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Cyathocrinites from the Silurian (Wenlock) Strata of Southeastern Indiana

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ABSTRACT

Three new species of *Cyathocrinites* are described from the Laurel Limestone-Waldron Shale succession in southeastern Indiana. The paleoecology of the species is discussed in detail. All Silurian members of *Cyathocrinites* are reviewed and assigned to three new subgenera (*Conicocyathocrinites, Rugosocyathocrinites,* and *Levicyathocrinites*). A phylogeny of the Silurian cyathocrinitids is suggested.

INTRODUCTION

The Silurian-Mississippian inadunate crinoid genus *Cyathocrinites* is extremely cosmopolitan; it has been reported from 12 nations on three continents. The majority of the 90 or so currently recognized species are Mississippian. About 13 heretofore described Silurian representatives are probably valid species and most of these are from rocks of Ludlow age. The three species described here considerably increase knowledge of the genus' early history. All sections of *Cyathocrinites* are in need of revision, but only the Silurian species are reviewed in this paper. The 16 accepted cyathocrinitid species are assigned to three new subgenera defined primarily on the basis of the characters of the dorsal cup. This approach is dictated mainly by the limitations of the available material (whole crowns or large series of specimens are exceptional) and thus ignores the features of the anal sac and tegmen which would unquestionably be of great taxonomic utility in subdividing the numerous Mississippian *Cyathocrinites.* A possible phylogeny of the Silurian species is presented which agrees well with the previously known facts concerning age and geographic distribution.

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Thanks are due to Drs. Eugene S. Richardson, Jr. and Matthew H. Nitecki, Field Museum of Natural History, for the loan of specimens of *Cyathocrinites striatissimus* (n. sp.) and for access to comparative material from the Museum's extensive Racine dolomite collections. All types are deposited in Field Museum; those with PE prefixes are in the Field Museum collections; those prefixed by the letters UC are Walker Museum (University of Chicago) specimens now permanently on loan to Field Museum. The photographs were taken by Kevin Frest. I would also like to thank N. Gary Lane for reviewing this paper, and Harrell L. Strimple for reading and helpful criticism of an earlier draft.

STRATIGRAPHY AND OCCURRENCES

The specimens described came from three early Late Silurian localities in rather close geographic proximity in southeastern Indiana (fig. 1). Collectively they span most of the Wenlock series of the British standard section. The exact age assignments of some of the formations involved has been a matter of debate. While echinoderms are encountered occasionally throughout the Indiana Silurian section, *Cyathocrinites* has been found only in very narrow stratigraphic intervals within a region of small areal extent, the western fringe of the "Ripley Island" positive area of Foerste (1904). The stratigraphy and age relationships of each occurrence are reviewed below.

St. Paul. In an attempt to locate the source of the large Laurel crinoid fauna monographed by Springer (1926) the accessible Laurel localities in the vicinity of St. Paul, Indiana were extensively investigated in 1973-1974. No additional specimens of *Cyathocrinites* were collected but the source of the preponderance of the Laurel echinoderms was most likely unit 3 (of Frest, 1975) of the Laurel Limestone at the disused Adams Quarry (SW¼ SW¼ SE¼ sec. 3 T11N, R8E, Adams quadrangle, Decatur Co., Indiana). The rationale for this conclusion and a section of the locality are given in the paper cited above and will not be repeated here. Other localities in the vicinity may also have produced echinoderms from time to time: most of these can be located but are presently practically barren.

There are two echinoderm faunas in the Laurel; they are readily distinguishable by the lithology of the surrounding sediments as well as by their paleoecology and generic composition. One, confined to unit 1 of the Adam's quarry section, is a sparse fauna char-

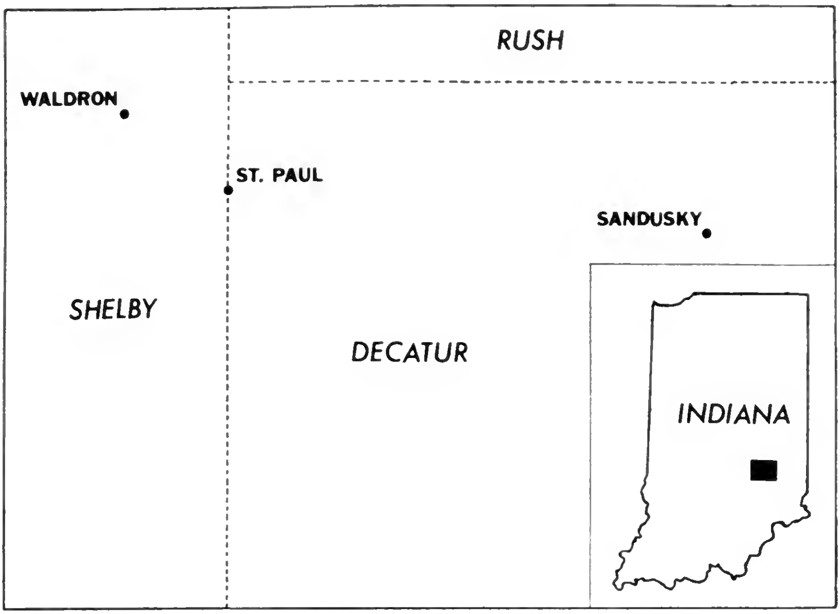

FIG. 1. Map of part of southeastern Indiana to show localities with *Cyathocrinites*.

acterized by crinoids with peculiar arm morphology (*Pisocrinus*, *Zophocrinus*, *Gissocrinus*, and *Petalocrinus*). The second, most typically developed in unit 3, contains the bulk of the Laurel crinoids. The provenance of the Laurel *Cyathocrinites* (*striatissimus* n. sp.), as indicated by matrix adhering to museum specimens, is unquestionably unit 3.

Sandusky. The bioclastic argillaceous limestones exposed near the top of the abandoned Vail Stone Co. quarry east of Sandusky (SE¼ NE¼ NW¼ sec. 12, T11N, R9E, Milroy quadrangle, Decatur Co., Ind.,) have been included in both the Laurel (Frest and Paul, 1971, p. 425) and in the Waldron (Berry and Boucot, 1970, p. 249): in this paper these beds are assigned to neither formation. Figure 3 is a composite section of the Silurian rocks exposed in the immediate vicinity of Sandusky. The boundaries between units are based primarily on the crinoid fauna; the contacts are believed to be conformable. The lower part of the section contains crinoids typical of unit 1 of the Laurel at the Adams quarry. The boundary marking the top of the Laurel is the bedding surface just above a zone of large crinoid stems (see fig. 2); the succeeding unit has common

