THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

November 30, 1967 Paper 24

REVISION OF SUBORDER CYATHOCRININA (CLASS CRINOIDEA)

N. GARY LANE

Department of Geology, University of California, Los Angeles

ABSTRACT

The suborder Cyathocrinina is divided into three superfamilies named Palaeocrinacea, Cyathocrinitacea and Codiacrinacea. Each of the first two includes families judged by MOORE & LAUDON (1943) to be closely related, one superfamily differing from the other in the presence or absence of an anal sac. The Codiacrinacea is a new superfamily containing crinoids which earlier were grouped in the family Codiacrinidae, but now are thought to represent three separate lineages that merit separation at the family level. The Codiacrinidae, as restricted, includes Codiacrinacea with five arm-bearing radials, and such crinoids range from the Devonian into the Permian. The new family Sycocrinitidae includes Lower Carboniferous to Permian genera that have only the *D* radial bearing an arm, the other radials being either present or absent. The new family Streblocrinidae consists of abrachiate (armless) crinoids in which the radials atrophied and disappeared during the Devonian, and pseudomonocyclic genera without radials which continue into the Permian.

INTRODUCTION

During preparation of materials on the suborder Cyathocrinina for Part T (Class Crinoidea) for the *Treatise on Invertebrate Paleontology*, it became evident that revision of the family Codiacrinidae BATHER, 1899, was called for before that group of crinoids would be in a taxonomic framework suitable for inclusion in the *Treatise*. The family included three phyletically distinct assemblages of crinoids that were thought to warrant separation at the family level, two of the three groups having separate evolutionary history from the Devonian through the Permian. Nevertheless, these three lineages are thought to have had a common, pre-Middle Devonian ancestry and to stand closer to each other than to other families of the Cyathocrinina. Consequently, the desirability of grouping these three families into a separate superfamily became evident.

For many years superfamilies were not used in the classification of fossil crinoids, which were ranked into subclasses and orders with their contained families. Relatively few suborders were recognized by BATHER (1899) and by MOORE & LAUDON (1943), but the classification was thoroughly revised in 1953 by UBAGHS who established several new suborders and superfamilies, especially among the camerate and inadunate crinoids. Consequently, ample precedent exists for division of the Cyathocrinina at the superfamily level.

MOORE & LAUDON (1943, p. 37) suggested that families which they classed in the Cyathocrinina fell into two relatively distinct groups, one consisting of earliest known cyathocrinoids as well as

specialized Silurian and Devonian families, all of which have a low tegmen and an anal opening directly through the tegmen or the side of the cup. These families are grouped here into the superfamily Palaeocrinacea. The remaining families in the suborder, exclusive of the codiacrinids, share several common features, the most important of which is that all have an elongate anal sac. These families are assembled as the superfamily Cyathocrinitacea (Fig. 1).

SUPERFAMILY CODIACRINACEA

The crinoids that have been grouped, until now, in the family Codiacrinidae are a diverse assemblage that includes 31 nominal genera. Paleontologists have disagreed concerning evolutionary trends within this group and their differing opinions about the phylogeny of its components never have been resolved satisfactorily, mainly because there has been no comprehensive review of all genera that attempts to fit them into a coherent evolutionary pattern. In recent years important new studies on oldest known codiacrinaceans from Devonian and Mississippian rocks have shed light on the evolutionary history of these crinoids. These factors need to be taken into account in a revision such as this, and necessitate discussion too lengthy for appropriate inclusion in the *Treatise*.

The superfamily Codiacrinacea is composed almost exclusively of small crinoids known from thecae with arms and columns rarely preserved. Some individuals are small, only 1 or 2 mm. in maximum dimension, and can be classed as microcrinoids, whereas others are several times larger, but rarely more than 1 cm. in height. The dorsal cup typically is higher than wide, with all plates visible in side view, and consists of either two or three circlets of plates. Infrabasals may number five, three, or be fused into a single plate; basals are the five largest plates in the cup, although exceptionally only three basals may be present. The radials are usually small, may or may not have arm-bearing articular facets developed on their distal edges, and may number five, three, or be absent. Those genera characterized by absence of radials have a two-circlet pseudomonocyclic cup, the remaining circlets being the infrabasals and basals, rather than the basals and radials, as in the true monocyclic condition. One important aspect of study of codiacrinaceans is the necessity for differentiating diminutive pseudomonocyclic members included in the superfamily from small, truly monocyclic crinoids of the disparid family Allagecrinidae.

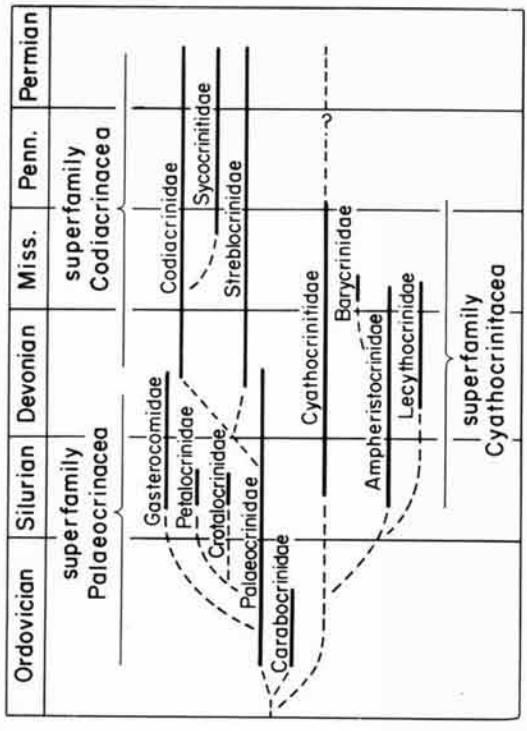

FIG. 1. Evolution of suborder Cyathocrinina.

CRITERIA FOR DISTINGUISHING DIMINUTIVE CODIACRINACEANS AND ALLAGECRINIDS

Small monocyclic allagecrinids, like *Kallimorphocrinus* and *Hybochilocrinus,* bear close resemblance to microscopic codiacrinaceans such as *Coenocystis* or *Hemistreptacron.* In these two unrelated groups the dorsal cup has only two circlets of plates, basals and radials in the allagecrinids and infrabasals and basals in the codiacrinaceans. In the latter assemblage the radials are postulated to have atrophied and disappeared, resulting in a pseudomonocyclic condition. The following morphologic criteria are available for distinguishing these two groups of microcrinoids.

