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REVISION OF CALCEOCRINIDAE

By Raymond C. Moore

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REVISION OF CALCEOCRINIDAE

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ILLUSTRATIONS

ABSTRACT

The family of monocyclic inadunate crinoids called Calceocrinidae (order Disparida) is a unique assemblage characterized by the recumbent position of the crown, with the dorsal cup and arms juxtaposed to the stem. Also, unlike any other crinoids, a muscular hinge along the boundary between the specialized basal and radial circlets of the dorsal cup allows back-and-forth movement of the crown with respect to the stem. The group displays a remarkable development of bilateral symmetry in a plane that coincides with the left anterior (E) ray and posterior-right (BC) interray, rather than with the so-called crinoidal plane through the anterior (A) ray and posterior (CD) interray. Representatives of the family range from Middle Ordovician (Blackriveran) rocks into the Lower Mississippian (Osagian) and are known from both North America and western Europe.

Study of the Calceocrinidae in connection with preparing text and illustrations for the volume on Crinoidea (Part S) of the *Treatise on Invertebrate Paleontology* has indicated a need for considerable taxonomic revision. This is demanded by the misidentification of the type-species of *Calceocrinus* as given by previous authors and by changes in evaluation of morphological features applied to definition of several genera. Formerly, the family was considered to contain five (or possibly six) genera: *Calceocrinus, Cremacrinus, Eucheirocrinus, Halysiocrinus, Senariocrinus,* and (according to some authors) *Deltacrinus.* As now understood, these nominal genera (excepting *Eucheirocrinus,* which is a junior objective synonym of *Calceocrinus*) are included in the family and in addition, *Chirocrinus* ANGELIN, 1878, *Synchirocrinus* JAEKEL, 1918, *Anulocrinus* RAMSBOTTOM, 1960, and *Chiropinna* MOORE, n. gen.

The revised definition of *Calceocrinus,* which depends essentially on corrected identification of its type-species, makes it equivalent to *Eucheirocrinus* of previous literature. Species formerly classed as belonging to *Calceocrinus* are now distributed among *Chirocrinus, Synchirocrinus, Deltacrinus,* and *Chiropinna.* The genus *Anulocrinus* is shown to have typical calceocrinid heterotomy of the lateral-ray axil-arms, instead of complete isotomy, as stated by RAMSBOTTOM. Analysis of the lateral rays demonstrates the presence of main-axil series in all calceocrinids except *Senariocrinus,* with range from ill-defined to highly developed. Axil-arms of all genera (except *Senariocrinus* and *Chiropinna*) bear unbranched ramules according to an invariable plan, the lowest (alpha-ramule) appearing on the abanal side of the axil-arm and higher ones on opposite sides in alternation. A striking enlargement of beta-ramules, accompanied by closely parallel arrangement of them so as to conceal higher parts of the axil-arms, distinguishes *Synchirocrinus. Chiropinna* differs radically from other calceocrinids, and possibly from all other Disparida, in having abundant true pinnules.

A comparative survey of the calceocrinids indicates that primitive genera have obscure main-axils and few axil-arms, whereas advanced genera are characterized by highly developed main-axils and relatively numerous axil-arms. Evolution of dorsal-cup features is not correlated with that of the arms in any systematic way.

Taken all together, the Calceocrinidae are now distributed in nine genera, which contain 58 species considered to be valid—11 of Ordovician age, 30 Silurian, 8 Devonian, and 9 Mississippian. Four genera are known from both North America and Europe, three from North America only, and two from Europe only. Among described species, 43 are North American and 15 European, none common to both continents being known.

INTRODUCTION

GENERAL NATURE OF CALCEOCRINIDAE

One of the most interesting groups of Paleozoic crinoids, both from the standpoint of their morphological specialization and adaptation to a particular mode of life, comprises the Ordovician-to-Mississippian family Calceocrinidae. These are monocyclic inadunates distinguished especially by deflection of the crown from a normal attitude, extending upward from the stem, to one in which it is bent very sharply backward or downward so as to parallel the stem (Fig. 1). The uniqueness of this arrangement has suggested the designation of bent-crown crinoids or "droopers."

Actually, it is by no means demonstrable that the crown hung pendent from the top of a subvertically standing stem. A plausible interpretation of the mode of life acquired by calceocrinids has been advanced by JAEKEL (1918, p. 88) in picturing these crinoids as dwellers on current-swept shallow sea-bottoms—for example, in reef environments—the stem in prone position attached to some up-current anchorage and the crown placed in down-current direction, capable of being elevated with outspread arms for feeding (Fig. 2). Hingement between the modified basals, not really a circlet, and the radials facilitated such back-and-forth movement in a plane that coincides with the strongly marked plane of bilateral symmetry found in these crinoids. Among earliest calceocrinids, symmetry was incompletely developed but in later genera it became remarkably perfected (Fig. 3). The orientation of the plane of bilateral symmetry calls for special notice because it is not anteroposterior, as one might expect, but disposed in the mid-plane of the left-anterior (E) ray, as in the Homocrinidae.

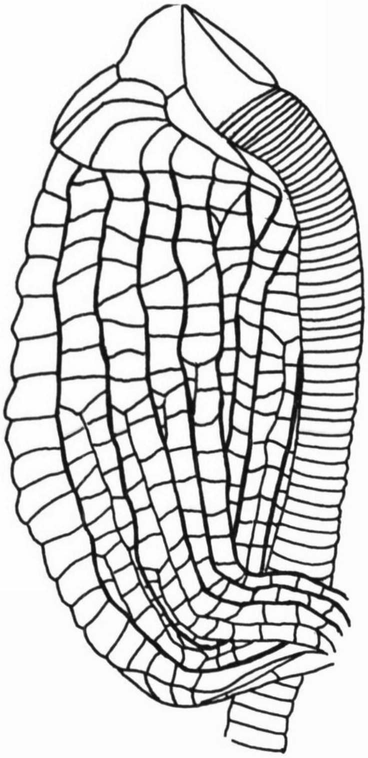


FIGURE 1. Typical calceocrinid with advanced evolutionary characters, showing crown closely recumbent on stem and tips of arms overlapping it; *Halysiocrinus nodosus* (HALL), Lower Mississippian, Borden Group, near Crawfordsville, Indiana, X1.5 (after Springer, 1926).