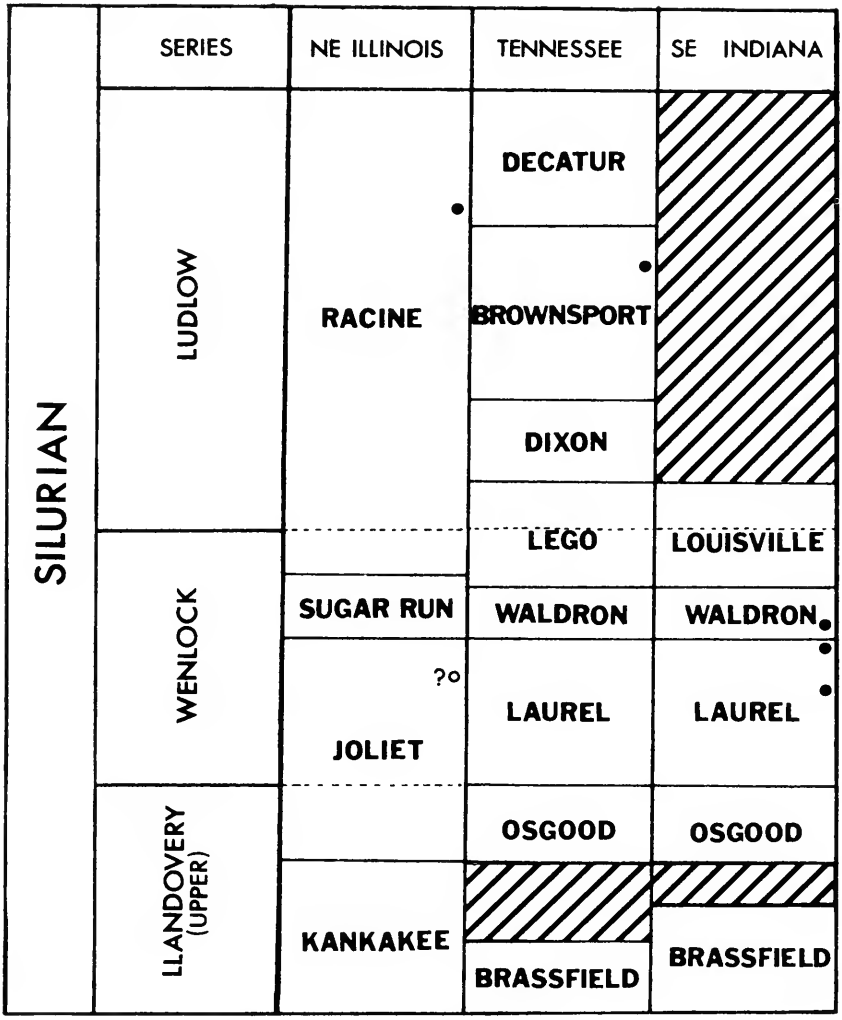

FIG. 2. Correlation diagram to show stratigraphic horizons in North America from which *Cyathocrinites* has been reported. Correlations based on Berry and Boucot (1970), Willman (1973), and author's fieldwork. Black dots indicate horizons with *Cyathocrinites*; open circle indicates doubtful record.

Eucalyptocrinites and *Dimerocrinites* at its base. The division between the transitional beds and the Waldron is somewhat arbitrary, as the shale content of this unit increases gradually from top to bottom. Strata succeeding the uppermost coherent limestone bed, 45 cm. (18 in.) thick, are assigned to the Waldron Shale. This 45 cm.

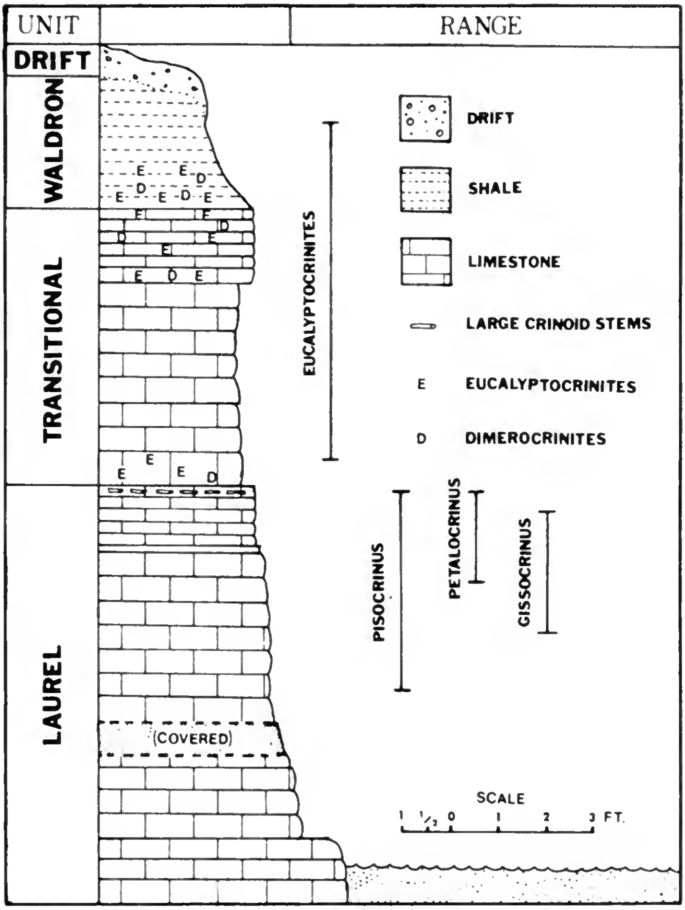

FIG. 3. Composite stratigraphic section of the Silurian strata exposed at the abandoned Vail quarry, Sandusky, Indiana, showing lithologies and ranges of selected echinoderms. Based on Frest and Paul (1971, fig. 1).

unit has an echinoderm fauna which incorporates some prominent elements of both the Laurel and Waldron faunas but also harbors some unique elements (*Callocystites brevis*, *Cyathocrinites sanduskyensis* n. sp., and an undescribed *Thalamocrinus*). These differences in faunal make-up are undoubtedly due at least in part to paleoecologic factors but the age of the Sandusky beds is believed to be intermediate between the fossiliferous Waldron and Laurel localities. Most earlier workers thought that the Laurel-Waldron contact was conformable, but Halleck (1973) presents convincing evidence refuting this contention. My own fieldwork supports Halleck's view in regard to most localities: Sandusky is exceptional. The Sandusky "transitional" beds may deserve formal ranking as either a member of the Waldron or Laurel or as a separate formation. No formal designation is proposed here, however, because Sandusky-type exposures are so limited in number and extent. A lengthier treatment of the paleoecology and relationships of the Silurian echinoderms of this region is in preparation.

Waldron. The type locality of *Cyathocrinites pauli* n. sp. is the Blue Ridge stone quarry, south of Waldron (center NE¼ sec. 6 T11N, R8E, Waldron quadrangle, Shelby County, Indiana). The Waldron Shale section is indicated diagrammatically in Figure 4. The stratum with *Cyathocrinites* is unit 5, a calcareous shale 30 cm. (1 ft.) thick whose base is about 63 cm. (2 ft.) above the Waldron-Laurel contact. The single known specimen was collected just above the contact with the underlying unit. The echinoderms at this level are substantially different from those in the hardground community described by Halleck (1973). The subcommunity containing *Cyathocrinites* consists of only a few genera of crinoids, mostly camerates (i. e., *Eucalyptocrinites* and *Lyriocrinus*), and other invertebrates which were able to maintain themselves on a very soft bottom. Less than a quarter of the full complement of Waldron crinoids persist to this level. The fauna of unit 5 corresponds roughly to Halleck's soft substrate community (Halleck, 1973, p. 250), although the actual community relationships in the Waldron are believed to be more complex than is implied by her model, which is essentially concerned with the lowermost Waldron.

The relations of the Waldron to the European standard are not yet settled; based on the presence of ostracods of the *Drepanellina clarki* zone the Waldron Shale is placed in the upper Wenlock (Berry and Boucot, 1970).