1) Allagecrinids, even small specimens less than 1 mm. in maximum dimension, have arm-

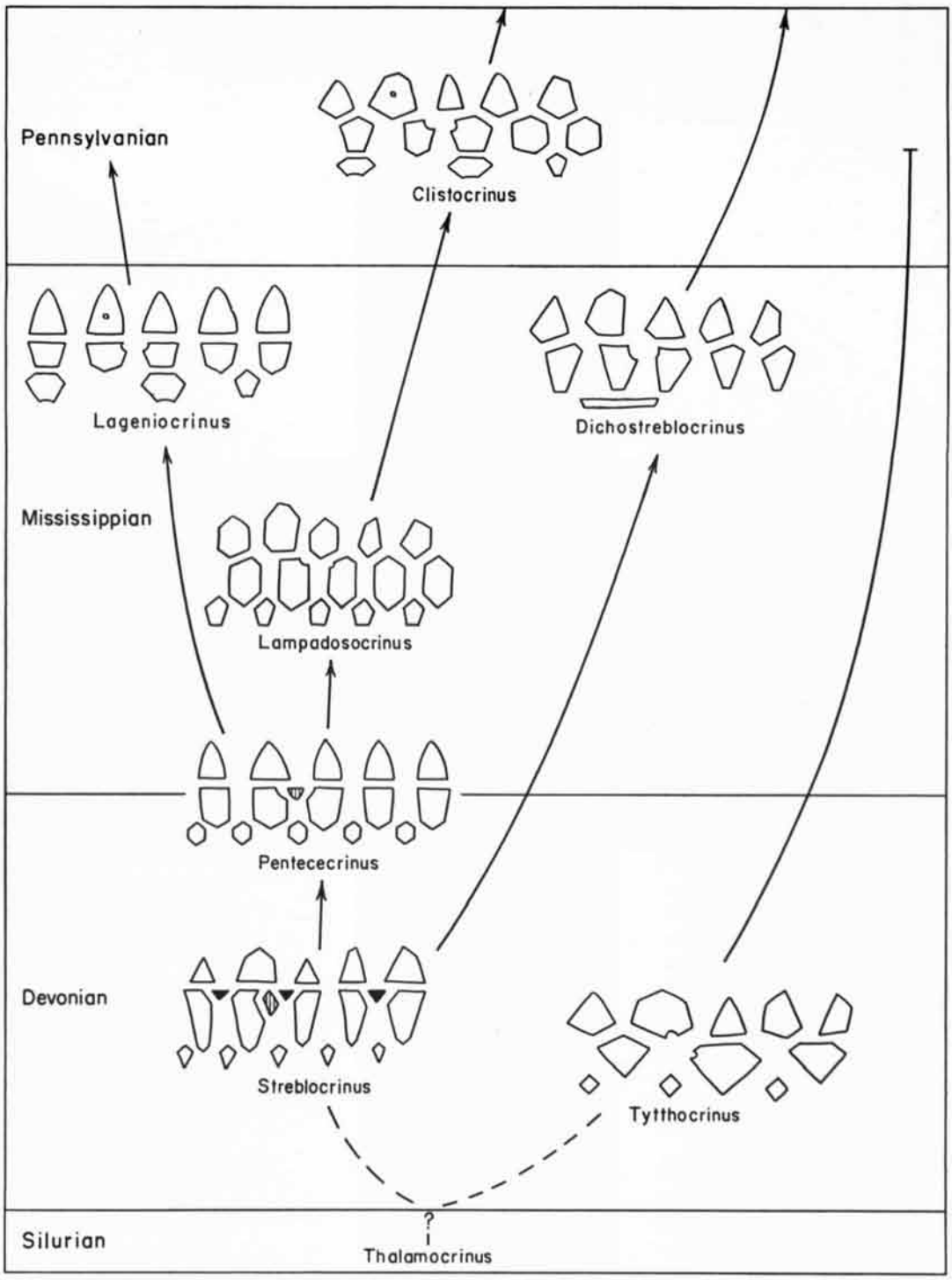

FIG. 2. Devonian-through-Pennsylvanian genera of Streblocrinidae, n.fam. [The *A* ray and *AE* interray are the farthest right plates in each diagram. Radials are black and anal plates have vertical ruling.]

bearing articular facets on the upper edges of one or more of the second circlet of cup plates. These plates are correctly designated as radials and the proximal circlet as basals. Codiacrinaceans with only two circlets of plates in the cup do not display articular facets on plates of the second circlet. These plates are judged to be basals and the proximal circlet infrabasals, the radials having atrophied and disappeared. The difference cannot be ascribed to ontogenetic change—that two-circlet cups without facets are immature monocyclic forms that have not yet developed facets on the second (radial) circlet—because many specimens of two-circlet codiacrinaceans are several times larger than much smaller arm-bearing allagecrinids, yet do not display facets. Conclusive evidence for this argument is found in codiacrinaceans with three-circlet cups like that of *Embryocrinus* (Perm.) or *Streblocrinus* (Dev.), in which the radials are much reduced in size, lack facets, and are at the point of disappearing.

2) Many allagecrinids have radial plates unequally developed in size, and some have differences in the number of arms borne by radials within the same cup. These allagrecrinids consistently display a bilateral symmetry plane in an *E-BC* direction. No reported codiacrinacean has this symmetry direction, even though asymmetric radials are known in several genera.

3) Microscopic allagecrinids typically do not have an anal opening in the side of the cup below the top of the radial circlet. Presumably the anal opening of these crinoids was situated internal to the oral plates, which probably were movable. All but a few codiacrinacean genera have an anus opening to the exterior through the theca, and all but two of the pseudomonocyclic codiacrinaceans have such an opening.

Utilization of these morphologic criteria should make the distinction clear between the two major groups of Paleozoic two-circlet microcrinoids.

EVOLUTION OF CODIACRINACEANS

Continuing disagreement among paleontologists on the phylogeny of codiacrinaceans (Yakovlev, 1928; Wanner, 1929; Weller, 1930; Peck, 1936; Kirk, 1940; Koenig & Niewoehner, 1959) will not be reviewed here in detail because this controversy has been adequately summarized in the readily available latest two cited papers. With the recent description of *Pentececrinus* Koenig & Niewoehner, from Devonian-Mississippian transition beds, which is the oldest known abrachiate (armless) codiacrinacean, it seems clear that two morphologically dissimilar groups of these crinoids persisted from Devonian through Permian time. One of the groups lacked radial plates from the beginning, so were pseudomonocyclic (Fig. 2, 3). The tendency for radials to atrophy and disappear is foreshadowed by the Middle Devonian genus *Streblocrinus* Koenig & Meyer (1965), which has only three small radial plates. Codiacrinaceans with five arm-bearing radials begin with *Codiacrinus* in the Devonian and continue through to the Permian (Fig. 4, 5). A third group, typified by *Sycocrinites,* has five radials, only one of which is arm-bearing, the others being reduced in size and lacking radial facets (Fig. 6). This group is first found in Lower Carboniferous rocks, and continues into the Permian.

At least two possible phyletic schemes may account for the temporal distribution of genera in the three morphologic groups distinguished on the basis of number of arm-bearing radials. Informally we may designate the three groups as abrachiate, monobrachiate, and pentabrachiate codiacrinaceans.

