of low-cupped, smooth-plated *Eucalyptocrinites* in the Racine Dolomite, and he did not note any transition between this group and other forms of *Eucalyptocrinites*.
Material: Thirty-six specimens are numbered SUI 31626 (11), 31636 (2), 31637, 31639 (2), 31641 (2), 31673 (3), 31675, 39894, 39896 (4), 39898 (5), 39897 (2), 39904 (2).
Horizon and Locality: ''*Cyrtia* beds;'' Localities 1, 2, 7, 10, 15, 42 (sec. 11).

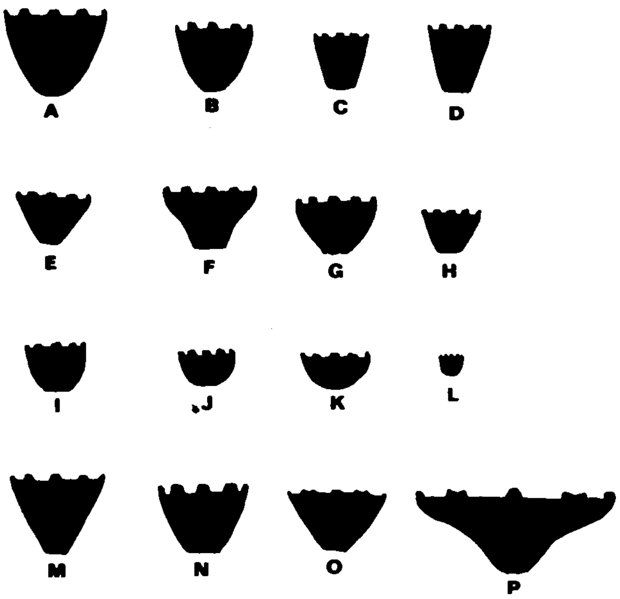


Fig. 18. *Silhouettes of* Eucalyptocrinites *dorsal cups. A-L are specimens of* E. *sp. from the Lower Silurian, Iowa. M-P are specimens chosen to illustrate some of the variation noted in populations of* E. crassus *from the Waldron Shale, Indiana and Tennessee (from Kesling et al., 1973); these are included for comparison. A) SUI 39874, B) SUI 39877, C) SUI 31666, D) SUI 39885, E) SUI 39884, F) SUI 39887, G) SUI 39878, H) SUI 39885, I) SUI 31645, J) SUI 39883, K) SUI 39882, L) SUI 31621. The classification of* Eucalyptocrinites *used in the Racine Dolomite sample by Weller (1900), if applied to the Iowa material, would probably assign A, B, and E to* E. crassus, *C and D to* E. egani, *F and G to* E. turbinatus, *and H-L to* E. ornatus. *In this study A-L are assigned to a single species. Approximately to scale.*

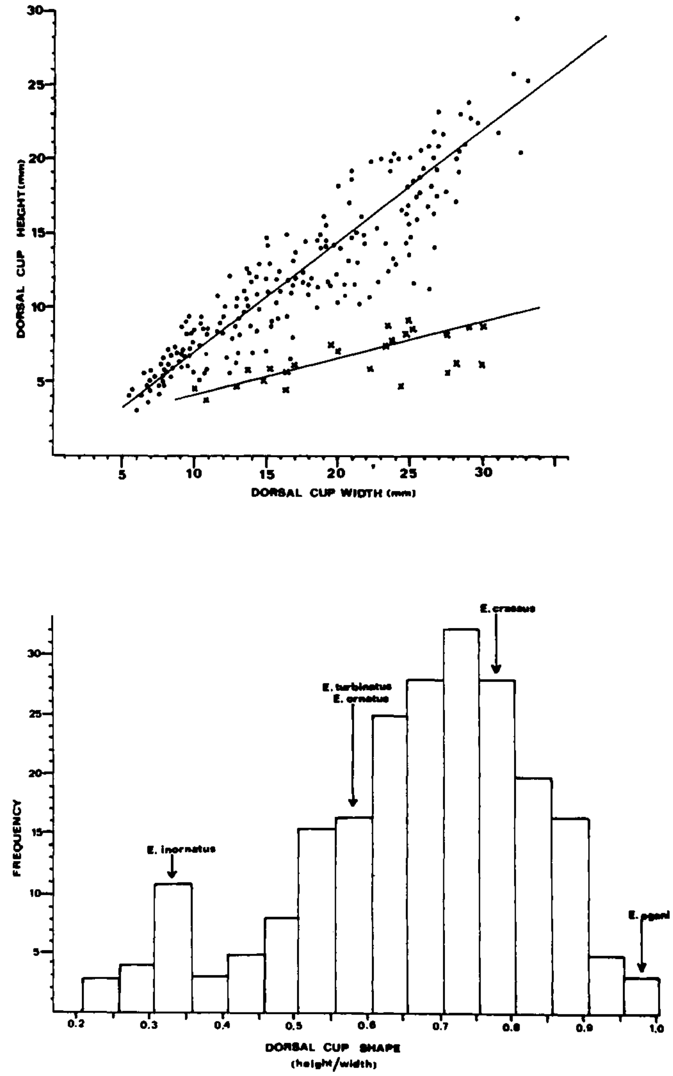


Fig. 19. *Bivariate plot of dorsal cup height vs. width (above) and a histogram of the frequency of occurrences of the dorsal cup shape (expressed as the ratio of height/width) in* Eucalyptocrinites. *The sample is from the Lower Silurian* "Cyrtia *beds" of Iowa. The two regression lines on the upper plot delineate the average slope for two different groupings of dorsal cups in the Iowa sample, each interpreted as a distinct species,* E. *sp. cf.* E. ornatus *(dots) and* E. inornatus *(x's). The approximate dorsal cup shapes of five species (sensu Weller, 1900) from the Racine Dolomite are shown on the histogram and are included for comparison.*