PURPOSE AND SCOPE OF PRESENT PAPER

The origin of descriptions and discussion given in this article is attributed to study by me called for in preparing part of the volume on Crinoidea to be included in the *Treatise on Invertebrate Paleontology,* published by the Geological Society of America and the University of Kansas Press. First, critical examination of the literature established the conclusion that virtually all previous workers had erroneously designated the type-species of *Calceocrinus,* type-genus of the family, and that the correctly determined type-species, according to application of the Rules, is the same as that cited universally for another calceocrinid genus, *Eucheirocrinus* MEEK & WORTHEN, 1869. As a result, unless appeal should be made to the International Commission on Zoological Nomenclature to abrogate the Rules in the case of *Calceocrinus* and *Eucheirocrinus,* the latter genus would have to be suppressed as an objective junior synonym of *Calceocrinus.* I have declined to draft such an appeal, preferring to follow stipulations of the Rules. Question then arose concerning disposition of species that commonly had been assigned to *Calceocrinus,* these species being clearly not congeneric with the true type-species of *Calceocrinus.* Inquiry needed to settle this problem led to study of the seemingly diagnostic characters of all nominal genera included in the Calceocrinidae. The main purpose of this paper is to record the results of this study.

Comparative morphology of the calceocrinid genera is described and illustrated, with notice that certain features of lateral-ray structures are through-going in nearly all genera and therefore of great importance for comparative studies, as well as for diagnosis of generic characters. Nine genera are recognized as members of the family, of which one is new *(Chiropinna)* and four *(Calceocrinus, Anulocrinus, Chirocrinus, Synchirocrinus)* call for revised diagnoses. The present paper undertakes to illustrate each genus and to record allocations of the 58 currently recognized species, but goes no farther in taxonomic directions.

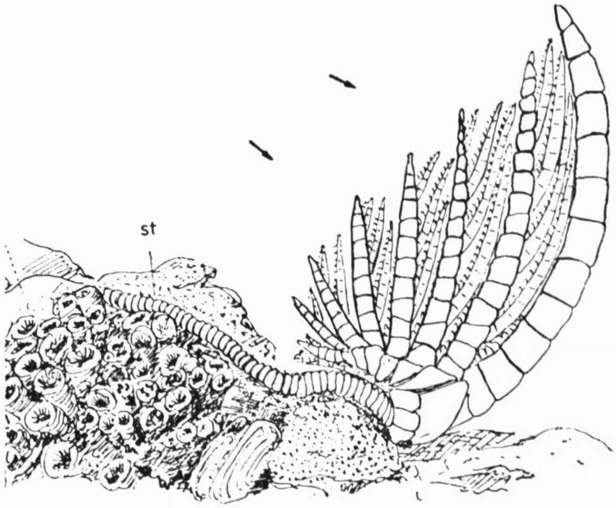


FIGURE 2. Reconstruction of a living calceocrinid, based on the postulate that the stem (st) lay flat on the sea floor and served as anchorage for the crown located in downcurrent (arrows) position. The arms are represented in spread-out erect arrangement for feeding. This drawing, labeled *Synchirocrinus anglicus,* n. gen., n. sp., accompanied JAEKEL'S (1918) diagnosis of the genus and although inaccurate in some morphological details, supports recognition of *S. anglicus* (type-species of *Synchirocrinus* by monotypy) as a junior synonym of *Calceocrinus nitidus* BATHER. The latter species, described from Middle Silurian rocks of Gotland, occurs also near Dudley, England, the sourse of *S. anglicus* (after Jaekel), 1918).

Discussion of evolution and phylogeny of the group is given, however.

PREVIOUS STUDIES

A brief review of work done by earlier authors, especially taking account of the important contributions of Bather (1893) and Springer (1926) toward understanding the peculiar morphological features of this crinoid group, is appropriate as an introductory part of the present paper. Numerous paleontologists have described species of calceocrinids, often with inadequate or misguided concepts of generic definitions and interrelationships, but few have helped significantly in the direction of interpreting evolution exhibited by this assemblage. In addition to Bather and Springer, Ulrich (1886), Ringueberg (1889), Schmidt (1934), Ramsbottom (1952, 1960) and Ubaghs (1953) have published contributions that rank as noteworthy advancements in knowledge of calceocrinids.

Hall (1852) first distinguished dorsal-cup remains obtained from Middle Silurian strata of New York as representing a previously unknown crinoid, publishing a description and illustrations of it under the name of *Calceocrinus,* but without providing any specific name. Subsequently, Hall (1860, 1862, 1863) described and figured several more complete fossils of similar sort, designating them by what he presumed was a new generic name—*Cheirocrinus.* Evidently, he overlooked his earlier *Calceocrinus* and was unaware of Eichwald's publication of *Cheirocrinus* (1856) for a genus of Ordovician cystoids from Russia. Salter (1859) had used *Cheirocrinus* for calceocrinids also, but without descriptions or illustrations, so that his generic and specific names rank as *nomina nuda* as of that date. Later Salter (1873) gave both descriptions and figures, still using the generic name *Cheirocrinus* but validating the specific names. Shumard (1866) in a catalogue of Paleozoic echinoderms described up to that date, listed Hall's species described in 1860 under *Cheirocrinus* and others published in 1862, and 1863, all cited by Shumard as questionably referred to *Calceocrinus.*

In 1869 Meek & Worthen described two species designated as *Calceocrinus? bradleyi* and *C? wachsmuthi* from Lower Mississippian rocks of Iowa and Indiana and provisionally introduced the family name Calceocrinidae. At the same time they proposed the new generic name *Eucheirocrinus* to replace Hall's junior homonym, *Cheirocrinus,* but they designated no type-species of *Eucheirocrinus.* S. A. Miller (1877) first definitely assigned to *Calceocrinus* some 12 previously described species but he did not select one of them as type-species. Angelin (1878) described a new species named *Chirocrinus gotlandicus* from Middle Silurian rocks of Gotland and published the family name Chirocrinidae. Wachsmuth & Springer (1886) listed genera classified as belonging to the Calceocrinidae and were first to designate explicitly a type-species for *Calceocrinus*; they named *Cheirocrinus chrysalis* Hall as the type-species.