PALEOECOLOGY OF *CYATHOCRINITES*

Cyathocrinites is uncommon but persistent in the Silurian rocks of the North American Continental Interior. In contrast to the abundant and varied Gotland material (Bather, 1893) most American Silurian species are known from but a few or single specimens. However, the American cyathocrinitids exhibit much wider time and geographic distributions. More than half of the Silurian *Cyathocrinites* reported thus far are endemic to the Gotland (Wenlock-

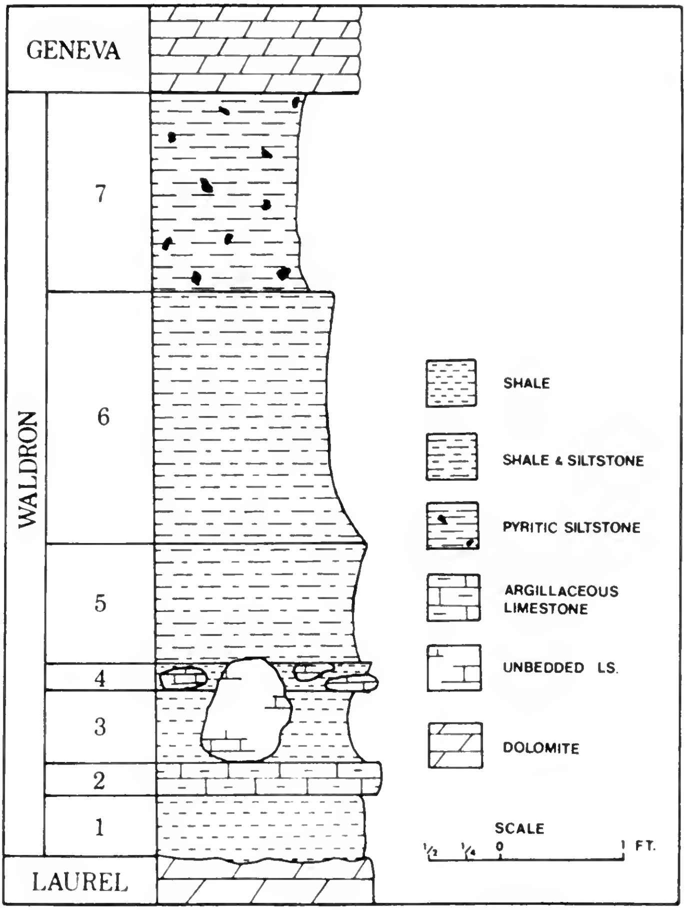

FIG. 4. Stratigraphic section of the Waldron Shale, Blue Ridge quarry, Waldron, Indiana, type locality of *Cyathocrinites* (*Rugosocyathocrinites*) *pauli*, n. sp. Units are distinguished on faunal and lithologic grounds.

Ludlow) reefs. Two Swedish species are found also in the English Wenlock (Bather, 1893 reviews the age and identities of English and Swedish species); *C. vallatus* (Bather) is known only from England (Bather, 1892, p. 221). In the United States species certainly ascribable to the genus have been mentioned in the literature as occurring in the Racine dolomite (Ludlow) of Illinois (Miller, 1881; Weller, 1900), the Laurel limestone (basal Wenlock) of Indiana, and the Brownsport formation (Ludlow) of Tennessee (Springer, 1926). Some fragmentary uncatalogued material labeled as having been collected from the Joliet dolomite at Romeoville, Illinois in Field Museum collections is probably *Cyathocrinites*. The specimens are too incomplete to be positively identified and attempts to secure better ones from the same area have been unsuccessful. Systematic collecting from the Silurian sequence in Indiana has turned up *Cyathocrinites* from three distinct stratigraphic levels, as detailed above. Supplementary material from St. Paul indicates that the Laurel crinoid placed by Springer (1926, p. 134) in the Gotland species *C. striolatus* (Angelin) is specifically distinct. New species were also recovered from the Waldron Shale near James Hall's classic locality and from beds intermediate in age and lithology between the typical Laurel and Waldron. Since beds of similar age and aspect in the adjoining states, as well as Iowa and Tennessee, also contain crinoids, the implication is that *Cyathocrinites* may have been more widespread than existing collections indicate. Figure 2 summarizes the known facts concerning the distribution of *Cyathocrinites* in North America. The correlations rely heavily on Berry and Boucot's work, with minimal modifications; for the northeastern Illinois sequence Willman's (1973) nomenclature and datings are preferred and the southeastern Indiana sequence is realigned slightly in accordance with the foregoing discussion. The Sandusky occurrence is arbitrarily included in the Laurel on the chart (uppermost plot in the Laurel).

I prefer to follow Berry and Boucot in retaining the Laurel Limestone as a separate formation, rather than as a member of the Salamonie Dolomite. The latter procedure is followed officially by the Indiana Geological Survey (Shaver et al., 1970; Shaver, 1974; Lane, pers. comm., 1975).

Invertebrate groups other than the Crinoidea will not be mentioned other than incidentally; fuller treatment of them will be found in the works cited above. The Gotland occurrences has been analyzed recently by Manten (1970, 1971). Generally the Swedish crinoids are closely associated with sizeable biohermal deposits that are true fossil reefs. Crinoids were found to be most abundant not on the upper surface of the reef itself but in flanking beds nearby or on the sides of the reef (Manten, 1971, p. 446). No specific data on *Cyathocrinites* itself is noted beyond the fact that it seems to be found in the crinoidal limestones surrounding the reef rather than in sediments formed near the core proper. The Gotland reefs are intermediate in size between that of the Racine Dolomite and those of the English Wenlock. The English reefs, according to Colter (1957,

p. 7), did not exceed 100 ft. (25 m.) in lateral extent; those studied by Penn (1971) in the Malvern Hills are typically much smaller. Neither of these authors note a very strong correlation between proximity to reefs and crinoid abundance. The association of crinoids with reefs, at least in the middle and later Paleozoic, has been generally accepted (Laudon, 1957, p. 961). The extension of the age of this association into the Silurian was suggested by Lowenstam (1957). Both Lowenstam and Lane (1971) see a tendency for selection in the vicinity of reefs to favor the proliferation of the camerates in, and the exclusion of the inadunates from, such environments. *Cyathocrinites,* at least, does not seem to have been so restricted. More detailed studies of reef genesis and faunal associates are needed to evaluate the consistency of the supposed camerate-reef association in the Silurian, since even individual genera or families within a subclass show some odd disparities in expected ecologic preference.

Cyathocrinites provides a good object lesson exemplifying the dangers of hasty generalization about adaptation to specialized habitats. It is extremely rare in the Racine which characteristically exhibits large scale reef development and is coextensive with some of the Gotland reef facies. The Brownsport species, also likely living contemporaneously with many of those in Gotland, probably derive from the limier portions of the Beech River facies (of Amsden, 1949) of the Brownsport formation, possibly from the so-called "*Coccocrinus*" (*Lyonicrinus*) zone of Pate and Bassler (1908; Springer, 1926, p. 6). They are not associated with reefs but the precise paleoecologic framework of the Beech River has not been well documented. Reefs are conspicuously absent from the southeastern Indiana Silurian but *Cyathocrinites* is found in a variety of non-reef habitats. This catholicity is typical of the genus as a whole but is especially striking in the Indiana cyathocrinitid species, three of which are closely related.

The two Laurel representatives (*wilsoni* (Springer) and *striatissimus* n. sp.) are both from unit 3 of the formation as seen at St. Paul, a limestone composed largely of comminuted echinoderm debris and chemically precipitated calcium carbonate. The unit is believed to have been deposited at some depth, the sedimentation rate was low and the currents low to moderate (supporting evidence is provided in Frest, 1975). The associated fauna is almost entirely echinoderms (crinoids, cystoids, blastoids, and cyclocystoids). *Cyathocrinites sanduskyensis* n. sp. occurs with a large and diverse invertebrate fauna (approximately 200 species). The same echinoderm classes are present as in the Laurel, but the genera are mostly dissimilar. The deposit (argillaceous limestone) was laid down in shallow, much-agitated water. The sedimentation rate varies locally but was usually high. *Cyathocrinites pauli* (n. sp.), the Waldron species, inhabited quiet shallow waters. The sea bottom was soft (it does not seem to have been a member of Halleck's hard substrate pioneer Waldron community) and the rate of deposition of the muddy sediment was high. Only a part of the prolific Waldron invertebrate fauna was present at this level and the reduced echinoderm fauna consists wholly of crinoids, mostly camerates.