Eucalyptocrinites sp. (cf. *E. ornatus* Hall, 1861)
Plate 4, Figs. 19-25; Plate 5, Figs. 1-7; Text-Figs. 18, 19

Diagnosis: Dorsal cup varies in shape between conical, turbinate, and low saucer-shaped; dorsal cup height/width ratio varies 0.36 to 0.98; basal concavity shallow to deep; plate surfaces ornamented with delicate sculptured ridges.

Discussion: A continuous range of variation in dorsal cup shape and degree of basal invagination within the Hopkinton *Eucalyptocrinites* collection is used to define a single species, *E.* sp. The collection shows similarities to *E. ornatus, E. turbinatus, E. egani* and *E. crassus (sensu* Weller, 1900) from the Racine Dolomite, although none of the diagnostic features of these species define the full range of variation noted in the Hopkinton sample. The great majority of the specimens are similar in general form to *E. crassus;* however, the presence of a delicate sculptured ornamentation (SUI 39879) precludes the assignment of the Hopkinton specimens to *E. crassus* (type from Waldron Shale), a form with smooth plates. SUI 39879 and 31622 external molds reveal the aboral nerve tract system at the base of the cup, an unusual state of preservation. *E. sculptilis* (Springer, 1926) from the Decatur Limestone has delicately sculptured plates, but *E.* sp. from the Hopkinton has an even finer and more delicate ornamentation. The delicate ornamentation of *E.* sp. is preserved on only one specimen (SUI 39879), all other specimens have recrystallized external molds that do not preserve any delicate external markings. Such delicate markings would probably be obliterated in the extensively recrystallized Racine Dolomite sample, and it will remain uncertain if the Racine forms also possessed similar markings.

Until the Racine sample is re-investigated, the total range of variation in dorsal cup shape defined, and synonymies of the included species discussed, the Hopkinton sample will remain in open nomenclature (*E.* sp.). If the range of variation in the Racine sample is found to be similar to that noted in the Hopkinton, the Hopkinton collection (*E.* sp.) should probably be referred to *E. ornatus* (Hall, 1861), the oldest described species of the series. *Eucalyptocrinites*, as exemplified by *E.* sp., exhibits one of the highest levels of intraspecific variation noted in any Paleozoic crinoid group. The reasons for the wide range of variation are unclear, although external environmental controls acting on the population during ontogeny are invoked as a major controlling factor in determining the dorsal cup shape of the individual crinoids. Kesling *et al.* (1973, pp. 49-50) invoked transportation of young crinoids from one environment to another in an effort to explain the wide variation in cup shapes generated during the ontogeny of the individual crinoids. A few specimens of *E.* sp. are noted adjacent to bioherms in coarse crinoidal dolomites (SUI 39878), although the vast majority of the specimens are found in the typical "*Cyrtia* bed" level-bottom paleocommunities associated with fenestellids, stricklandids, and numerous other echinoderms and brachiopods. It seems doubtful if transportation from one environment to another can be invoked to explain the variation in dorsal cup shape noted in the Hopkinton sample.

Material: Four hundred eighty-six specimens are numbered 3482 (10), 31605, 31606 (22), 31608 (17), 31609 (2), 31610 (7), 31611 (2), 31616 (31), 31620, 31621 (90), 31622, 31623, 31625, 31630, 31640, 31645, 31646, 31647 (28), 31648, 31666 (16), 31667 (5), 31671 (10), 31672, 31674, 39873 (106), 39874 (8), 39876 (6), 39877 (25), 39878, 39879, 39880 (30), 39881 (4), 39882 (9), 39884 (7), 39885 (9), 39886, 39887 (6), 39888, 39889, 39895 (9), 39982.

Horizon and Locality: Adjacent to Bioherms at Locality 33. "*Cyrtia* beds" at Localities 1, 2, 4, 6, 7, 10, 15, 18, 30, 34, 42 (SW sec. 10; sec. 11; SW sec. 35).

Genus CALLIOCRINUS d'Orbigny, 1850

Type species: Eugeniacrinites ? costatus Hisinger, 1837; M

Diagnosis: A genus of the Eucalyptocrinitidae with two primibrachs per ray; BB and proximal portion of RR gently to deeply invaginated at base of dorsal cup; 20 vertical partition plates restricted to the lowermost circlet of plates on the tegmen which do not form alcoves for complete arm enclosure; four fourth level (uppermost) tegmen plates enclose a quadrangular anal opening, often extended horizontally into wing-like extensions forming a broad umbrella-like covering over the arms; calyx plates ornamented with spines, nodes, or ridges.