Ulrich (1886), in connection with studies on Ordovician crinoids from Minnesota, introduced descriptions and illustrations of three new calceocrinid genera, *Cremacrinus, Deltacrinus,* and *Halysiocrinus,* publishing also the family name Cremacrinidae as replacement of Calceocrinidae, because he did not recognize *Calceocrinus* as a valid genus. Ringueberg (1889) undertook to straighten out classification of calceocrinid fossils by redescribing and figuring Hall's original dorsal cup named *Calceocrinus,* naming it *C. halli,* and then in order better to establish the genus, he described a more complete specimen as *C. typus,* which he designated (illegally) as type-species of the genus. In addition, he proposed two new genera (*Castocrinus, Proclivocrinus*).

Bather (1893), in a monographic work on the Silurian inadunate crinoids of Gotland, published a penetrating analysis of calceocrinid arm structures and described a number of new species from this area, all referred to *Calceocrinus.* A comprehensive review by Bather of the diverse, largely conflicting morphological terms used by previous authors for the strangely specialized structural elements of the Calceocrinidae furnished him with the basis for a revised terminology which has been accepted by most later workers. Bather's treatment of calceocrinid systematics, however, must be judged not only inadequate but in part quite erroneous. Twenty-five previously described species considered by him to be valid were distributed among four genera—*Castocrinus, Calceocrinus, Euchirocrinus* (incorrect spelling of *Eucheirocrinus*), and *Halysiocrinus*—and to these he added six new species of *Calceocrinus.* He validly fixed the type-species of *Euchirocrinus* (=*Eucheirocrinus*) but wrongly designated the type-species of *Calceocrinus* and *Halysiocrinus.* Bather (1900, p. 147) very briefly described the Calceocrinidae in Lankester's *Treatise on Zoology,* referring the same four genera mentioned above to the family.

Jaekel (1918) summarized morphological features of the calceocrinids and introduced the new genus *Synchirocrinus,* which later authors, until now, have classed as a junior synonym of *Calceocrinus*. Goldring (1923) recognized *Deltacrinus* and *Halysiocrinus* in her monograph on Devonian crinoids of New York.

In many ways the most illuminating description of the Calceocrinidae, accompanied by discussion of their evolution, was contributed by Springer (1926) in his memoir on American Silurian crinoids. After