The Indiana *Cyathocrinites* are the oldest yet discovered but display the ecologic versatility of the genus well. None are from reef habitats but this may well be an indication of the type of accessible and well-investigated deposits rather than genuine expression of any ecologic limitation of the genus at this early point in its history. Still it is not otherwise obvious why nearly all American species are from non-reef sediments whereas most European ones are found solely near reefs. This contrast is particularly striking when corresponding Ludlow faunas are compared. Despite an abundance of crinoid-bearing outcrops and continuing investigations by paleontologists since the 1860's *Cyathocrinites* is both extremely rare and extremely limited in diversity in the Racine fauna, at a time when the genus reached its (Silurian) zeinth in Gotland. Paleogeographic considerations alone do not provide a satisfying answer to the problem. The similarities in crinoid generic constitution between the Gotland and Racine reefs were noted long ago (Weller, 1898, 1900). Several highly specialized and short-ranging genera are found on both sides of the Atlantic (e. g., *Petalocrinus* and *Crotalocrinites*) and the general aspect of both faunas is quite similar.

As far as the fossil record is presently known, *Cyathocrinites* originated in North America near to the commencement of Wenlock sedimentation and had arrived in Europe (England and Sweden) by the middle Wenlock. There is evidence, though it is spotty, that the genus existed continually in both North America and Europe after the initial migration at least through the Ludlow. The peculiarities of its distribution were probably brought about by a combination of factors, of which phylogeny and paleogeography were most important. Each of the subgenera defined herein appears to exhibit habitat preferences of varying strength and it is suggested below that the phylogeny of this group of species (Silurian) is best explained as a reaction to two different environmental regimens; reef *versus* non-reef. Given the rarity of *Cyathocrinites* in most Silurian crinoid faunas the effects of even initially very slight tendencies toward ecologic specialization would have been substantial, especially since habitat diversification may have increased from the Ordovician through the Silurian (Lane, 1971, p. 1430), at least as far as reefs are concerned. The small size of individual *Cyathocrinites* populations (as inferred from the limited fossil record) would tend to enhance the development of new species whether or not ecologic incentives to adaptation were initially present. In this instance all the requisite factors were soon present and certainly reinforced one another.

SYSTEMATIC DESCRIPTIONS

List of Abbreviations

B (plural BB)	basal, basals
IB (plural IBB)	infrabasal, infrabasals
RA	radianal
R (plural RR)	radial, radials
X	anal X

Class Crinoidea Miller, 1821
Subclass Inadunata Wachsmuth and Springer, 1885
Order Cladida Moore and Laudon, 1943
Suborder Cyathocrinina Bather, 1899
Superfamily Cyathocrinitacea Bassler, 1938
Family Cyathocrinitidae Bassler, 1938

Diagnosis.—Dicyclic, dorsal cup low conical or bowl-shaped. IBB 5, one anal plate, X (no RA present), in line with RR. Tegmen strong, simple, anal sac stout, not prominent. Arms heavy, branching isotomously several times.

Genera.—*Anarchocrinus* Jackel, 1918; *Ceratocrinus* Wanner, 1937; *Cyathocrinites* Miller, 1821; *Gissocrinus* Angelin, 1878.

Range.—Ordovician; Silurian-Permian.

Genus **Cyathocrinites** Miller, 1821

Definition.—A genus of Cyathocrinidae with bowl-shaped cup, smooth thin plates, short anal sac with terminal opening, and a tegmen consisting largely of orals. Arms strong, non-pinnulate, nearly round in cross-section. Column round.

Genotype.—Cyathocrinites (Cyathocrinites) planus Miller, 1821.

Subgenus **Levicyathocrinites** (n. subgen.)

Definition.—A subgenus of *Cyathocrinites* with deeply bowl-shaped dorsal cup generally constructed somewhat below the RR, and thin usually unornamented non-plicate plates. Sides of cup convex, IBB and BB prominent, making up more than half the total height of the cup. Tegmen nearly flat, filling most of the oral surface. Anal sac small, barely protrusive, composed of numerous irregularly arranged plates. Arm facets on RR rounded, with separate opening for axial nerve canal, oriented vertically.

Type.—Cyathocrinites (Levicyathocrinites) acinotubus (Angelin), 1878.

Assigned species.—Cyathocrinites (Levicyathocrinites) acinotubus (Angelin); *C. (L.) brittsi* (Miller and Gurley); *C. (L.) dianae* (Bather); *C. (L.) distensus* (Angelin); *C. (L.) glaber* (Angelin); *C. (L.) monilifer* (Angelin); *C. (L.) muticus* (Angelin); *C. (L.) vallatus* (Bather).

Remarks.—Levicyathocrinites is predominately European in its distribution and confined to the upper Wenlock and Ludlow. Of the eight species definitely assigned to it, five are endemic to Gotland and one to the English Wenlock; the genotype is reported to occur in both English and Swedish rocks. Only one species, *C. (L.) brittsi,* is American (Brownsport of Tennessee), although the poorly known *C. vanhornei* (Miller) may also belong here (see section on unassigned species below).

The subgenus is believed to have evolved from European representatives of *Conicocyathocrinites* (n. subgen.) in the lower Wenlock. One evolutionary trend in *Levicyathocrinites* is a tendency toward flattening of the dorsal cup, achieved by greatly expanding the width of the RR and depressing the IBB, which in early representatives are nearly vertical, to an almost planar configuration. The area of the RR included in the arm facets also progressively increases, as does the width of the stem facet (in proportion to the greatest width of the cup).

Subgenus **Conicocyathocrinites** (n. subgen.)

Definition.—A subgenus of *Cyathocrinites* with elongate subconical dorsal cup with straight sides. Plates unornamented, without ridges, thin. RR arm facets elliptical, broad, oriented obliquely outward. Arm facets with separate opening for axial nerve canal. RR and BB about equal in height; IBB prominent.

Type.—*Cyathocrinites* (*Conicocyathocrinites*) *wilsoni* (Springer), 1926.

Assigned species.—*Cyathocrinites* (*Conicocyathocrinites*) *decatur* (Springer); *C.* (*Conicocyathocrinites*) *longimanus* (Angelin); *C.* (*Conicocyathocrinites*) *ramosus* (Angelin); *C.* (*Conicocyathocrinites*) *wilsoni* (Springer).

Remarks—The *Conicocyathocrinites* group of species spans the whole of the Wenlock and Ludlow series. The earliest and latest known species are American; the remaining two are found in the Gotland deposits, and one of these (*C.* (*C.*) *longimanus*) has also been reported from the Wenlock. In the course of evolution the dorsal cup tends to become more broadly conical and the width of the RR comes to exceed their height. A corresponding expansion of the width of the radial arm facets (which are broad for the genus) also takes place.

Subgenus **Rugosocyathocrinites** (n. subgen.)

Definition.—*Cyathocrinites* with broadly conical straight-sided dorsal cup. Plates thick, usually ornamented, sculptured with heavy ridges from centers of plates normal to plate sutures. Radial arm facets elliptical, about one half width of RR, sloping inward; no separate canal for axial nerve cord.

Type.—*Cyathocrinites* (*Rugosocyathocrinites*) *pauli* (n. sp.)

Assigned species.—*Cyathocrinites* (*Rugosocyathocrinites*) *pauli* (n. sp.); *C.* (*R.*) *sanduskyensis* (n. sp.); *C.* (*R.*) *striatissimus* (n. sp.); *C.* (*R.*) *striolatus* (Angelin).