Discussion: The twenty small vertical tegmen partitions of *Calliocrinus* contrast markedly with the 10 large tegmen partitions of *Eucalyptocrinites*. With few exceptions (e.g., *E. depressus*), *Calliocrinus* has a more deply excavated basal concavity than *Eucalyptocrinites*; the plates of *Calliocrinus* are ornamented with prominent spines, nodes, or ridges whereas *Eucalyptocrinites* has smooth, gently sculptured, or gently nodose plates. *Eucalyptocrinites* may have one or two primibrachs per ray, all *Calliocrinus* have two primibrachs per ray, and *Chicagocrinus* has only one reduced primibrach per ray. The dorsal cup plate arrangement is remarkably similar in all members of the Eucalyptocrinitidae with the exception of the primibrach series in the North American *Calliocrinus-Chicagocrinus* lineage. Most *Calliocrinus* possess quadrangular IBr1 and pentagonal IBr2; a trend toward reduction and loss of one primibrach is first evident in *Calliocrinus primibrachialis* in which the first primibrach is reduced to a small ovoid rudimentary plate surrounded by the IBr2 and R (Busch, 1943). The continued reduction of IBr2 and the loss of IBr1 would lead toward the extreme condition noted in *Chicagocrinus* in which the remaining primibrach is reduced to a small triangular plate and the first secundibrachs share a suture with the radials (see Text-Figure 20).

Many species of *Calliocrinus* have adjacent IIBr1 in lateral contact, a condition alligning *Calliocrinus* more closely with *Archaeocalyptocrinus* than *Eucalyptocrinites*. *Calliocrinus* probably originated in North America from a form like *Archaeocalyptocrinus nodosus* during the late Llandoverian. The oldest *Calliocrinus* are noted from the Hopkinton Dolomite (late Llandoverian). By the Wenlockian *Calliocrinus* had spread to Europe. The last occurrence of *Calliocrinus* is noted from Emsian (L. Devonian) rocks in the Urals.

The development of umbrella-like winged terminal plates surrounding the anal vent in *Calliocrinus* is among the most curious of features developed in any crinoid group. The functional significance of this feature is unclear. In the closely related genus, *Eucalyptocrinites*, tegmen partitions allowed for enclosure of the arms which apparently functioned to protect the pinnulated arms during periods of quiescence. The winged terminal plates in *Calliocrinus* could also have served as a protective cover over the arms; small retractive slots at the base of the tegmen could help protect the arm bases. Additionally, the winged

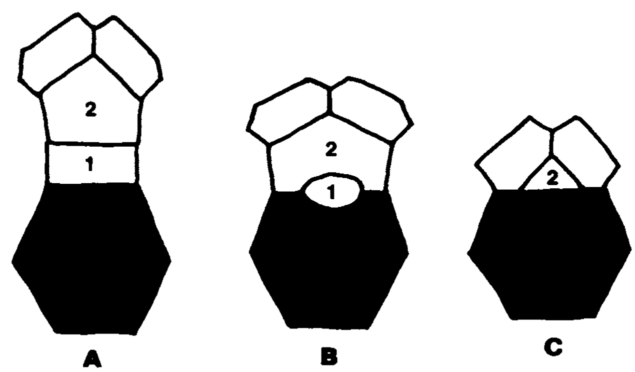
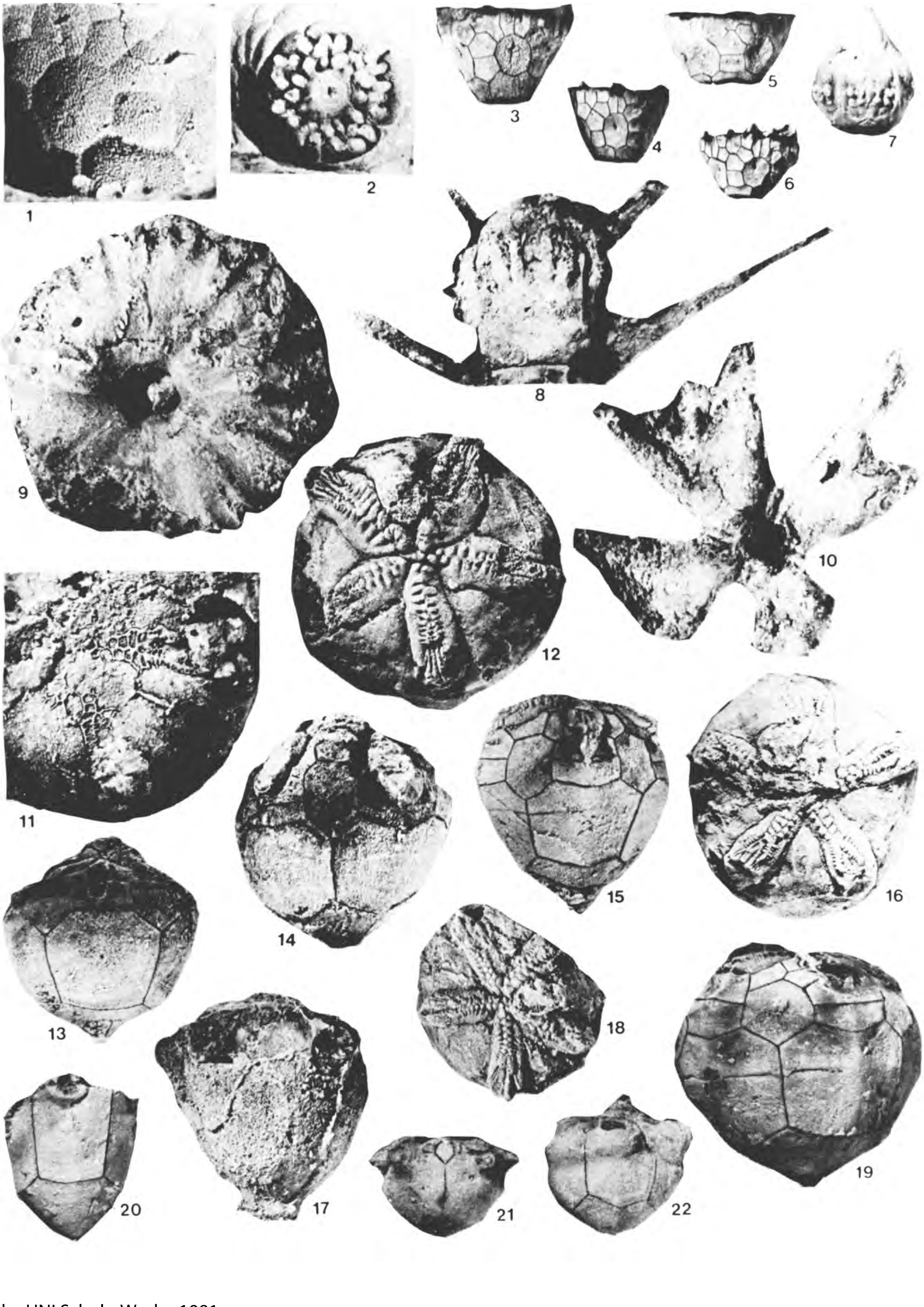