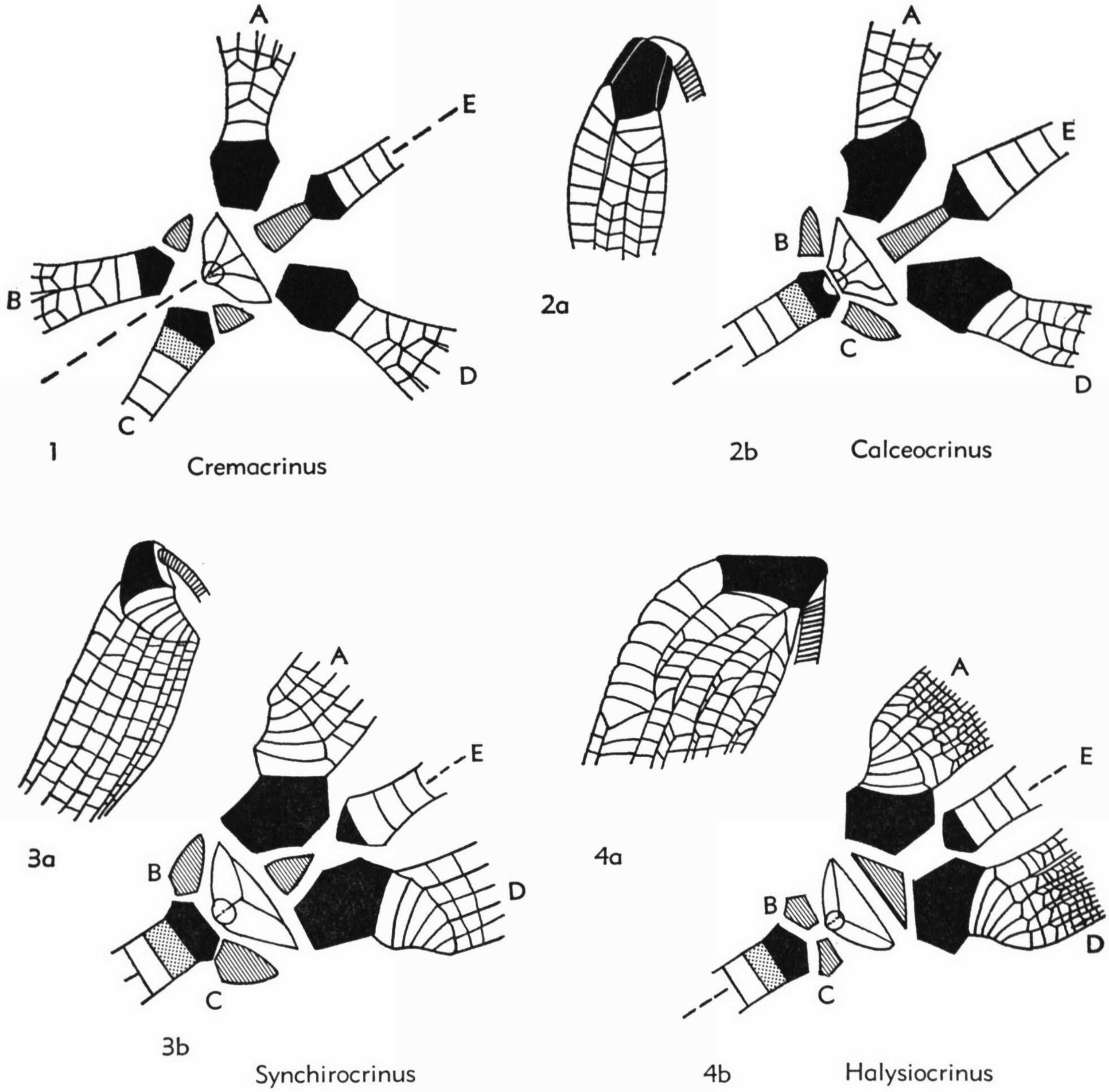


Figure 3. Diagrams illustrating bilateral symmetry of calceocrinid genera: *1, Cremacrinus,* M.Ord.-M.Sil.; *2a,b, Calceocrinus,* M.Ord.-U.Sil.; *3a,b, Synchirocrinus,* L.Sil.-M.Dev.; *4a,b, Halysiocrinus,* M.Dev.-L.Miss. The plane of this bilateral symmetry is not the so-called crinoidal plane, through the anterior (A) ray and posterior (CD) interray, but coincides with the left anterior (E) ray and mid-line of the postero-right (BC) interray. The plane of symmetry is perpendicular to the hinge-line separating the basal circlet from radials of the A-, D-, and E-rays. In *Cremacrinus,* which has four arm-bearing radials, symmetry is almost but not quite complete, whereas in the other genera illustrated it is perfectly developed, with structures on opposite sides of the median plane mirror-image duplicates of one another. (Explanation: superradials and undivided radials, solid black; inferradials, ruled; proximal plate of anal tube, designated as anal X, stippled; other parts without pattern.) (Modified from Moore in Moore, Lalicker, & Fischer, 1952.)

surveying the comparative morphology of the group, he concluded that four distinct stages in evolutionary progression, each definable as a genus, were adequate for classification of all known species. These genera, in order of advancement from most primitive to most highly specialized, according to SPRINGER, are *Cremacrinus, Eucheirocrinus, Calceocrinus,* and *Halysiocrinus.* He described and illustrated 10 new species, but most useful are the numerous excellent figures of various already-known forms which previously had been very inadequately illustrated.

SCHMIDT (1934) added a strange new genus to the Calceocrinidae when he described and figured *Senariocrinus* from Lower Devonian rocks of Germany. He speculated on its mode of life, arriving at the conclusion that probably it was a free-swimming pelagic crinoid. BASSLER (1938) and BASSLER & MOODEY (1943) published taxonomic lists and bibliographic data of much value on Paleozoic crinoids, including the Calceocrinidae. Considered to be valid members of this family, the following genera were recorded: *Calceocrinus, Cremacrinus, Deltacrinus, Eucheirocrinus, Halysiocrinus, and Senariocrinus.* MOORE & LAUDON (1943, 1944) accepted these genera as members of the family, illustrated morphological features, and described them briefly.

MOORE (1952) and UBAGHS (1953) in paleontological textbooks discussed the calceocrinids from the standpoint of their specialized evolution, stressing the remarkable bilateral symmetry developed in a plane other than the prevalent plane of crinoid symmetry in anteroposterior position.

RAMSBOTTOM (1952) undertook to restudy the calceocrinids of the important Wenlockian deposits near Dudley, England, and as a result of his work three ill-known species of *Calceocrinus* introduced by SALTER (1873) were put on firm ground for recognition. Also, he described a new species referred to this genus and added discussion of SPRINGER'S *Eucheirocrinus anglicus.* In 1960, RAMSBOTTOM (p. 8) published excellent illustrations of two Upper Ordovician species of a new calceocrinid genus that resembles *Cremacrinus* in having four arm-bearing radials. This genus, named *Anulocrinus,* was reported to be characterized by completely isotomous branching of the arms, whereas it is demonstrated in the present paper that branching of the lateral rays is actually heterotomous and accords with the all-but-universal pattern of arm branching observed in calceocrinids.

ACKNOWLEDGMENTS

Assistance in preparing some of the drawings reproduced in this article has been given by ROGER B. WILLIAMS, a member of my staff who works on illustrations needed for the *Treatise on Invertebrate Paleontology.* Also, J. S. VAN SANT and DORIS E. N. ZELLER aided in organizing the list of references. Financial support toward publication is acknowledged to the United States National Science Foundation, which has made a grant for the purpose of accelerating completion of the *Treatise.*

MORPHOLOGICAL FEATURES

DESIGNATION OF RAYS

Before proceeding with description and discussion of various calceocrinid genera, it is needful to explain the method of designating ray and interray elements of crinoids which has been adopted for use in the *Treatise* and which is employed in this paper. As illustrated in Figure 4, capital letters (A to E) are assigned to the rays, beginning with A for the ray (anterior) opposite the interray (posterior) that contains the anal plate(s) or anal opening (or both). In ventral (tegminal) view, other rays then are indicated by B, C, D, and E, proceeding in clockwise direction; in dorsal (aboral) view, the order of sequence is counter-clockwise. Any interray is readily defined in terms of its bordering rays, as AB, BC, etc. This is the system of designation introduced by CARPENTER (1884). It is favored on the grounds of clarity, convenience, and brevity, especially in referring to interray portions of the crinoid skeleton, although equivalent directional designations (e.g., right posterior, left anterior, etc.) are also used to some extent in descriptions and discussions. In illustrations, it is preferable to place the anterior (A) ray upward uniformly (not downward in dorsal views, as oriented by some authors for the purpose of having left and right sides of the crinoid in positions corresponding to those of the viewer).

DORSAL CUP

Distinctive characters of the dorsal cup of calceocrinids are seen in the number, shapes, and arrangement of basal plates, relation of the facet for attachment of the stem to these plates, and structures of the radial circlet. In addition, the nature of rectilinear hingement between the asymmetrically disposed basals and the higher part of the cup composed of radials is unique among crinoids. The anal tube and pattern of arm structures also call for notice. To some extent, terminology differing from that suited to other crinoids is helpful for purposes of description and for bringing out in simplest, clearest manner the highly significant features of ray structure that, with modifications important for generic diagnoses, are common to all calceocrinids.