Remarks.—Three of the four species ascribed to *Rugosocyathocrinites* are American; one is from Gotland. One other poorly known crinoid, *C. turbinatus* (Weller) from the Racine dolomite, may also belong here. Eliminating doubtful ascriptions the subgenus is confined to the Wenlock. These four species are obviously closely related and their phylogeny is likely best represented as a single line without branches once the initial separation from the subgenus' ancestors occurred.

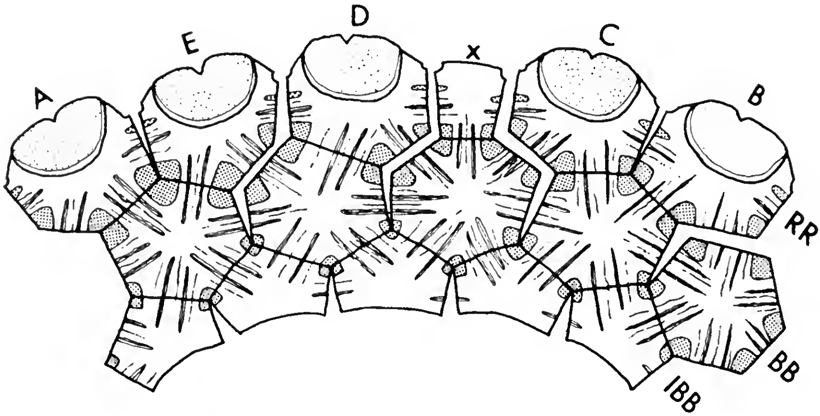

FIG. 5. Plate diagram of *Cyathocrinites (Rugosocyathocrinites) striatissimus* n. sp., based on holotype. Rays lettered A-E; IBB-infrabasals, BB-basals, RR-radials, x-anal X.

Cyathocrinites (Rugosocyathocrinites) striatissimus n. sp. Figures 5, 6b, 7.

Cyathocrinites striolatus (Angelin) Springer, 1926, Smithsonian Inst. Misc. Pub. 2871, p. 134, pl. 31, figs. 4-7.

Cyathocrinites striolatus (Angelin) (pars) Bassler and Moodey, 1943, Geol. Soc. Amer., Spec. Pap. 45, p. 396.

Diagnosis.—A species of *Rugosocyathocrinites* with strongly sculptured radial ridges and small deep corner areas on each plate, subequal IBB dimensions, and wide stem facet.

Type.—UC 33636a (holotype); UC 33636b (paratype), Walker Museum collection.

Material.—Eight dorsal cups. FMNH and National Museum of Natural History (Springer collection).

Horizon and locality.—Unit 3, Laurel limestone, Adams quarry, St. Paul, Ind.

Description.—Dorsal cup subconical. Greatest R width about equal to height. Plate configuration normal for genus (fig. 5). Stem facet width about one-half maximum diameter of cup. Sides of cup straight, making an angle of about 55° from the horizontal (fig. 6b). Plates slightly convex with deeply indented corners and prominent ridges directed to centers of adjacent plates, forming small triangles surrounding plate corners. Ornamentation on ridges deeply sculptured, consisting of incised ridges and pits oriented parallel to the main strike of the radial ridges, somewhat irregular. Plate corners depressed, unornamented.

IBB subequal, forming circlet, high for subgenus, about one third height of cup, rather variable in number, usually five. Each IB pentagonal with sides nearly equal in length. Two prominent ridges radiate from base of IB toward BB, with smaller ridges linking adjacent IBB.

BB forming uninterrupted circlet, unequal in size and shape, averaging two-fifths height of cup. BB of AB, BC, DE, and AE interrays subequal, hexagonal; CD interray B considerably taller, slightly wider than other BB, heptagonal with X situated centrally on top. All BB with strong radial ridges to adjacent plates.

RR large, approximately one-half height of cup, equal and pentagonal with arm facets extending above the general R level. R arm facets rounded, about one-half width of RR, inclined obliquely inward. All RR with heavy highly ornamented ridges to adjacent plates. Single anal (X) level with adjacent RR, wider than high, about one-half maximum width of RR, rectangular.

Arms, tegmen, and column unknown. Dimensions of holotype: height, 7.30 mm.; width, 6.94 mm.; width and height of IBB respectively 2.0 mm. and 1.69 mm.; of BB 2.92 mm. and 2.77 mm.; of RR 4.15 mm. and 3.38 mm. Width of R facet of 2.30 mm.; dimensions of

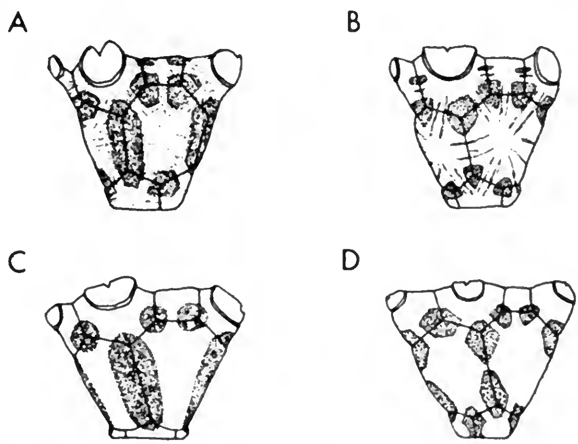

FIG. 6. Diagrammatic side view of the cups of four species of *Rugosocyathocrinites*. A, *C.* (*R.*) *striolatus* (Angelin); B, *C.* (*R.*) *striatissimus* n. sp.; C, *C.* (*R.*) *sanduskyensis* n. sp.: D, *C.* (*R.*) *pauli* n. sp. Not to scale.

anal X 2.00 mm. (width) by 1.54 mm. Dimensions of stem facet: width, 2.10 mm.; lumen, 1.54 mm.

Remarks.—This species was uncommon in the Laurel, judging from the number of specimens in museum collections. Springer (1926) referred his Laurel specimens to the Gotland species *C.* (*R.*) *striolatus* (Angelin), but there are a number of differences which justify separation. The plate ridges in *C.* (*R.*) *striolatus* have broad gentle slopes and the triangular depressions at the corners are shallow. Both the ridges and corner areas are ornamented with very fine striae, and the B-B ridges are absent or very faint (fig. 6a). Lastly the RR are considerably smaller and only one-third or less the height of the cup. Most Laurel specimens have eroded surfaces which tend to obscure plate ornamentation and even out the ridges and depressions (fig. 7-6). This probably accounts for Springer's misidentification.

Cyathocrinites (Rugosocyathocrinites) sanduskyensis n. sp. Figures 6c, 8, 9-1-9-7.

Diagnosis.—*Rugosocyathocrinites* with unornamented radial ridges but ornamented plate corners, wide elliptical R facets, and narrow short IBB.

Type.—FMNH Pe 28336 (holotype).

Material.—One nearly intact dorsal cup, the holotype, one incomplete dorsal cup, and numerous isolated plates.

Horizon and Locality.—Argillaceous limestones transitional between the Laurel and Waldron, Vail Stone Co. quarry, Sandusky, Ind.