Each of these three groups could represent a separate phyletic lineage. The abrachiate genera developed in the Devonian from an ancestor like *Streblocrinus* with complete atrophy of the radials by Late Devonian or Early Mississippian time *(Pentececrinus).* The pentabrachiate forms began with *Codiacrinus* in the Devonian and continued through to the Permian. The monobrachiate genera, which first appear in the Lower Carboniferous, would have been derived initially from a pentabrachiate genus by loss of arms on all but one of the radial plates, and then continued on as a separate lineage into the Permian.

Alternatively, the abrachiate genera could represent a series of unrelated but homeomorphic genera that repeatedly evolved from pentabrachiate forms by loss of radials. This pattern of evolutionary reiteration would be similar to that of Mesozoic ammonoids. If this were the case, then one might postulate that the monobrachiate genera represent transitional stages in the evolutionary lines leading to abrachiate types.

Various workers (Kirk, 1940; Peck, 1936) have suggested that the Permian *Embryocrinus,* which has five small abrachiate radials, may have

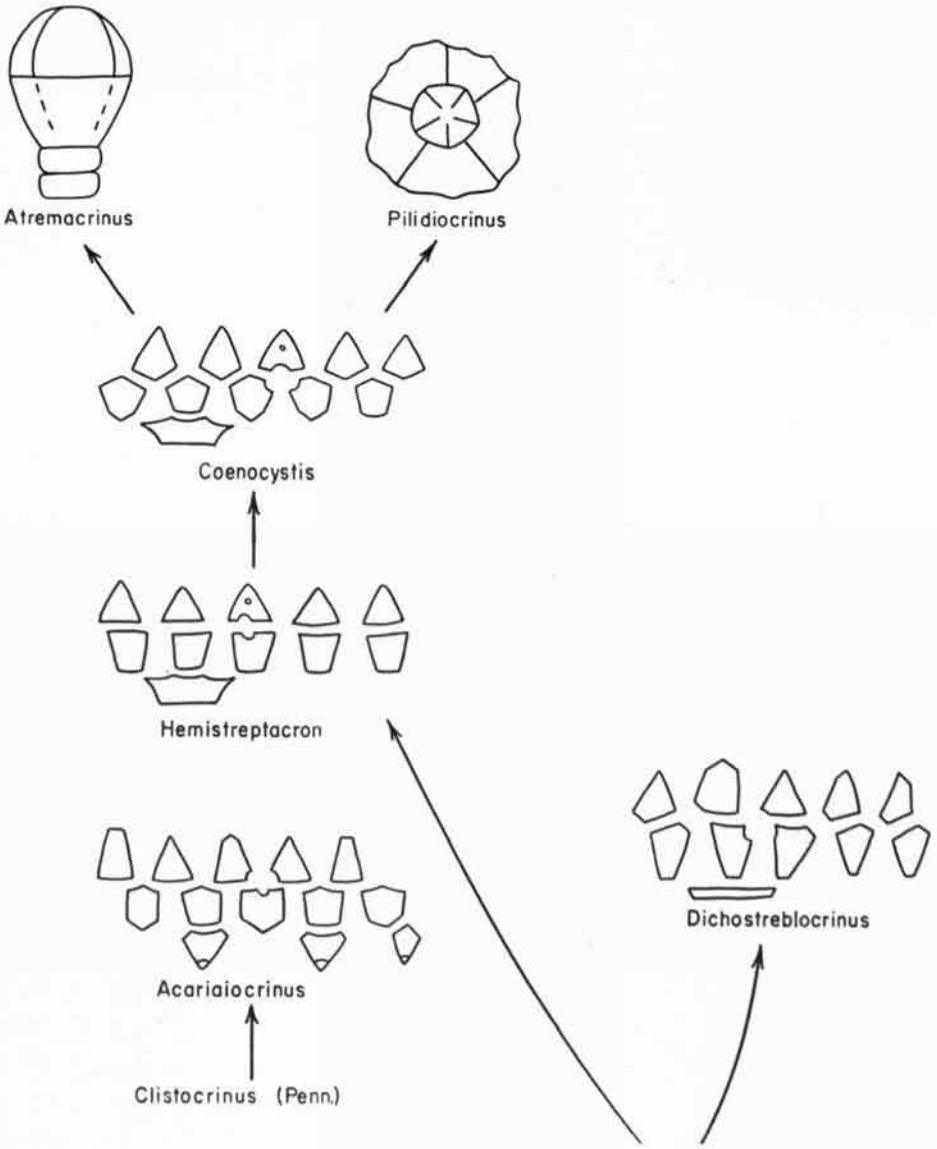

FIG. 3. Permian representatives of the Streblocrinidae. [Explanation of orientation and symbols as for Fig. 2.]

evolved from a pseudomonocyclic form like *Lageniocrinus* de Koninck, of the Lower Carboniferous, by a secondary reappearance of radial plates late in the evolutionary history of the group. It seems more reasonable, however, to regard *Embryocrinus* as a descendant of pentabrachiate codiacrinaceans, which only began to effect reduction in radial plates in the Permian, a process that the abrachiate group began in the Devonian. In this view the dicyclic forms with radials still present are a conservative, more slowly evolving group than the abrachiate types.

If one differentiates three groups of codiacrinaceans on the basis of the number of arm-bearing radial plates, as was done above, several other morphologic features serve to establish the morphologic distinctiveness of the groups and buttress the argument that each is a separate phylogenetic entity, at least from the Early Carboniferous through the Permian.