The basal "circlet" of most calceocrinids is a firmly joined group of four or three plates that together form a triangle with wide, straight or nearly straight base along the hinge and with stem facet covering all or part of the apex (Fig. 5). In one genus (*Senariocrinus,* Dev.) the basals seem to be fused into a single triangular plate. The homologies of individual plates with the basals of other crinoids are by no means determinable at a glance, and how to designate them has offered problems. The two median plates have been termed left posterior and left anterior (or when fused together as left basal), others being designated as posterior and right anterior; except posterior, these are confusing terms because in monocyclic crinoids basal plates are interradial—not radial—in position. Letter designations employed in the CARPENTER system are preferable. Figure 6 illustrates inferred steps in evolution of calceocrinid cup plates, including basals, from a homocrinid ancestral form to *Cremacrinus.* This depicts diminution and ultimate suppression of the BC-basal, located in the plane of bilateral symmetry opposite the E-ray, and it shows rotation of the other basals into symmetrical positions touching the long straight hinge. The pair of small median basals observed in *Cremacrinus* consist of DE and EA, and the laterally disposed pair prove to be CD and AB.

Undivided radials, which belong to the A- and D-rays, occur on opposite sides of the crown and support the main arm structures, accenting bilateral symmetry of the crown (Figs. 3, 6). The median radial (in the E-ray) is compound, as are radials of B- and C-rays adjacent to the anal tube and stem. The shapes of the infer- and superradials and the nature of their contacts (or separation of these elements which may be seen in the median radial), and fusion of superradials in the B- and C-radials of all calceocrinid genera except *Cremacrinus* and *Senariocrinus* are morphological variations that have generic value.

Divided radials occur in three rays (B, C, and E) and thus the radial circlet as a whole has the basic pattern of the Homocrinidae (Fig. 4). Among calceocrinids this is most clearly defined in *Cremacrinus;* it is somewhat modified in other genera. The infer- and superradial of the E-ray are well marked in all calceocrinids, touching one another widely *(Chiropinna)* to narrowly *(Calceocrinus, Cremacrinus, Anulocrinus, Chirocrinus, Synchirocrinus, Senariocrinus)* or separated slightly *(Calceocrinus, Chirocrinus, Synchirocrinus)* to strongly *(Deltacrinus, Senariocrinus, Halysiocrinus)* (Fig. 5). In some genera the length of the inferradial-superradial suture, if present, varies appreciably among species or even among individuals, and in a few species variations range from a clearly developed contact to moderate separation of these radial elements. Wide separation of the E-ray infer- and superradial plates by interposition of the lateral radials is a constant character in *Deltacrinus* and *Halysiocrinus,* and therefore, in combination with other features, has diagnostic generic value. The length (height) of the E-inferradial may greatly exceed that of the superradial or conversely may be

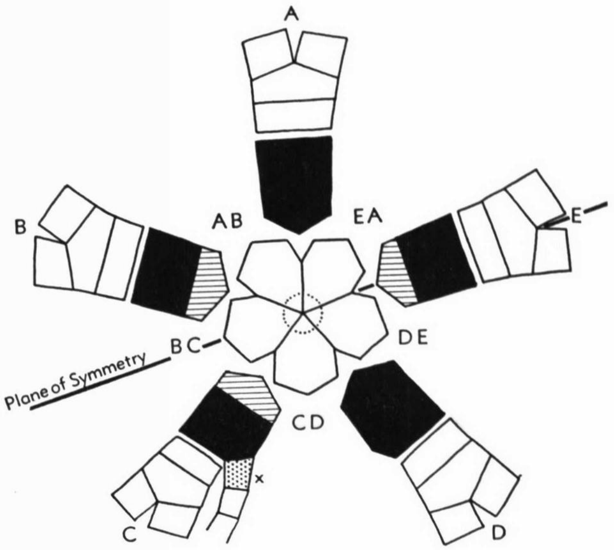


FIGURE 4. Structure of dorsal cup and proximal parts of arms and anal tube of *Ectenocrinus* (Ord.), a typical genus of the Homocrinidae, showing positions of the two undivided radials and three compound radials. Designations of the rays and interrays by capital letters of the Carpenter system are indicated, the anterior (A) ray being directed upward so that the conventional left and right sides of the crinoid are opposite to those of a viewer. Very noteworthy is placement of the anal tube as an armlike appendage borne by the right posterior (C) superradial. The structure of *Ectenocrinus* is identical to that of calceocrinid genera except for shapes and number of basal plates and shapes and lateral contacts of radial plates. (Explanation: superradials and undivided radials, solid black; inferradials, ruled, proximal plate of anal tube, designated as anal X, stippled; other parts without pattern.)

smaller, and not uncommonly lengths of the two plates are observed to be subequal. The ratios of length to width determined for each plate are fairly constant within a given species or genus, but they commonly differ materially for infer- and superradials of an individual form both in degree and sign—that is, length may considerably exceed width or be smaller than width. The characters discussed seem to have a low order of taxonomic value, despite their use for differentiation of some genera and species and notwithstanding effort to employ them as marks of evolutionary changes.

Broad contact between the lower and upper parts of a compound radial can be accepted as a primitive character, because it is universal in oldest crinoids having such radials (e.g., Homocrinidae, Heterocrinidae, Anomalocrinidae), among which the antecedents of calceocrinid radial structures must belong. It fol-