Description.—Dorsal cup subconical, wider than high (holotype: width 5.70 mm., height 4.31 mm). Sides of cup straight, making an angle of 55° with the horizontal (fig. 6c). Stem facet width 2.45 mm.,

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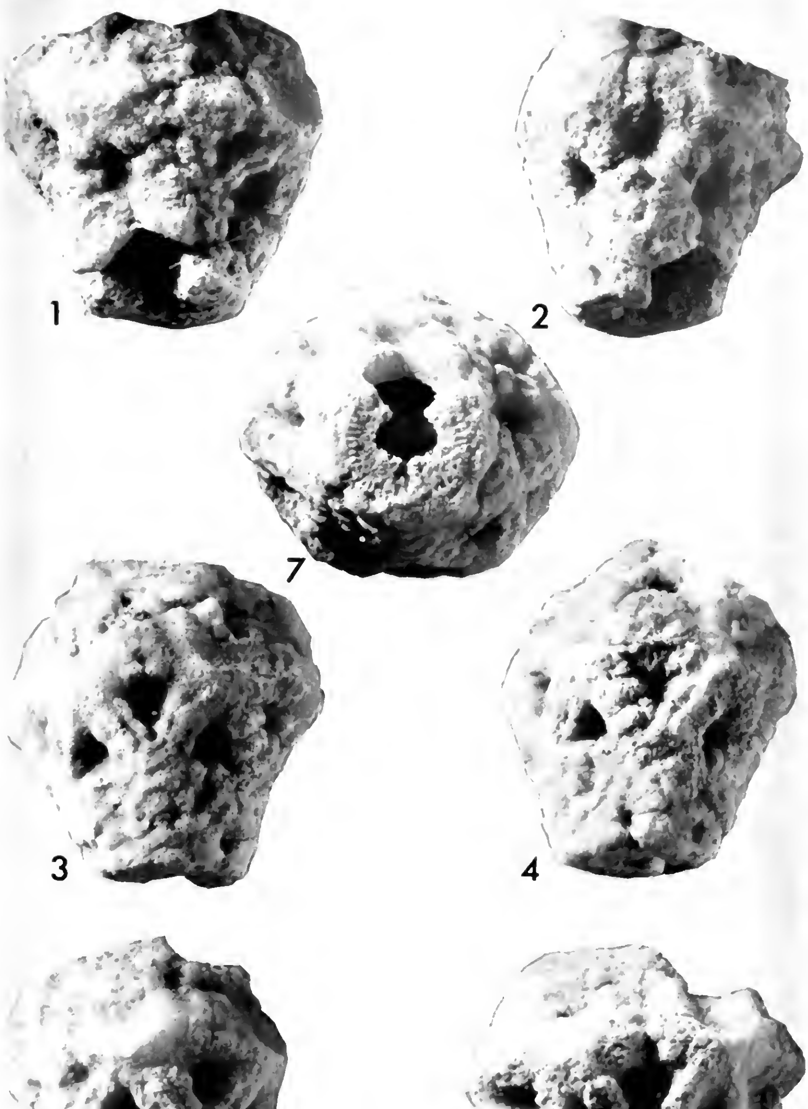
Opposite:

FIG. 7. *Cyathocrinites* (*Rugosocyathocrinites*) *striatissimus* n. sp. 1-5, 7, holotype UC 33636a. 6, paratype UC 33636b. 1-5, views centered on CD, DE, AE, AB, and BC interrays respectively, to show plate proportions and arm facets and ornament. 6, side view of paratype. 7, basal view to show stem facet. Note absence of ornament and enlarged interareas at plate corners due to erosion produced by weathering. All figures coated with ammonium chloride sublimate. All figures magnified 6.5 × approximately.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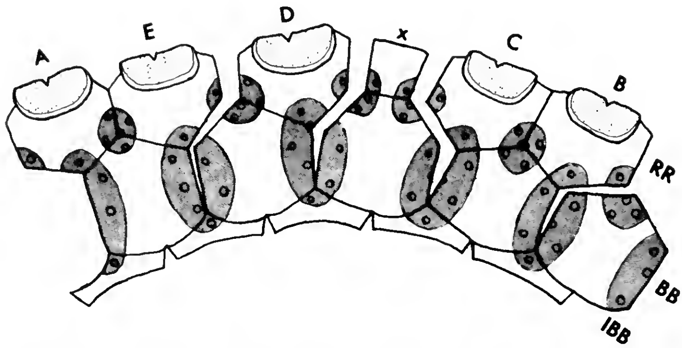


FIG. 8. Plate diagram of *Cyathocrinites* (*Rugosocyathocrinites*) *sanduskyensis* n. sp., based on holotype. See Figure 5 for key.

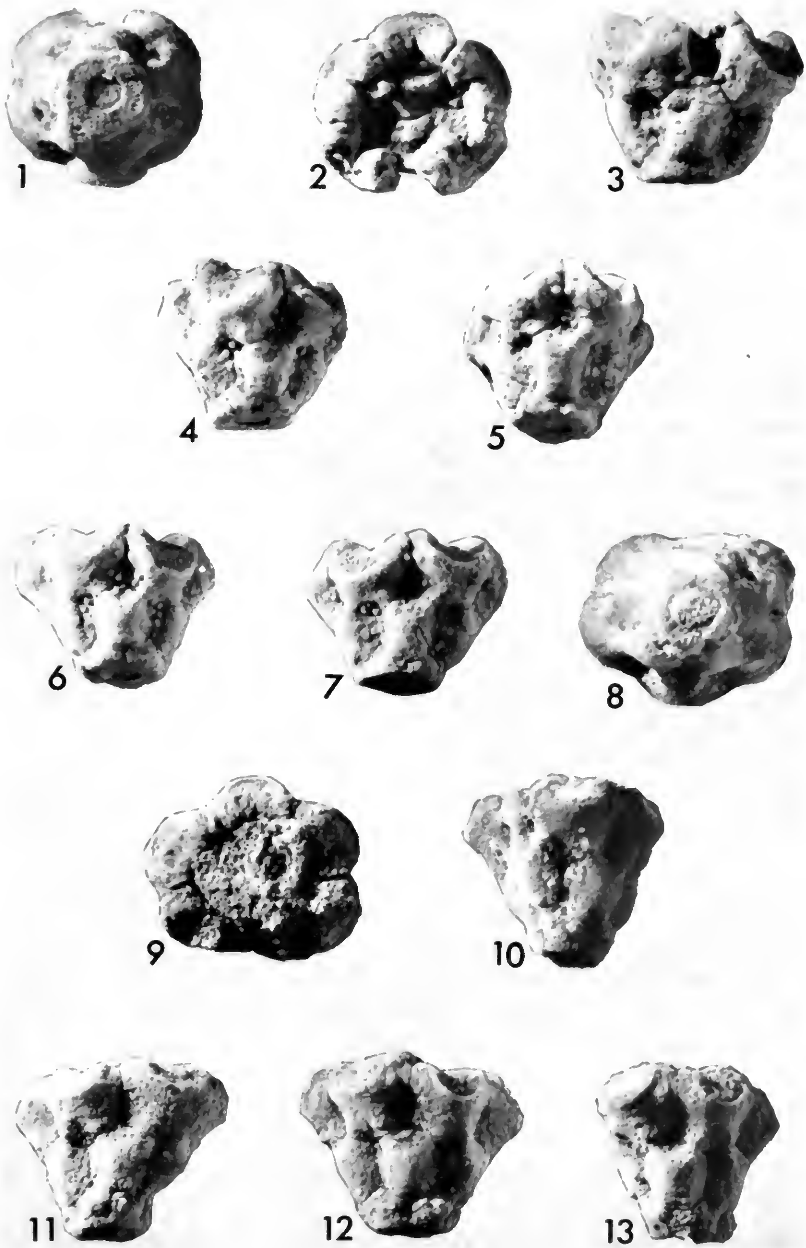
about one-half maximum width of cup. Plate configuration as usual for genus (fig. 8). Plates barely convex, plicate; ridges wide, coalescing toward center of plate, broadly rounded, smooth; ridges between IBB and BB very broad: IBB BB interareas very shallow or absent. Areas at plate corners and sides not involved in ridges ghallow, generally elliptical; ornamentation consists of a few wide tubercles.

IBB constitute closed circlet; all five identical in size and shape, much wider than high (dimensions: height, .69 mm.; width 1.31 mm.). Apex of each IB plate depressed: rest of IBB involved in ridges leading from BB and coalescing at base of IB. Height of IBB small for *Cyathocrinites,* only one-sixth cup height.