Fig. 20. *Evolutionary trend in the primibrach series of the North American* Calliocrinus-Chicagocrinus *lineage. Radials black; primibrachs numbered; first secundibrachs unnumbered. A)* "*Typical*" Calliocrinus *(e.g.* C. cornutus*), B)* Calliocrinus primibrachialis, *C)* Chicagocrinus inornatus.

PLATE 5. *1-7.* Eucalyptocrinites *sp. cf.* E. ornatus *Hall: 1,2. external mold with plate ornamentation and base of cup with aboral nerve tracts (SUI 39879), 3. dorsal cup, side view (SUI 39884), 4. dorsal cup, side view (SUI 31666B), 5. dorsal cup, side view (SUI 31646), 6. dorsal cup, side view (SUI 39885), 7. dorsal cup, side view with tegmen exclusive of partitions (SUI 39883). 1. x3, 2. x2, 3-7. x1.5. 8-10.* Calliocrinus longispinus *Weller: 8. calyx with spines, side view (SUI 39990), 9. terminal anal disc (SUI 31676), 10. terminal anal disc (SUI 31684). All x1.5. 11-19.* Theleproktocrinus davidsoni *n. gen. et sp.: 11. summit view, external mold with ambulacrals (SUI 39986), 12. calyx, summit view with ambulacra (SUI 39530), 13. calyx, side view (SUI 39532), 14. calyx, side view with posterior interray (SUI 39986), 15. calyx, side view (SUI 39533), 16. calyx, summit view with ambulacra (SUI 42275), 17. calyx, latex cast of external mold, side view (SUI 39534), 18. calyx, summit view with ambulacra (SUI 39531), 19. calyx, side view (SUI 39998). All x1.5 except 11. x3. 20.* Hagnocrinus *sp.: dorsal cup, side view (SUI 39926). x1.5. 21,22.* Lyonicrinus *sp.: 21. dorsal cup, side view (SUI 39974A), 22. dorsal cup, side view (SUI 39974B). 21. x3, 22. x2.*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terminal plates could have created a current-baffling effect allowing for more efficient feeding. Welch (1978) described tegmen wing plates in the Carboniferous genus *Pterotocrinus* which he suggested served a dual feeding and protective function, and the bizarre tegmen of *Calliocrinus* with winged terminal plates may have served a similar dual function. During feeding periods *Calliocrinus* must have held its arms out laterally; large spines, such as those noted in *C. murchisonianus* and *C. longispinus*, could serve to protect or support the laterally extended arms at that time. If *Eucalyptocrinites* and *Calliocrinus* developed these unique tegmen features for arm protection, it remains uncertain as to why other successful crinoid groups with exposed arms found it unnecessary to have analogous structures.

Isolated umbrella-like terminal plates were first noted by Hall (1867) from Wisconsin who named them *Cryptodiscus*. The affinities of the plates remained unclear until Weller (1897) found the terminal plate positioned on a *Calliocrinus*-like anal tube from Racine, Wisconsin. Weller (1900, p. 122) also suggested that some of the terminal anal discs may belong to *Chicagocrinus*. Weller (1897, 1900) assigned six new species from the Racine Dolomite to *Calliocrinus* based solely on isolated terminal anal discs. All six species are regarded herein as tentative since "two names may be given to two distinct portions of the same species, one to the dorsal cup and one to the terminal anal disk" (Weller, 1900, p. 122). The dual nomenclature that can result is highly undesirable, and an effort to correlate isolated anal discs with associated *Calliocrinus* dorsal cups should be made. In the Hopkinton Dolomite the terminal anal discs are found in strata in which *Calliocrinus longispinus* dorsal cups are also found; the discs are tentatively assigned to that species.