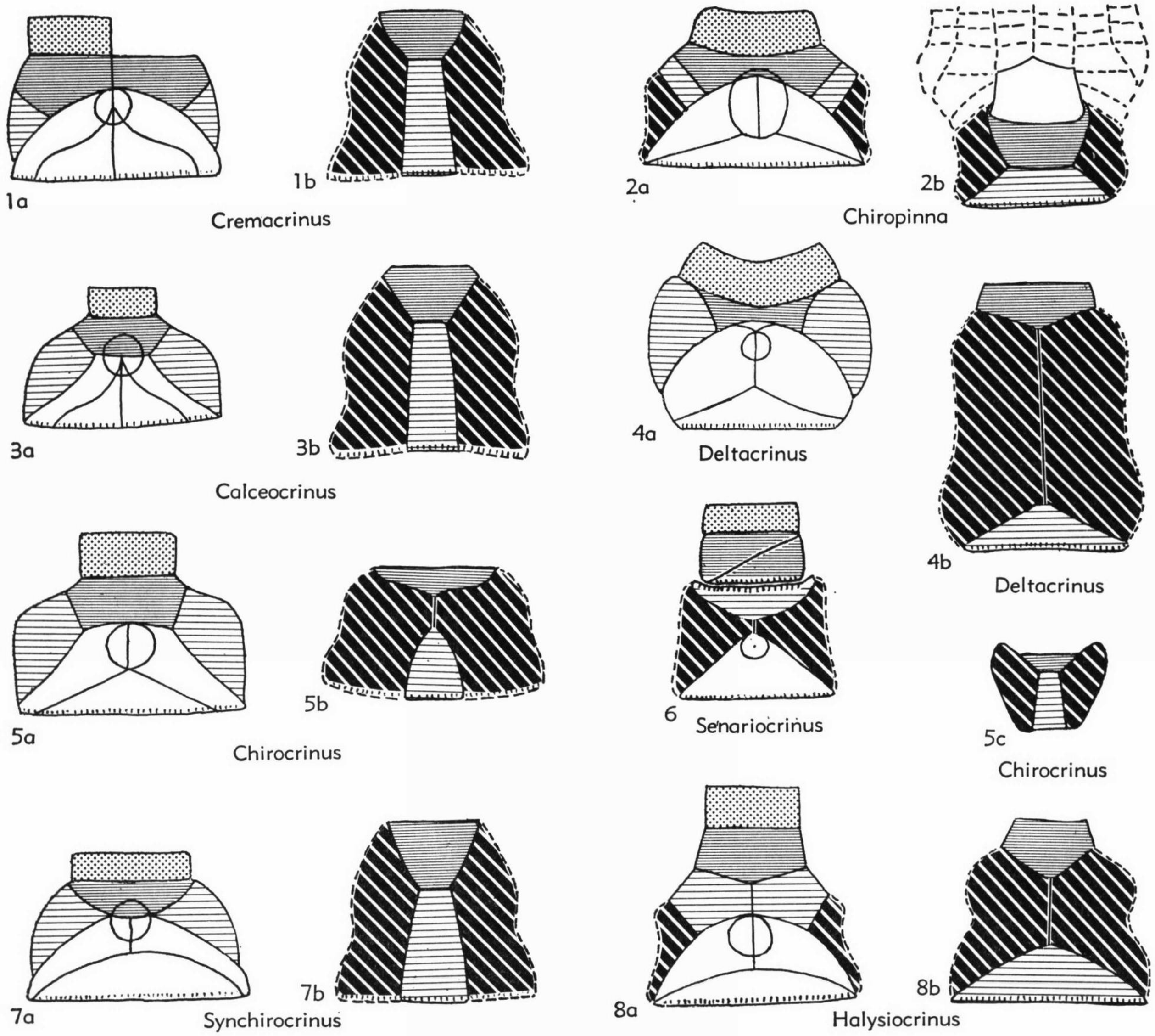


FIGURE 5. Structure of dorsal cup and placement of anal X in calceocrinid genera. The features illustrated, in conjunction with characters of the arms, furnish the basis for generic distinctions. The drawings are diagrammatic, mostly based on type-species of each genus; the small figure showing the left anterior side of the cup of *Chirocrinus* (at right of *Senariocrinus*) represents *C. fletcheri*. (Explanation: A- and D-radials, which are undivided, obliquely ruled; inferradials, wide-spaced horizontally ruled; superradials, close-spaced horizontally ruled; anal X, stippled; other plates without pattern.)