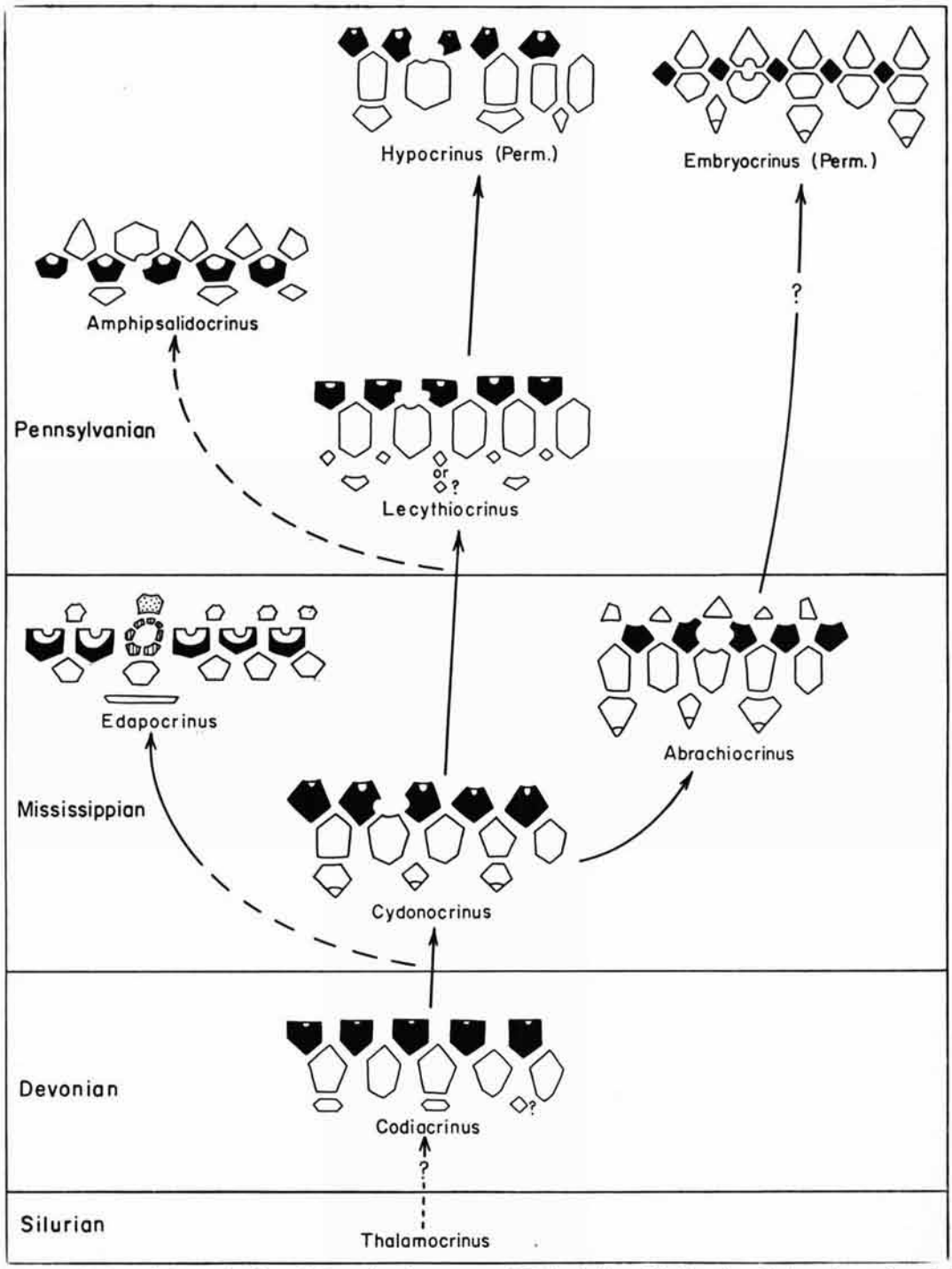

FIG. 4. Evolution of Devonian-through-Pennsylvanian genera of Codiacrinidae. [Explanation of orientation and symbols as for Fig 2, except for stippled madreporitic posterior oral.]

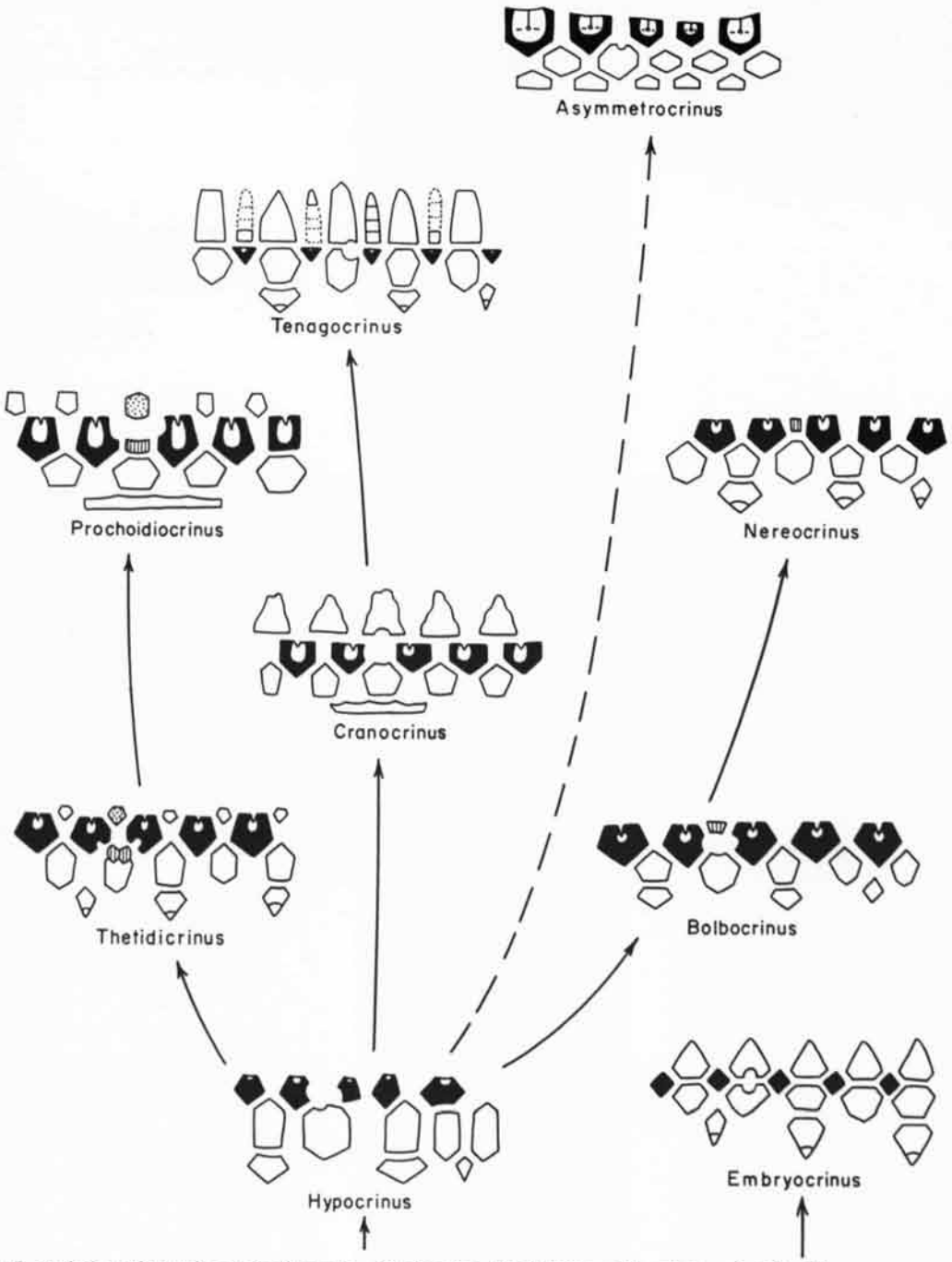

FIG. 5. Evolution of Permian codiacrinaceans. [Explanation of orientation and symbols as for Fig. 2.]