Calliocrinus longispinus Weller, 1900
Plate 5, Figs. 8-10

Diagnosis: Dorsal cup with deep basal excavation whose outer margin is roughly pentagonal; radials, first interbrachs, and lowermost circlet of plates on tegmen produced into long spines; interspinal nodes developed on cup; terminal anal disc probably present.
Discussion: The Hopkinton specimens appear to be conspecific with *C. longispinus*, a species originally described from the Racine Dolomite. However, the Hopkinton specimens preserve structures not noted on the Racine specimens; the lowermost circlet of tegmen plates bears spines (SUI 39900) and interspinal nodes are present on the cup (SUI 31680). *C. longispinus* closely resembles *C. murchisonianus* from Gotland but differs in possessing interspinal nodes and a more deeply excavated base. *C. cornutus*, also from the Racine Dolomite, is closely similar to *C. longispinus* but has shorter spines that are developed only on the radial plates (Weller, 1900, p. 119). Busch (1943, p. 109) proposed the synonymy of *C. costatus* (Gotland) with *C. cornutus* (Racine); this synonomy is regarded herein as unlikely since *C. costatus* is ornamented with low ridges whereas *C. cornutus* has spined and nodose plates.

Two types of terminal anal discs are found at the same horizon as *C. longispinus*, and these are tentatively included in the species. Using a dual nomenclature, the discs would be referrable to *C. hydei* and *C. corrugatus*. Weller (1900) described from the Racine Dolomite six species of *Calliocrinus* based on terminal anal discs and three species based on dorsal cups. It seems highly likely that one species of *Calliocrinus* could have more than one type of anal disc. The radial spines are directed upward forming a 25° angle with the base of the cup. SUI 39900 has a cup 27 mm wide with radial spines in excess of 30 mm long. Two other dorsal cups (SUI 31680, 31678) have a width of 25 and 20 mm respectively. Two terminal anal discs (SUI 31676, 31684) have a minimum width of 47 and 55 mm respectively.
Material: Dorsal cups and calyces are numbered SUI 31678, 31680, 31683, 39900, 39901, 39902, 39983 (14). Terminal anal plates are numbered 31676, 31679, 31684.
Horizon and Locality: "*Cyrtia* beds;" Localities 1, 2, 7, 10.

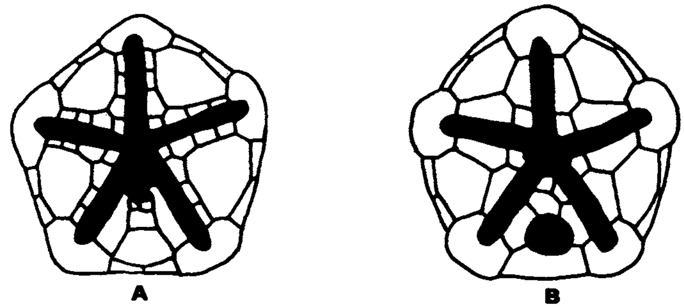

Fig. 21. *Oral views of A)* Lyonicrinus bacca, *Silurian, Tenn. and B)* "Cyttarocrinus" jewetti, *M. Devonian, N.Y. (from Goldring, 1954). Ambulacral grooves (colored black) probably covered by small ambulacral plates.*

Superfamily PLATYCRINITACEA Austin & Austin, 1842

Family HAPALOCRINIDAE Jaekel, 1895

Discussion: The platycrinitacean families (Hapalocrinidae, Hirneacrinidae, Prokopicrinidae, Platycrinitidae) are distinguished primarily on tegmen morphology. The hapalocrinids are characterized by a tegmen dominated by displaced interbrachs or enlarged orals; no axillary ambulacrals are present. Ubaghs (1978) indicated that "no interambulacrals" are present; however. *Theleproktocrinus, Cordylocrinus plumosus, "Cyttarocrinus" jewetti,* and *Lyonicrinus* all possess tegmen plates properly termed interambulacrals (apparently the interambulacrals are displaced interbrachs and may alternatively be termed as such). Ubaghs (1978) described "C" *jewetti* as having "2 interambulacrals in each interray." Tegminal plates in the hapalocrinids have been given a variety of names; Breimer (1962, p. 142) believed that the large plates interambulacral in position of "*C.*" *jewetti*, considered by Goldring (1954, p. 9) and Frest and Strimple (1977a) as interradials, could alternatively be considered as orals. The distinction between tegminal interbrachs and orals is of primary importance in tracing lineages. The large tegminal plates on "*C.*" *jewetti* are best interpreted as interbrachs (interradials); the orals are greatly reduced.

Theleproktocrinus, the oldest described hapalocrinid, was probably derived from a North American patelliocrinid (e.g., *Macrostylocrinus)* during the Llandoverian by the distal movement of the interbrachs onto the tegmen. Three general trends in mid Paleozoic platycrinitacean development can all be related back to an ancestral form like *Theleproktocrinus*. The first trend is characterized by general expulsion of the iBrr from the cup to form the largest tegminal plates; general reduction or displacement of the orals correspondingly takes place. Adambulacrals may be present, the posterior interambulacral area is differentiated by extra plates (anus protuberant), and ambulacral covering plates are present. This trend is evident in the *Lyonicrinus*-"*Cyttarocrinus*" *jewetti* (Sil.-Dev.) lineage (see Text-Figure 21). The second trend is characterized by the development of five large orals; the proximal portion of the iBrr is generally incorporated into the cup. This displacement of the iBrr from the tegmen by the orals is seen in several

Devonian genera (*Amblacrinus, Cantharocrinus,* and *Culicocrinus*). The third trend, also characterized by displacement of the iBrr from the tegmen by the orals, exhibits additional developments such as a more sharply differentiated and loosely-sutured tegmen and a single primibrach per ray (Frest & Strimple, 1977a). This third group, the hirneacrinids, includes the Silurian genera, *Hirneacrinus* and *Hagnocrinus*. Another group of small Silurian platycrinitaceans, probably derived from a hirneacrinid stock, was assigned to a distinct family, the Prokopicrinidae, by Frest and Strimple (1977b, 1980). The tegmen of the prokopicrinids is unknown, although, like the hirneacrinids, the distal margin of the RR extends onto the oral surface (ibid., p. 145).