B circlet consisting of five plates approximately equal in size and shape, height (2.46 mm.) exceeding width (2.14 mm.) slightly. AB, BC, DE, and AE interray BB equal, hexagonal; B of CD interray heptagonal although height nearly identical to that of other BB. Each BB with broad radial ridges to RR and IBB; none, or very weak, indications of infra-B ridges. B-B contact sutures and plate

Opposite:

FIG. 9. 1-7, holotype of *C.* (*R.*) *sanduskyensis* n. sp. 1, top view to show arm facets; 2, basal view to show stem facet. 3-7, side views of cup centered on CD, DE, AE, AB, and BD interrays in succession to show plate configuration and ornamentation. 8-13, holotype of *C.* (*R.*) *pauli* n. sp.; 8, top view to show arm facets; 9, basal view to show stem facet. 10-13, side views of holotype of *C.* (*R.*) *pauli* n. sp., centered on CD, AE, AB, and BC interrays showing plate proportions and plate to plate ridges. Specimens photographed coated with ammonium chloride sublimate. Magnifications: all figures 6.5× approximately.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corners depressed to form rounded depressed areas with a few large tubercles.

RR with ridges and ornamentation like those of BB; R height (2.1 mm.) one-half that of cup; width about one-quarter greater than height (2.76 mm.). All RR equal, pentagonal. R arm facets elliptical, extending over three-quarters of the maximum width of the RR, width about 2.14 mm. Anal X (missing on holotype but inferred from adjacent plates) elongate trapezoidal with height exceeding greatest width (1.38 mm. and 1.23 mm., respectively).

Arms, tegmen, and column unknown.

Remarks.—Although only one complete cup of *C.* (*R.*) *sanduskyensis* has been recovered, the abundance of isolated plates (mostly RR) at the type locality indicates that the species was uncommon but not rare. It bears little resemblance to other Silurian *Cyathocrinites* aside from *C.* (*R.*) *pauli* (n. sp.), from which it may readily be distinguished by its wide IBB, elongate trapezoidal X, wider R arm facets and ornamented plate corners.

Cyathocrinites (Rugosocyathocrinites) pauli n. sp. Figures 6d, 9-8-9-13, 10.

Diagnosis.—A species of *Rugosocyathocrinites* with narrow R arm facets, unornamented plate corners, and small square anal X.

Type.—FMNH Pe 28337 (holotype).

Material.—A single dorsal cap.

Horizon and locality.—Unit 5 of the Waldron shale, Blue Ridge quarry, near Waldron, Ind.

Description.—Dorsal cup subconical, slightly crushed laterally, 4.90 mm. in height, width as preserved 6.16 mm.×4.90 mm.; inferred original width about 5.6 mm. Stem facet small, approximately three-eights of cup width (2.10 mm.). Sides of cup straight, angling about 60° from horizontal (fig. 6d). All plates with narrow radial ridges extending across sutures, coalescing in center, ridges between BB faint, absent between IBB. Plate corners and B-B sutures depressed to form low roughly polygonal interareas. Neither ridges nor depressions ornamented; number of plates in each circlet and their disposition as normal for genus (fig. 10).

IBB pentagonal, equal, in contact all around, height of IBB about equal in length. Each IB with elevated central area filling most of

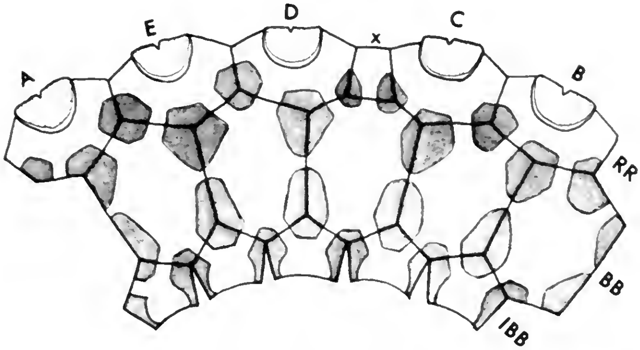

FIG. 10. Plate diagram of *Cyathocrinites* (*Rugosocyathocrinites*) *pauli* n. sp., holotype Pe 28337. See Figure 5 for key.

plate formed by merger of IB-B ridges; no ridges join adjacent IBB.

BB arranged in circlet, four (those of AB, BC, DE, and AE interrays) hexagonal, identical in size. The fifth B (CD interray) is heptagonal and its height exceeds that of adjacent BB. Width and height of BB nearly equal (dimensions: 1.82 mm. for former, 1.96 mm. for latter). All BB with narrow radial ridges to adjacent plates; those between BB not developed prominently.

RR dimensions: width 2.94 mm, height 2.10 mm, three-sevenths of cup height. R arm facets elliptical but only about one-half greatest radial width 1.68 mm), slanting inward toward the mouth. Ridges link adjoining plates and expand toward plate centers to form a large elevated node occupying most of plate aside from arm facets. Anal X level with flanking RR, small, rectangular, width greater than height (dimensions: 1.50 mm. and 1.26 mm., respectively).

Arms, tegmen, and column unknown.

Remarks.—*C.* (*R.*) *pauli* most closely resembles *C.* (*R.*) *sanduskyensis* n. sp.; the differences have been noted under the latter species. The species is named for C. R. C. Paul.

UNASSIGNED SPECIES

Under this heading are gathered several specific epithets applied to Silurian crinoids which for one reason or another are excluded from any of the subgenera erected above, "*Cyathocrinites*" *macrostylus* (Phillips) has not been illustrated and was founded on stems only; the state of the art is not advanced enough to allow determination of the generic affinities of isolated columnals or pluricolumnals except in rare cases. *Cyathocrinites* ? *nanus* (Grubbs) is almost certainly not *Cyathocrinites*; further analysis is hampered by the fact that the two known specimens are likely juveniles and are apparently missing from the Field Museum collections. Similarly sized crinoid cups collected at Sandusky proved to be juvenile *Lecanocrinus pusillus* (Hall); these specimens have an anal plate (X) projecting above the level of the RR identical in appearance to that shown by one of Grubb's (1939, pl. 61, fig. 61) specimens.

The two Racine "species" present more complicated problems. Most Racine crinoids are known solely from internal molds; only a few have plates adhering and most collectors did not bother to save external molds. *Cyathocrinites turbinatus* (Weller) is an undoubted *Cyathocrinites* but subgeneric ascription is not possible unless better material comes to light. The raised ridges on some steinkerns suggest *Rugosocyathocrinites* but there is a chance that they mark the positions of the branches of the aboral nerve system. *Cyathocrinites vanhornei* (Miller) may well be an American representative of *Levicyathocrinites*: Miller's type preserves some of the plates, which are smooth, and indicates a strong constriction of the cup beneath the radials. Weller (1900, p. 64) originally accepted it as *Cyathocrinites*; later he (1902, p. 533) states that the species "is probably another member of the genus Crotalocrinus." Bassler and Moodey (1943, p. 370) place *vanhornei* in *Crotalocrinites,* apparently following Weller though no reference is made to his 1902 paper. Weller does not state explicitly his reasons for the change; but in the earlier work he mentions that the radial arm facets seem far down on the plates (based on molds of the interior of the cup and the bases of the arms): this is a characteristic of *Crotalocrinites,* whose arms branch repeatedly near their base which is set into the R about one-third its total height. Weller illustrates a specimen, supposedly *vanhornei* (1900, pl. 14, fig. 5), which shows the filling of an arm extending most of the way down the R. Unfortunately, I have not been able to locate specimens which unequivocally show this structure and have plates preserved.