The Devonian and some Lower Carboniferous abrachiate genera have five unfused infrabasal plates, which surely is a generalized condition denoting little evolutionary advancement of this feature. On the other hand, the oldest pentabrachiate genus *(Codiacrinus)*, and only known Devonian crinoid of this type, has only three infrabasals, four of the original five being fused into two larger

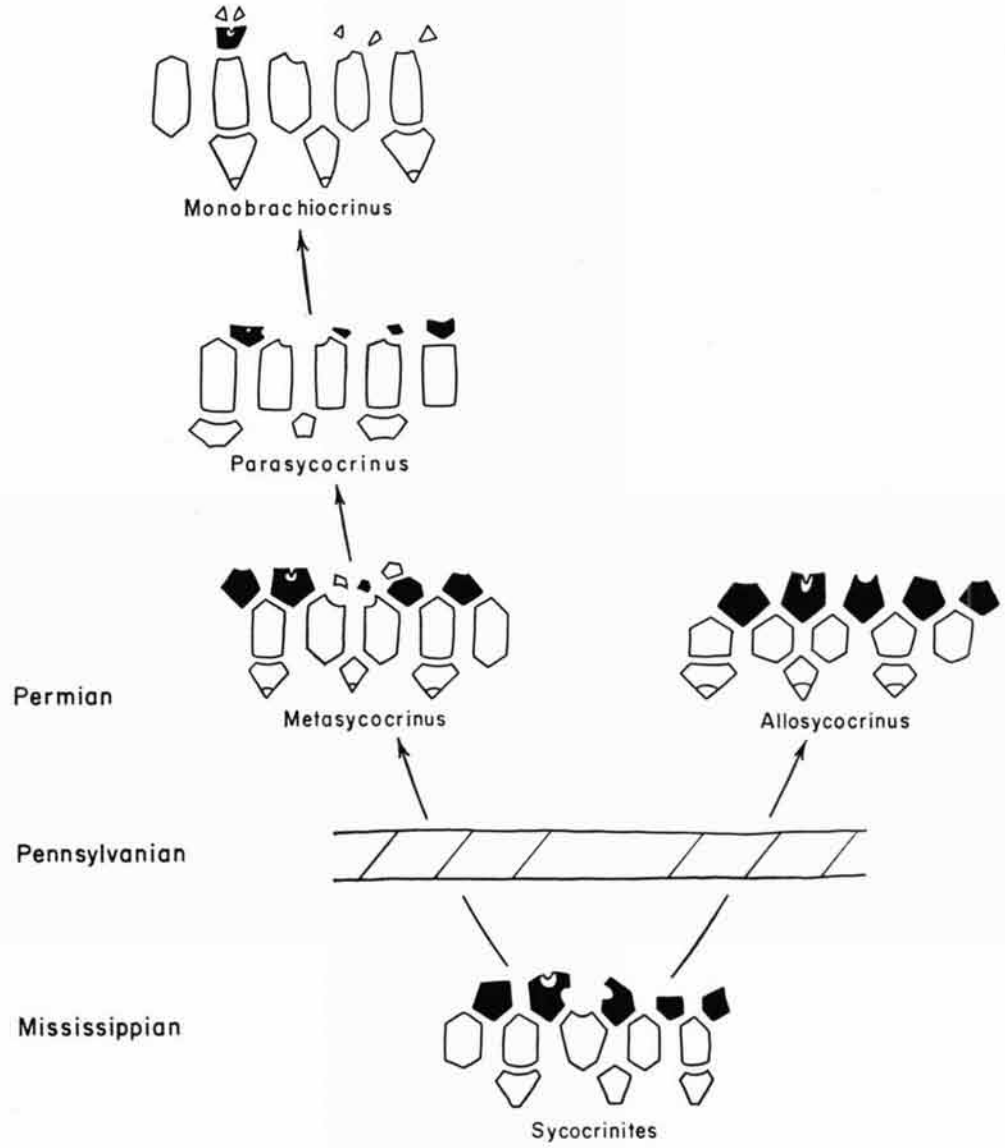

FIG. 6. Evolution of Sycocrinitidae, n.fam. [Explanation of orientation and symbols as for Fig. 2.]

plates. Consequently, the oldest known abrachiate forms could not have evolved from the oldest pentabrachiate type, which is evolutionarily more advanced in structure of the infrabasal circlet. The condition of the infrabasals then suggests either a separate origin for the two groups or a common but as yet unknown pre-Middle Devonian ancestor.

Another morphologic feature that seems to indicate a long separate phyletic history for the pentabrachiate and abrachiate groups is relative orientation of the anal opening. In pentabrachiate forms the anal opening typically is directly above the posterior basal, either between basals and radials, between radials, or between radials and orals. In abrachiate genera, however, the anal opening is above and to the right of the posterior basal from Devonian to Permian time, when a trend begins for leftward shift of the anal opening until it is directly above the posterior basal (Fig. 7).

A third feature that can be cited is that all pre-Permian pentabrachiate genera typically are pre-

served without oral plates, since the latter do not form an integral part of the theca, but apparently are loosely articulated so that they tend to fall off soon after death of the crinoid. All abrachiate forms typically have the orals preserved in place.

The combination of morphologic features discussed—number of arm-bearing radials, number of infrabasals, position of anal opening, and preservation of oral plates—supports the hypothesis that three separate, distinctive, long-continued phylogenetic lines were developed within the crinoids previously classed in the family Codiacrinidae. Consequently, it is judged desirable to recognize each of these groups as a separate family in order to effect a phyletic classification of these crinoids.

ANCESTRY OF CODIACRINACEANS

It has been postulated that the codiacrinaceans evolved from, or had a common ancestor with, the Gasterocomidae (Moore & Laudon, 1943). This relationship can no longer be supported, especially in view of more recent knowledge of oldest known (Devonian) Codiacrinacea. The gasterocomids are a group of Silurian and Devonian genera characterized by such specialized features as a completely fused infrabasal circlet, peripheral canals in the stem, and an anal opening below the top of the radial circlet. As pointed out previously, some primitive codiacrinaceans have five unfused infrabasals and all lack peripheral canals in the stem and axial canals in the radials and brachials; also, codiacrinaceans with an anal opening below the top of the radials are not found until Mississippian time, indicating that this characteristic was developed independently in the two groups of crinoids. Consequently, the gasterocomids and codiacrinaceans are judged not to be closely related.

A literature search for a potential pre-Middle Devonian ancestor for all of the Codiacrinacea reveals that only the Silurian palaeocrinid *Thalamocrinus* possibly qualifies as an ancestral type. This genus consists of small individuals with a relatively high theca, five infrabasals, large basal plates, five small arm-bearing radials, and two anal plates in the cup. If the anal plates were expelled from the cup and infrabasals fused into three plates, *Thalamocrinus* would resemble *Codiacrinus*, the oldest pentabrachiate codiacrinacean. If two of the radials disappeared and one anal were eliminated, the former genus would resemble *Streblocrinus*, which is judged to be ancestral to the abrachiate types.