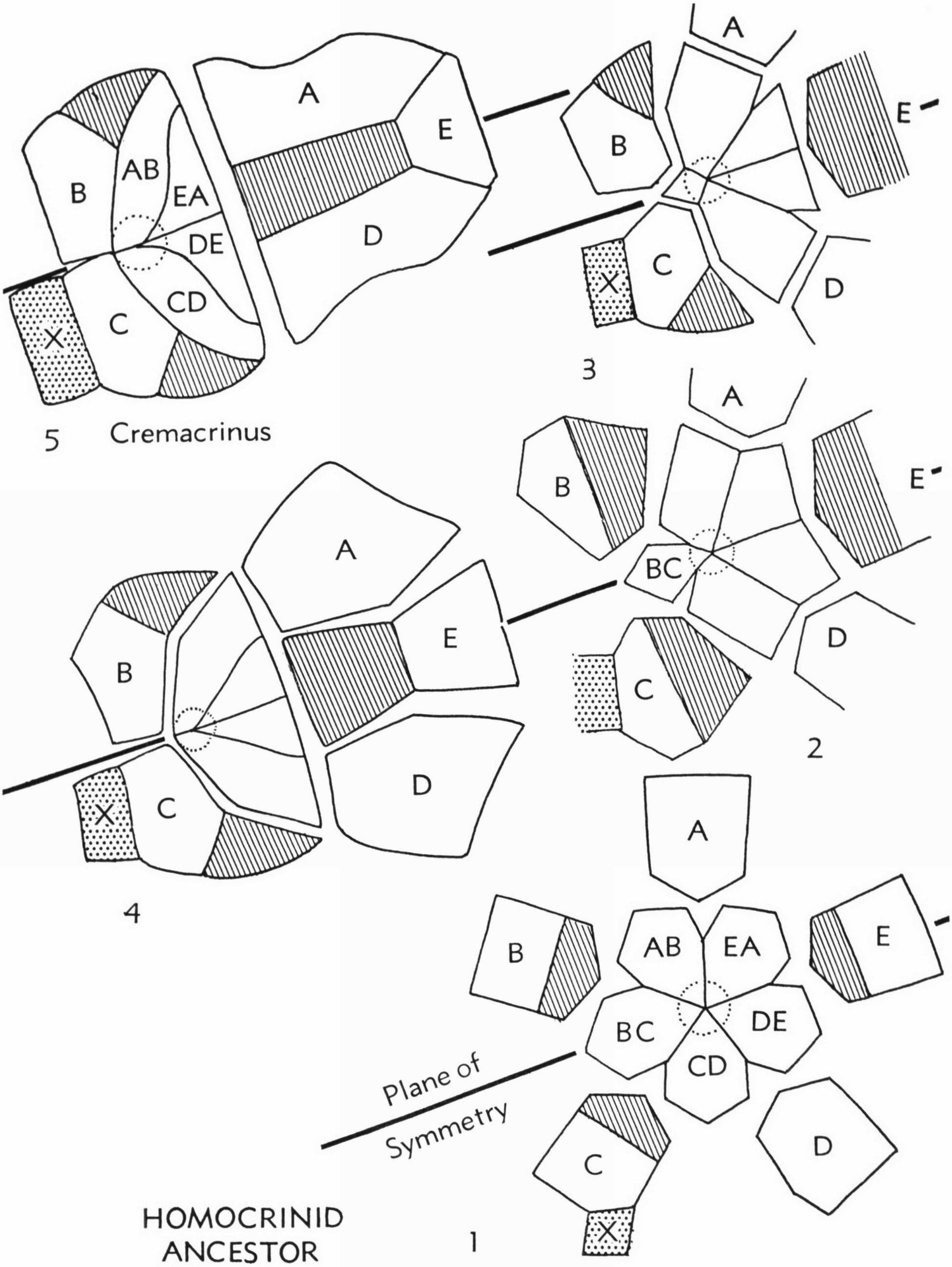


FIGURE 6. Inferred structural changes of dorsal cup in derivation of a primitive calceocrinid *(5, Cremacrinus)* from its postulated homocrinid ancestor *(1)*. Successive intermediate stages are suggested in *2-4*. Elements are correspondingly lettered in each figure as an aid to observation of homologies; inferradials ruled, anal **X** stippled.

lows that a narrowing and ultimately a disappearance of contact between infer- and superradials are doubtless interpreted correctly as signs of evolutionary progression away from ancestral conditions. If this is accepted, the E-radial elements of *Chiropinna* represent the least advanced observed stage in evolution of this ray among all calceocrinid genera, in contrast to *Deltacrinus, Halysiocrinus,* and some individuals of *Senariocrinus,* which represent the greatest advance (Fig. 5). Subsequent discussion indicates that no such single feature is a trustworthy guide for interpreting the evolutionary status of a given genus or species.

Cremacrinus differs from all other calceocrinids except *Senariocrinus* in having separate superradials above the inferradials of the B- and C-rays (Fig. 5). These superradials adjoin each other laterally, whereas the inferradials are separated by intervening plates of the basal circlet. The arrangement of these four plates (infer- and superradial of B-ray and infer- and superradial of C-ray) is identical to that in *Homocrinus, Ectenocrinus,* and other homocrinid, anamesocrinid, and haplocrinitid genera except for lack of lateral contact between the inferradials in *Cremacrinus.* The B- and C-superradials of *Senariocrinus* are separate plates which laterally adjoin each other along an obliquely disposed suture and in wholly unique manner they lie with movable hingement on a broadly triangular plate that seemingly consists of the B- and C-inferradials solidly fused together (Fig. 5).

In calceocrinid genera other than *Cremacrinus* and *Senariocrinus* the inferradials of the B- and C-rays occur obliquely beneath a transversely extended single plate located in the E-BC plane of bilateral symmetry slightly above the stem impression. Evidently, this plate is the product of lateral fusing together of the B- and C-superradials; it was called the T-piece by Bather (1893, p. 62, 65) and the subanal plate by Springer (1926, p. 89), Moore & Laudon (1944, p. 145) and Ramsbottom (1952, p. 35). It was interpreted as a superradial by Moore & Laudon (1943, p. 27). Because of its unquestioned status as an element of the radial circlet, the plate is better designated as the posterior or BC-superradial. The fact that it supports