Theleproktocrinus represents a highly successful patelliocrinid derivative that was probably directly ancestral to later hapalocrinids and hirneacrinids. The origin of the Platycrinitidae is presently not as clear; the presence of axillary ambulacrals on the Ludlovian *"Culicocrinus" spinosus* from Tennessee (Springer, 1926) seems to suggest that the platycrinitids diverged from a hapalocrinid stock sometime in the latter half of the Silurian.

Genus THELEPROKTOCRINUS n. gen.

Type species: Theleproktocrinus davidsoni n. sp.
Diagnosis: Small basal alligned with CD interray. Two primibrachs fused into cup above RR and between iBrr. Tegmen gently convex; distal half of iBrrl incorporated into tegmen, followed by 2 interambulacrals (displaced iBrr); single small oral in the 4 lateral interambulacral areas. Primanal distally incorporated into tegmen, followed by 3 interambulacrals (iBrr) in next range, with 3 plates in next range adjacent to anus. Anus protruberant. Ambulacra suprategminal, covered by alternating ambulacrals. 10 arms.
Discussion: Theleproktocrinus is most similar to *Lyonicrinus* (Brownsport Fm., Tennessee) from which it differs in having the proximal portions of the iBrr incorporated well into the cup, in adambulacrals, and in the arrangement of the plates in the posterior interambulacral area. Gerontic individuals of *Theleproktocrinus* are the largest known hapalocrinids.

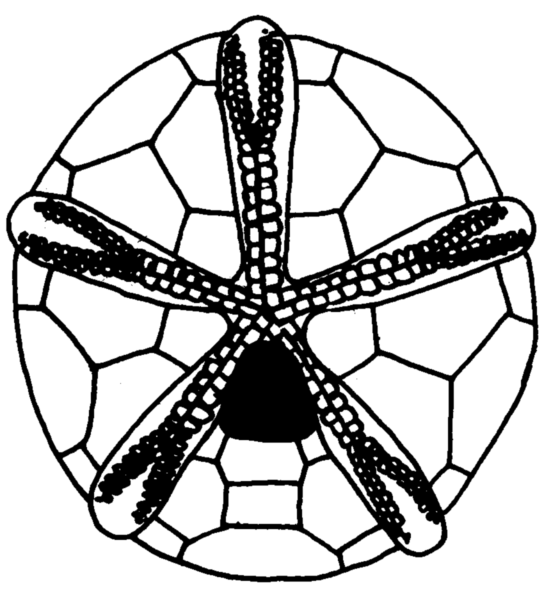

Fig. 22. *Oral view of* Theleproktocrinus davidsoni. *Anus shown in black.*

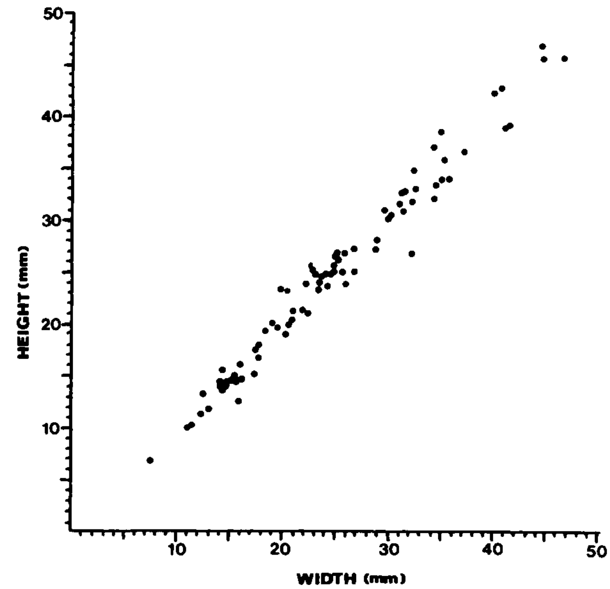

Fig. 23. *Scatter plot (height vs. width) of measurable dorsal cups of* Theleproktocrinus davidsoni.

Derivation of name: Thele (Greek), nipple-like protruberance; prokto (Greek), anus ("crinoid with protruberant anus").