SUPRAGENERIC CLASSIFICATION OF CYATHOCRININA

Order CLADIDA Moore & Laudon, 1943

Suborder CYATHOCRININA Bather, 1899

Superfamily CYATHOCRINITACEA Bassler, 1938 (Roemer, 1854)

[*nom. transl.* Lane, herein (*ex* Cyathocrinitidae Bassler, 1938) (Roemer, 1854)]

Diagnosis.—Theca bowl-shaped; radianal small or absent; anal-X large; one or more additional anal plates may be in cup. Tegmen produced into stout anal sac with terminal anal opening. Arms atomous, isotomous with few or many branches, or heterotomous. *Sil.-Perm.*

Families.—Cyathocrinitidae Bassler, 1938 (Roemer, 1854); Ampheristocrinidae S. A. Miller, 1890; Lecythocrinidae Kirk, 1934; Barycrinidae Jaekel, 1918.

Remarks.—The Cyathocrinitacea are judged to comprise an advanced stock of families that developed several morphologic features paralleling the more successful evolutionary trends of the dendro- and poteriocrinoids. The cyathocrinitaceans possessed an anal sac, like all more advanced cladid crinoids, but the sac is short, confined to the posterior part of the tegmen, and is composed of heavy, imperforate plates with a terminal anal opening. A porous or reflexed sac, or one with a wide spinose cap was not developed. Most of the genera in the superfamily have isotomous arms with relatively numerous branches; only the Barycrinidae have heterotomously arranged branchlets, suggesting a trend toward pinnulation. These crinoids show another trend parallel to those of more advanced cladids in having radial facets relatively wider than in most other Cyathocrinina and the facet may develop an obscure transverse ridge in advanced types.

Superfamily PALAEOCRINACEA Bather, 1899

[*nom. transl.* Lane, herein (*ex* Palaeocrinidae Bather, 1899)]

Diagnosis.—Theca bowl-shaped; radianal and

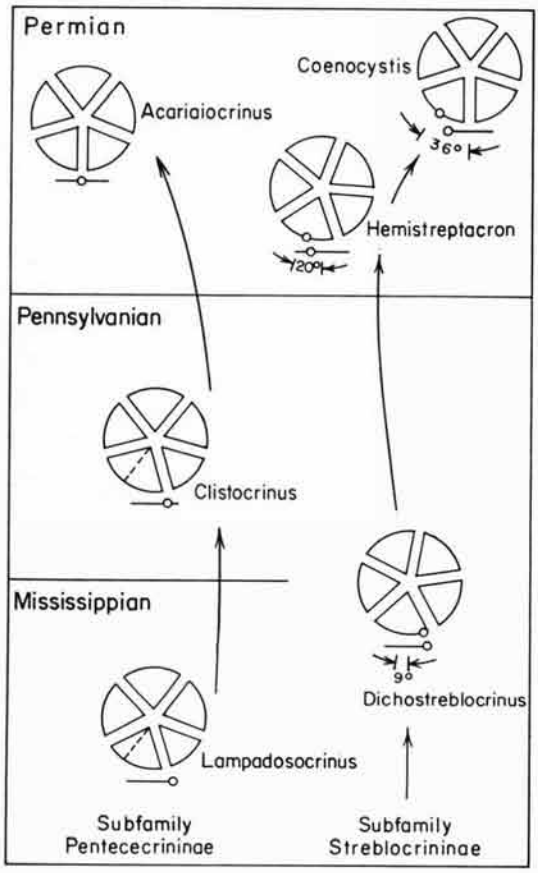

FIG. 8. Different modes of anal opening and oral relationship in subfamilies Pentececrininae and Streblocrininae of the family Streblocrinidae. Line beneath each oral rosette represents the posterior basal.

anal-X present, or one or both may be absent; infer- and superradianal present primitively. Tegmen low, flat, anal opening directly through tegmen or side of cup; posterior oral with hydropore or developed as madreporite. Arms atomous or isotomous; brachials fused in each ray, or laterally united in specialized families. *Ord.-Dev.*

Families.—Palaeocrinidae BATHER, 1899; Carabocrinidae BATHER, 1899; Crotalocrinitidae BASSLER, 1938 (*pro* Crotalocrinidae ANGELIN, 1878); Petalocrinidae WELLER & DAVIDSON, 1896; Gasterocomidae ROEMER, 1854.

Remarks.—The Palaeocrinidae and Carabocrinidae are the oldest and structurally most primitive of the Cyathocrinina. Both families have egg-shaped thecae reminiscent of the monocyclic disparid suborder Hybocrinina, differing from that monocyclic group mainly in the possession of infrabasals. The Carabocrinidae are the only inadunate crinoids having a double radianal plate, with upper and lower parts caller super- and inferradianal. The Palaeocrinidae have a single radianal and atomous arms, in contrast to the isotomously divided arms of the carabocrinids. The three families which are judged to have evolved directly from palaeocrinids are highly specialized, short-lived Silurian and Devonian crinoids characterized by a low, bowl-shaped cup, and isotomously branched arms. In the Gasterocomidae the anal opening has migrated downward into the posterior side of the cup to a position just above the posterior basal. The stem is distinctive in having three or four peripheral canals surrounding the main axial canal. The Petalocrinidae have no anal plates in the cup and the brachials of each ray are fused into a single solid plate with branching ambulacral canals on the ventral surface of each ray plate. The Crotalocrinitidae have many-branched arms with brachials laterally joined to form a flexible meshwork. All three of these families have separate axial canals piercing the radials and brachials.

Superfamily CODIACRINACEA Bather, 1899

[*nom. transl.* LANE, herein (*ex* Codiacrinidae BATHER, 1899)]

Diagnosis.—Theca small, radials five, three, one, or absent. Radianal absent, anal-X present only primitively or secondarily. Tegmen low, composed of five orals, posterior one large, separating *BC* and *DE* orals, commonly with hydropore, or rarely and secondarily developed as madreporite. *Dev.-Perm.*

Families.—Codiacrinidae BATHER, 1899; Sycocrinitidae LANE, n.fam.; Streblocrinidae LANE, n. fam.

Family CODIACRINIDAE Bather, 1899

[=Hypocrinidae JAEKEL, 1918; Embryocrinidae WANNER, 1916]

Diagnosis.—Codiacrinoids with five facet-bearing radials, or rarely with five secondarily reduced, nonfacet-bearing radials of equal size. Anal opening between radials and basals, or radials and orals. Anal-X absent, or secondarily developed above or below anal opening in advanced genera. Posterior oral with a hydropore or developed as a madreporite. *Dev.-Perm.*

Subfamilies.—Codiacrininae BATHER, 1899; Bolbocrininae WANNER, 1916; Thetidicrininae WANNER, 1916.