A small crinoid with basally constricted cup and *Crotalocrinites*-type arms (as illustrated by Weller) does undoubtedly occur in the Chicago area Racine; but it is not the same animal as the type of *C. vanhornei.* The holotype of this species (FMNH UC 7887) is not as well preserved as Miller's (1881, pl. 6, fig. 3) figure indicates, and there is a possibility that it is a *Botryocrinus,* such as *B. polyxo*

(Hall), which is known from both the Waldron Shale and Racine Dolomite (Weller, 1900, p. 66). Internal molds of a definite *Cyathocrinites* are preserved in Field Museum collections (uncatalogued) and these do show a constriction beneath the RR like that in *Levicyathocrinites,* but better material is needed to permit description.

PHYLOGENY OF SILURIAN *CYATHOCRINITES*

A possible phylogeny of the Silurian species of *Cyathocrinites* taking into account the evolutionary trends mentioned above is outlined in Figure 11. All of the species which could definitely be assigned to subgenera are included; all unassigned forms are excluded. Consequently, even though the occurrence of *Cyathocrinites* (s. l.) in the Racine is regarded as certain no Racine forms are incorporated into the dendrogram.

Taken as a whole the Silurian forms display some interesting trends. The earlier forms (*Conicocyathocrinites* and *Rugosocyathocrinites*) are environmental generalists seemingly well adapted to a variety of sediment types and depths but not particularly successful in reef habitats. By way of contrast *Levicyathocrinites* was spectacularly successful in the vicinity of large reefs while only occasionally showing up in non-reef sediments. Evolutionary trends in the morphology of the dorsal cup include the modification of the shape of the cup from conical and straight-sided to low bowl-shaped with convex sides. The surface area of the RR as compared to that of the BB and IBB increases and the average thickness of the plates decreases. The predominant orientation of the arm facets shifts from oblique sloping inward to vertical or even oblique directed outward. The axial nerve cord opening on the RR is separate in more advanced *Cyathocrinites* but combined with the ventral food grooves in *Rugosocyathocrinites.* This developmental trend is reflected in the ontogeny of the brachials of many cyathocrinitids (Brower, 1974, p. 26). The selective advantage of these characters is not clear. Other progressive tendencies within subgenera have been noted separately in the remarks on each subgenus.

The preponderance of species and individuals belong to *Levicyathocrinites* while representatives of the other two subgenera are almost invariably quite rare. As might be expected, the *Levicyathocrinites* section of the phylogeny has a number of "twigs" but the phylogenies of the remaining subgenera are straightfor-

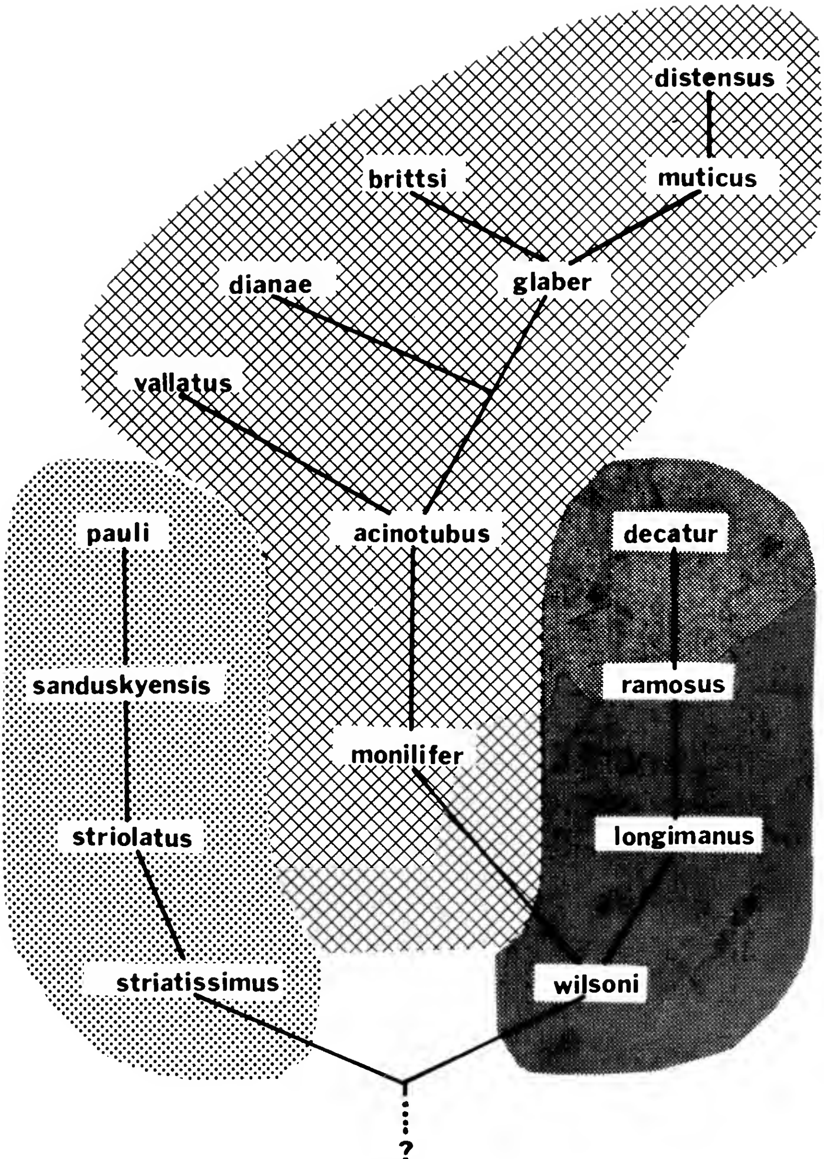

FIG. 11. Phylogeny of the Silurian species of *Cyathocrinites*. *Rugosocyathocrinites* branch indicated by dotted area: *Levicyathocrinites* by open crosshatching; and *Conicocyathocrinites* by close (dark) crosshatching.

ward. Likewise the distribution of the former subgenus is readily explicable: it probably originated in the middle Wenlock of Europe from *Conicocyathocrinites.* The actual direct antecedent of *C.* (*L.*) *monilifer* is uncertain but a generalized conicocyathocrinitid like *wilsoni* is favored over the more advanced and specialized *longimanus* and *ramosus*, even though these latter species are nearer to being contemporaneous both in age and locale with the earliest *Levicyathocrinites.* The subgenus flourished in the Ludlow rocks of Sweden and England and reached North America in the middle Ludlow, after which it continued to survive in both areas through the close of the Silurian. All three subgenera had Devonian representatives, but the majority of later species including the bulk of the Mississippian species are believed to have descended from *Levicyathocrinites.*

The earliest *Rugosocyathocrinites* and *Conicocyathocrinites* appear simultaneously in the Laurel. As the two are quite distinct, a long period of prior evolution is supposed. If *Anarchocrinus* Jackel is truly a cyathocrinitid the most likely evolution of the genus would be directly from it, with *Conicocyathocrinites* being the first subgenus to appear, probably in the uppermost Ordovician. *Rugosocyathocrinites* would then have derived from *Conicocyathicrinites* possibly in the lower Silurian. Alternatively, the development of both from an as yet unknown genus is also possible. This interpretation is preferred here since *Rugosocyathocrinites* and *Levicyathocrinites* have more characters in common than either one has with *Anarchocrinus.* As shown in Figure 11, the origin of both subgenera was in the North American Wenlock; shortly thereafter both migrated to Europe and the last known Silurian species of each is American (Ludlow). This rather patchy geographic distribution may be due to exigencies of preservation and collecting or to the seemingly small size of each species population. In the former case the phylogeny of the two subgenera as now depicted could be oversimplified: still, the consistent progression of some morphologic developments and the close resemblance to each other of the species within each grouping support the suggested phylogeny.

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