Theleproktocrinus davidsoni n. sp.
Plate 5, Figs. 11-19; Text-figs. 22,23

Description: Calyx subglobose, height and width roughly equal, widest at distal level of RR. Three basals; two large pentagonal BB are second largest plates in calyx; one small quadrangular basal aligned with CD interray; basal pentagon occupies about two-thirds total cup width. Radials very large, roughly equidimensional, about one-half as high as calyx, in contact all around; RR hexagonal, distal margin concave. First primibrachs quadrangular, proximal margin in contact with RR convex; IBrl over twice as wide as high. Primaxil (IBr2) incorporated in cup, similar in size to IBrl, supporting two arm facets; no secundibrachs incorporated into cup. Proximal interbrachs visible in lateral and oral view, being eliminated from cup onto tegmen; iBrr hexagonal (or octagonal if lateral margins of IBrl and IBr2 are not aligned), higher than wide, next in size to BB. Tegmen gently convex; interambulacral areas composed of two pentagonal interambulacrals (displaced iBrr) following iBrl, each in contact with ambulacra, and one small quadrangular plate resting between adjacent ambulacra here termed the orals. All interambulacral areas of equal width; posterior interambulacral area differentiated; primanal heptagonal, occupying a position analogous to iBrr, bearing 3 interambulacral plates (displaced iBrr), two hexagonal plates adjacent to ambulacra, one rectangular plate in series above primanal. Three plates in next range adjacent to anus; 2 small quadrangular plates adjacent to ambulacra and a central hexagonal interambulacral in series with anus above rectangular plate. Anus large, subcentral, protruding on internal molds, in contact with adjacent ambulacra. Ambulacra prominent, suprategminal, protruding laterally on internal and external molds, bifurcating at about one-half their total length. Ambulacrals hexagonal, alternating in two rows before bifurcation; after bifurcation ambulacrals smaller, alternating. Surface of plates smooth. Ten arms of unknown structure. Lumen pentalobate.

Size variation noted (height exclusive of anal protruberance × maximum width): smallest specimen, 7 mm × 7.6 mm; largest specimen, 46 mm × 47 mm.
Discussion: Grontic *Theleproktocrinus davidsoni* reach exceptionally large sizes and, along with *Dimerocrinites (Eucrinus),* are the largest crinoids in the "*Cyclocrinites* beds." A scatter-plot of the measurable specimens (Text-figure 23) reveals a linear trend in the growth-series; *Theleproktocrinus* maintained the same general shape throughout the series, from the smallest specimens to the largest ones. The individual plates of *Theleproktocrinus* (simplified cup geometry with RR & BB predominating) maintained their same proportions during growth unlike the mode of growth noted, for example, in *Eucalyptocrinites* (Macurda, 1968; Kesling *et al,* 1973), *Eopatelliocrinus,* and *Macrostylocrinus* (Brower, 1973). Wachsmuth and Springer (1897, p. 735, pl. 75, fig. 14) illustrated a specimen of *T. davidsoni* from "Maquoketa, Iowa" and believed the specimen represented a *Culiococrinus* or *Marsupiocrinus.*
Derivation of name: Named in honor of the late D.B. Davidson (Davenport) whose collection has been an invaluable asset to this study.
Holotype: SUI 39986 (internal, external; Loc. 11)
Material: Six paratypes, SUI 39529, 39530, 39531, 39532, 39533, 39534 (int., ext.). One hundred eleven additional specimens: SUI 39987 (4), 39988 (8), 39989, 39990 (2), 39991, 39992, 39993 (3), 39994 (3), 39995, 39996 (2), 39997 (2), 39998, 39999 (4), 42265 (3), 42266 (2), 42267 (7), 42268 (15), 42269, 42270 (8), 42271 (2), 42272 (2), 42273 (5), 42274 (int., ext.), 42275 (31), 42276.
Horizon and Locality: "*Cyclocrinites* beds;" Localities 6, 9, 11, 14, 16, 19, 22, 23, 24, 26, 27, 28, 31, 32, 35.

Genus LYONICRINUS Springer, 1926

Type species: Coccocrinus bacca Roemer, 1860; OD
Discussion: The protruberant anus of *Lyonicrinus* is similar to that noted in *Theleproktocrinus.* The similarities between *Lyonicrinus* and "*Cyttarocrinus*" *jewetti* are striking; the latter species, a form significantly different from the type species of *Cyttarocrinus,* should probably be moved to another genus (Koenig, 1965, p. 412; Ubaghs, 1978, p. 514).

Lyonicrinus sp.
Plate 5, Figs. 21,22

Description: Three BB, 1 large, 2 small. Radials largest plates in cup. Primibrachs on lobes, not rigidly incorporated into the calyx. Interbrachs largely excluded from cup, although the proximal portion of the interbrachs can be seen on two of the three specimens in the notch between adjacent RR at the proximal margin of the cup. Tegmen unknown. Cup measurements (height × width): 8.5 mm × 11.8 mm, 7.5 mm × 8.2 mm, 5.7 mm × 7.8 mm.
Discussion: Until the tegmen of the Hopkinton specimens becomes known, the assignment of the species to *Lyonicrinus* is tentative. The dorsal cup of the Hopkinton species is most similar to *Lyonicrinus bacca,* Brownsport Fm. of Tennessee. The presence of *Lyonicrinus* in the "*Cyrtia* beds" of Iowa indicates that a considerable advancement in hapalocrinid evolution (exclusion of iBrr from cup) had occurred between the mid Late Llandoverian *(Theleproktocrinus)* and C_6 Late Llandoverian.
Material: Three specimens are numbered SUI 39974.
Horizon and Locality: "*Cyrtia* beds;" Locality 15.

Family HIRNEACRINIDAE Frest & Strimple, 1977

Genus HAGNOCRINUS Frest & Strimple, 1977
Type species: Hagnocrinus crenus; OD.