Subfamily CODIACRININAE Bather, 1899

[*nom. transl.* LANE, herein (*ex* Codiacrinidae BATHER, 1899)] [=Hypocrininae WANNER, 1929; section Hypocrinites WANNER, 1929]

Diagnosis.—Codiacrinids that lack madreporite and anal-X.

Genera.—*Codiacrinus* SCHULTZE, 1866; *Cydonocrinus* BATHER, 1913; *Abrachiocrinus* WANNER, 1920; *Lecythiocrinus* WHITE, 1879 (=*Menocrinus* S. A. MILLER, 1889); *Amphipsalidocrinus* WELLER, 1930; *Hypocrinus* BEYRICH, 1862; *Cranocrinus* WANNER, 1929; *Tenagocrinus* WANNER, 1929; *Embryocrinus* WANNER, 1916; *Asymmetrocrinus* WANNER, 1937.

Remarks.—The central evolutionary stock of this subfamily is judged to be one that includes *Codiacrinus* (Dev.), *Cydonocrinus* (L.Carb.), *Lecythiocrinus* (Penn.), and *Hypocrinus* (Perm.). These genera show trends for the anal opening to migrate from the tegmen down into the side of the cup *(Codiacrinus* to *Cydonocrinus),* and gradual reduction in size of the radials, resulting in change of cup form from an essentially conical shape in *Codiacrinus* to an egg-shaped theca in *Hypocrinus.* In this main evolutionary line the anal opening is persistently above the posterior basal, and oral plates are not preserved above the radials. During Early Carboniferous time the aberrant *Abrachiocrinus* developed, which has five subequal radials that lack articular facets. A form like this genus may have led to the Permian genus *Embryocrinus,* which differs from it mainly in having the armless radials reduced to the point where they are completely separated by basals and orals.

Hypocrinus is judged to have been the radicle from which the Bolbocrininae and Permian genera of the Thetidicrininae evolved. Other offshoots from *Hypocrinus* include *Cranocrinus,* with completely fused infrabasals and asymmetrically arranged facets on the radials, *Asymmetrocrinus,* which has five infrabasals and radials and radial facets of quite unequal size, and *Tenagocrinus,* the only Permian codiacrinid for which the arms are known. This genus has five small triangular radials completely separated from each other by basals, as in *Embryocrinus,* but unlike that genus, *Tenagocrinus* possesses five atomous uniserial arms and its anal opening, instead of being directly above the posterior basal, has shifted to the right, indenting the upper right shoulder of the posterior oral next to the *C* radial. The position of the anal opening in this genus is comparable to that of the Pennsylvanian abrachiate genus *Clistocrinus,* but the presence of radials and arms in *Tenagocrinus* is thought to preclude any relationship of the two forms.

Subfamily BOLBOCRININAE Wanner, 1929

[*nom. transl.* LANE, herein (*ex* section Bolbocrinites WANNER, 1929)]

Diagnosis.—Codiacrinids with anal opening in side of cup, bounded above or below by secondarily developed anal plate; without madreporite.

Genera.—*Bolbocrinus* WANNER, 1916; *Nereocrinus* WANNER, 1924 (=*Oceanocrinus* WANNER, 1924).

Remarks.—The two genera of this subfamily are closely related, differing mainly in whether the anal plate is above *(Nereocrinus),* or below *(Bolbocrinus)* the anal opening. The presence of an extra plate in the posterior interray is thought to be a secondary, advanced development, not a holdover from a more primitive condition. All post-Devonian, pre-Permian codiacrinids except *Edapocrinus* (an unusual, specialized Lower Carboniferous form), lack any trace of an anal plate in the theca. Development of an extra plate in the posterior part of the theca may be related to a tendency for the radial plates to decrease in size in Permian Codiacrinidae, and the resultant necessity for filling up of space around the anal opening. There is no indication that the anal plate of the Bolbocrininae is homologous with the anal-X, radianal, or right tube plate of most inadunate crinoids.

Subfamily THETIDICRININAE Wanner, 1929

[*nom. transl.* LANE, herein (*ex* section Thetidicrinites WANNER, 1930)]

Diagnosis.—Codiacrinids with madreporitic posterior oral, and one or two anals in dorsal cup.

Genera.—*Thetidicrinus* WANNER, 1916; *Prochoidiocrinus* WANNER, 1937; *Edapocrinus* WRIGHT, 1935 [=*Edaphocrinus* WANNER, 1937 *(nom van.)*].

Remarks.—This subfamily is clearly polyphyletic, for there is little reason to assume that the two Permian genera described by WANNER evolved from the only known Lower Carboniferous genus *Edapocrinus.* The latter differs from most codia-

crinids in having a flat base, with infrabasals hidden in side view, relatively large radial facets, and more than five plates in the tegmen. The five orals are large, interradial plates, of which the posterior one is pierced by numerous canals to form a typical madreporite. The summit of the tegmen is covered by five small tegminal plates which alternate with the orals, so as to be situated radially. WRIGHT called these plates epiorals. Several small plates surround the anal opening, located on a slightly protuberant part of the posterior side of the cup. This projection is not sufficient to warrant designation of it as an anal sac in the usual sense. *Edapocrinus* is judged to have evolved from a form like *Cydonocrinus* by fusion of the infrabasals into a single plate and development of the characteristic features discussed. The two Permian genera are thought to have evolved from a generalized Permian form like *Hypocrinus* by development of one or two accessory anal plates below the anal opening, a madreporitic posterior oral, and in *Prochoidiocrinus,* fusion of three infrabasals into a single plate.

Family SYCOCRINITIDAE Lane, new family

Diagnosis.—Codiacrinaceans with one arm-bearing radial, other radials present or absent, commonly unequal and reduced in size; three infrabasals; anal plate absent; anal opening bounded by basals and radials or by radials. Orals small, commonly not preserved. *L.Carb.-Perm.*

Genera.—Sycocrinites AUSTIN & AUSTIN, 1842 (=*Sycocrinus* BATHER, 1900); *Allosycocrinus* WANNER, 1924; *Metasycocrinus* WANNER, 1920; *Monobrachiocrinus* WANNER, 1916; *Parasycocrinus* MAREZ OYENS, 1940.

Remarks.—This group of genera is thought to be closely related and to represent a single phyletic lineage even though no Pennsylvanian representatives have been found. The major difference between Lower Carboniferous *Sycocrinites* and Permian *Allosyocrinus* is in the position of the anal opening, which is directly above the posterior basal in the older form and notches the top of one of the radials in the younger. Although the small infrabasal is in a different position in these two genera, being in the *C* radius in *Sycocrinites* and in the *D* radius in *Allosycocrinus,* this difference is thought not to be of generic importance, considering the variation in position of the small infrabasal in other genera of the Codiacrinacea.

Both of the genera just mentioned differ from *Metasycocrinus* in having radials that are approximately of equal size, although the arm-bearing *D* radial is consistently the largest plate of the circlet. In *Metasycocrinus* the *C* radial is reduced to small size, and the anal opening scallops the tops of both the posterior and *BC* basals. In *Monobrachiocrinus,* clearly a descendant of *Parasycocrinus*, the anal opening is in the same position but all of the radials except the arm-bearing *D* radial have disappeared.

Family STREBLOCRINIDAE Lane, new family

Diagnosis.—Codiacrinaceans with no arm-bearing radial plates; radials absent in all but most primitive genus; anal plate absent in all post-Devonian genera; orals five, large, posterior oral commonly with hydropore and separating *BC* and *DE* orals. Orals primitively above basals and anal opening is on the lower right side of posterior basal. *Dev.-Perm.*

Subfamily STREBLOCRININAE Lane, new subfamily

Anal opening shifted toward left of anteroposterior axis and orals uniformly rotated clockwise to a radial position. *Dev.-Perm.*

This subfamily is represented in the Middle Devonian by *Streblocrinus* and *Tytthocrinus,* the latter an unusual codiacrinacean that lacks radials, has five orals but only three basals and infrabasals. *Tytthocrinus* ranges into the Pennsylvanian and is thought to be a specialized offshoot of the Streblocrininae that did not lead to any other genera. *Streblocrinus,* on the other hand, has several morphologic features which indicate that it may be close to an ancestral type for all other, younger, genera in the family Streblocrinidae. There are five infrabasals, five large basals, and three small triangular radials that lack articular facets. These radials are in the *A, C* and *D* rays. Five large orals surmount the basals, and although the only known specimen is imperfect in the posterior area, a single anal plate is thought to be present below and at left of the *D* radial. Whether this plate was anal-X or a radianal is not known. By loss of the three radials, *Streblocrinus* leads to the Pennsylvanian genus *Dichostreblocrinus,* which ranges into the Permian. Two other abrachiate genera found in the Permian appear to have evolved from *Dichostreblocrinus*, which differs from its Devonian predecessor, *Streblocrinus,* mainly in having

the orals uniformly shifted about 9° to the left of the basals. In the Permian there is a clear trend for the position of the anal opening to shift to the left, until in *Coenocystis* it notches the upper left corner of the posterior basal and is in the mid-line of the posterior oral (Fig. 7). The shift in position of the anal opening is accompanied by a uniform rotation of the oral plates to the left until in *Coenocystis* they occupy a radial position, having rotated 12° to 20° in *Hemistreptacron* to 36° in *Coenocystis*. Except for *Streblocrinus*, all of the genera in this subfamily have fused infrabasals.

Genera.—Streblocrinus Koenig & Meyer, 1965; *Dichostreblocrinus* Weller, 1930; *Hemistreptacron* Yakovlev, 1926; *Coenocystis* Girty, 1908; *Tytthocrinus* Weller, 1930 (=*Octocrinus* Peck, 1936); *Atremacrinus* Wanner, 1929; *Pilidiocrinus* Wanner, 1937.

Subfamily PENTECECRININAE Lane, new subfamily

Anal opening shifted secondarily to anteroposterior axis and orals moved to a radial position by left-lateral extension of the posterior orals. *Dev.-Perm.*

Pentececrinus, a Late Devonian genus judged to be a direct descendant of *Streblocrinus*, is a primitive streblocrinid possessing five infrabasals, five large basals, and five orals in interradial position directly above the basals. A single anal plate is inserted within the basal circlet between the upper right corner of the posterior basal and upper left corner of the right posterior basal. In the next succeeding Mississippian genus *Lampadosocrinus*, expansion of the left side of the posterior oral indicates the beginning of a trend in which the oral plates shift to a radial position and the anal opening moves to the mid-line of the posterior basal (Fig. 7). This trend culminates in the Permian genus *Acariaiocrinus*. Except for *Pentececrinus* and *Lampadosocrinus*, which have five infrabasals, all other genera in this subfamily have three.

Genera.—Pentececrinus Koenig & Niewoehner, 1959; *Lampadosocrinus* Strimple & Koenig, 1956; *Lageniocrinus* de Koninck, 1854; *Clistocrinus* Kirk, 1937 (=*Clithrocrinus* Kirk, 1937, *nom. van.*); *Acariaiocrinus* Wanner, 1924 (=*Streptostomocrinus* Yakovlev, 1927).

ACKNOWLEDGMENTS

The author is indebted to Raymond C. Moore for critical review of this paper, and to John W. Koenig, Missouri Geological Survey, who suggested several substantial changes in treatment of the Streblocrinidae which are reflected in both the text and illustrations concerning this family.

REFERENCES

Bather, F. A., 1899, *A phylogenetic classification of the Pelmatozoa:* British Assoc. Rept., 1898, p. 916-923.

Kirk, Edwin, 1940, *A redescription of* Lageniocrinus *de Koninck:* Am. Jour. Sci., v. 238, p. 129-139, fig. 1-12.

Koenig, J. W., & Meyer, D. L., 1965, *Two new crinoids from the Devonian of New York:* Jour. Paleontology, v. 39, p. 391-397, fig. 1-4.

——— & Niewoehner, Walter, 1959, Pentececrinus, *a new microcrinoid from the Louisiana Formation of Missouri:* Same, v. 33, p. 462-470, 3 text-figs.

Moore, R. C. & Laudon, L. R., 1943, *Evolution and classification of Paleozoic crinoids:* Geol. Soc. America Special Paper 46, x+167 p., 18 fig., 14 pl.

Peck, R. E., 1936, *Lower Mississippian microcrinoids from the Kinderhook and Osage Groups of Missouri:* Jour. Paleontology, v. 10, p. 282-293, pl. 46-47.

Strimple, H. L., & Koenig, J. W., 1956, *Mississippian microcrinoids from Oklahoma and New Mexico:* Jour. Paleontology, v. 30, p. 1225-1247, fig. 1-4.

Ubaghs, Georges, 1953, *Classe des Crinoïdes:* in Traité de paléontologie, Jean Piveteau (ed.), v. 3, p. 658-733, 166 fig.

Wanner, Johannes, 1929, *Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor, II,* Hypocrinites: Dienst van den Mijnb. Nederl.-Indië, Wetenschap. Medel. no. 11, 116 p., 16 fig., 7 pl.

Weller, J. M., 1930, *A group of larviform crinoids from Lower Pennsylvanian strata of the Eastern Interior basin:* Illinois Geol. Survey, Rept. Investig., no. 21, 38 p., 2 pl.

Yakovlev, N. N., 1928, *Sur la teratologie et la morphogenie des crinoïdes abrachiates:* Acad. Sci. U.R.S.S., Comptes Rendus, no. 16-17, p. 313-315, fig. 1-3.