Hagnocrinus sp.
Plate 5, Fig. 20

Discussion: Frest and Strimple (1977a) briefly considered the placement of a small collection of platycrinacean crinoids from Locality 15;

> All are dolomite internal casts of a subconical crinoid with a simple plate configuration (three unequal basals and five radials); beyond that little can be established from the available material. The plates of the oral surface are unknown; the assignment to *Hagnocrinus* is based mostly on the resemblance of these casts to the internal cast of *Platycrinus augusta* (=*Hagnocrinus* ? *augusta* (Slocum) Frest and Strimple, n. comb).

Hagnocrinus "occupies a position among the Platycrinacea closely analogous to that of the Marsupiocrinidae in the Patelliocrinacea" (*ibid.*). The abundance at some localities (e.g., Loc. 15) of isolated conical basal circlets indicates that the basal plates were tightly fused together and did not disarticulate as quickly as the remainder of the calyx. Tightly fused basal circlets are also a characteristic feature of the Marsupiocrinidae.
Material: Primary reference specimens numbered SUI 39926 (5) and 39975 (int., ext.); additional specimens numbered SUI 31735, 39927 (30).
Horizon and Locality: "*Cyrtia* beds;" Localities 15 and 42 (sec. 10).

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APPENDIX: LOCALITY REGISTER

All locality numbers mentioned in the text are listed below according to county. The beds cropping out at each locality are recorded as follows: P (*Pentamerus* beds), Cc (*Cyclocrinites* beds), F (*Favosites* beds), B (bioherm and upper quarry beds), Cr (*Cyrtia* beds), Pd (*Pentameroides* beds).

Cedar County

1. NW¼ sec. 13, T82, R1W; cliffs and small abandoned quarry along Wapsipinicon River in county park; Cr.
2. NW¼ sec. 5, T82, R1W; the "Orelup locality," a small quarry; Rowser (1929, p. 29) recorded it in NW¼ sec. 6; Cr.
3. NW¼ & SW¼ sec. 10, T82, R1W; small quarry and roadcut; Cr.

Clinton County

4. SE¼ NW¼ sec. 8, T83, R2E; Elwood Quarry; B (bioherm), Cr.
6. NW¼ NE¼ sec. 17, T83, R2E; Wirth Quarry; Cc, F, B, Cr.
7. NW¼ SW¼ sec. 2, T81, R3E; Behr Quarry; B, Cr.
8. c. sec. 1, T80, R5E; unknown outcrop; Cr.
9. n. sec. 34, T83, R4E; abandoned quarry 1 mi. SW of Charlotte; Cc.
10. "Clinton;" unknown locality labels for specimens found in the vicinity of Clinton; Cc, Cr.

Delaware County

11. SE¼ SE¼ sec. 23, T89, R3W; Krapfl Quarry; Cc, F.
14. NE¼ SW¼ sec. 36, T90, R6W; Sedgwick Quarry; Cc, F.

Dubuque County

15. SE¼ SE¼ sec. 2, T87, R2W; Lux Quarry; F, B, Cr.
16. SE¼ NE¼ & NE¼ SE¼ sec. 16, T87, R2W; Clarence Martin Quarries; Cc, F, B.
17. SW¼ SW¼ sec. 36, T87, R2E; Zwingle roadcut on U.S. 61; P, Cc.
18. SE¼ SW¼ sec. 36, T88, R2W; John's Creek Quarry; Cc, F, B (bioherm), Cr.
19. SW¼ SW¼ sec. 31, T89, R2W; roadcut on U.S. 20 in Dyersville; Cc, F.
20. "roadcut on Hwy. 136 1.3 miles south of Dyersville;" a D. B. Davidson label; Cc.

Jackson County

21. c. sec. 24, T85, R2E; U.S. 61 roadcut in Fulton; P, Cc.
22. NE¼ sec. 3, T84, R1E; roadcut and river bluffs; Cc, F, Cr, Pd.
23. NW¼ SE¼ sec. 20, T84, R2E; Joiners Quarry; Cc.
24. SE¼ sec. 12, T84, R2E; Hurstville Quarry; P, Cc.
25. NE¼ SE¼ SE¼ sec. 26, T86, R3E; Rowhn Quarry; Cc, F.
26. "near Maquoketa;" old S. Calvin labels; Cc.
27. "Monmouth;" unknown locality label; Cr.

Jones County

28. NE¼ NE¼ sec. 14, T86, R3W; Farmer's Lime Quarry; P, Cc, F.
30. SE¼ sec. 7, T85, R2W; Willms Quarry; B, Cr.
31. SW¼ sec. 32, T86, R2W; river bluffs, Picture Rock Park; Cc, F, B, Cr.
32. SE¼ NE¼ sec. 22, T86, R3W; River quarry near Monticello; Cc, F.
33. NW¼ NW¼ sec. 24, T86, R4W; Monticello Quarry; B (bioherm), Cr.
34. "8 miles northwest of Monticello;" unknown locality; B and/or Cr.
35. sec. 23, T86, R3W; unknown outcrop; Cr.
36. NW¼ sec. 4, T85, R3W; Hwy. 151 roadcut; B (bioherm), Cr.
40. secs. 27 & 33, T86, R3W; unknown outcrops; Cc, B.
41. secs. 19 & 36, T86, R3W: unknown outcrops. Davidson collection; Cr.
42. secs. 9, 10, 11, 25, 26 & 35, T84, R1W; numerous natural outcrops and roadcuts; Cr.
43. NW¼ sec. 33, T84, R1W; Wyoming Quarry; bioherms.