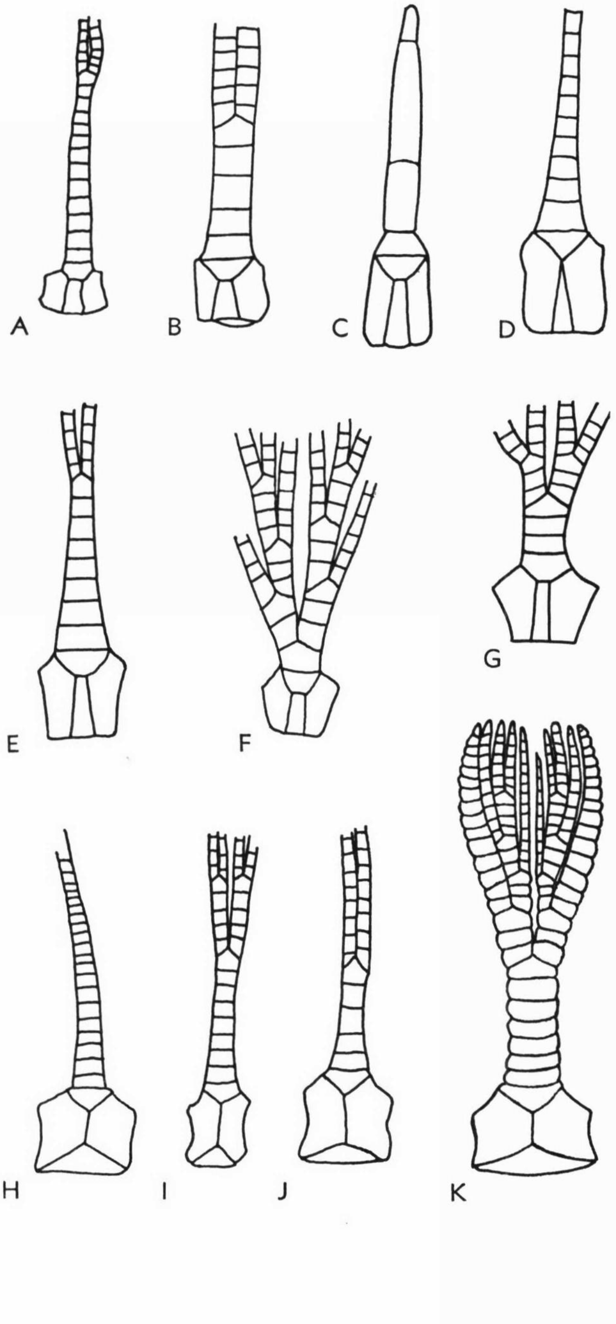


Figure 7. Left anterior views of dorsal cup and arm structure of E-ray in various calceocrinid species (not to scale).—*A. Cremacrinus kentuckiensis* (M.Ord.), isotomous branching on IBr$_{13}$.—*B. Chirocrinus incertus* (L.Sil.), isotomous branching on IBr$_{5}$.—*C. Calceocrinus minor* (M.Sil.), arm unbranched.—*D. Calceocrinus barrandei* (M.Ord.), arm unbranched.—*E. Calceocrinus chrysalis* (M.Sil.), isotomous branching on IBr$_{8}$.—*F. Calceocrinus anglicus* (M.Sil.), isotomous branching on IBr$_{1}$ followed by heterotomous branching in at least three higher positions.—*G. Calceocrinus ontario* (L.Sil.), isotomous branching on IBr$_{3}$, higher branching seemingly isotomous but probably heterotomous.—*H. Halysiocrinus elephantinus* (M.Dev.), arm unbranched.—*I. Halysiocrinus dactylus* (L.Miss.), isotomous branching on IBr$_{8}$, higher branching apparently isotomous but may be heterotomous.—*J. Halysiocrinus bradleyi* (L.Miss.), isotomous branching on IBr$_{5}$.—*K. Halysiocrinus nodosus* (L.Miss.), isotomous branching on IBr$_{7}$ followed by heterotomous branching in at least four higher positions.

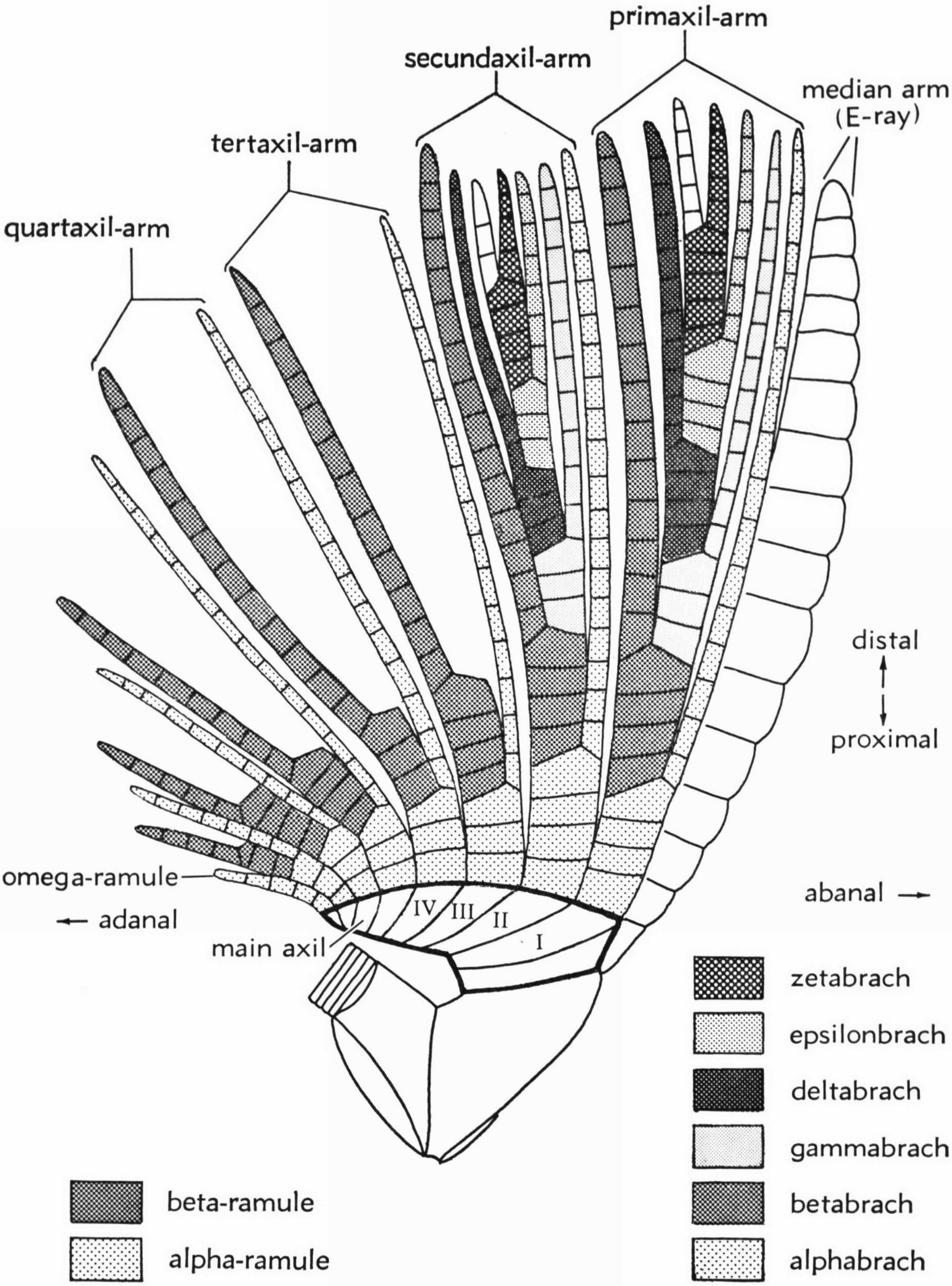


FIGURE 8. Arrangement of plates in main-axil series and structural pattern of axil-arms with their ramules given off from opposite sides at various levels. The plan illustrated appears to be invariable throughout all genera and species of the Calceocrinidae (except *Senariocrinus* and *Chiropinna*), although varying a great deal in perfection of its development. The nomenclature adopted for designation of individual elements is indicated and the identity of branching in each axil-arm is emphasized by patterns.

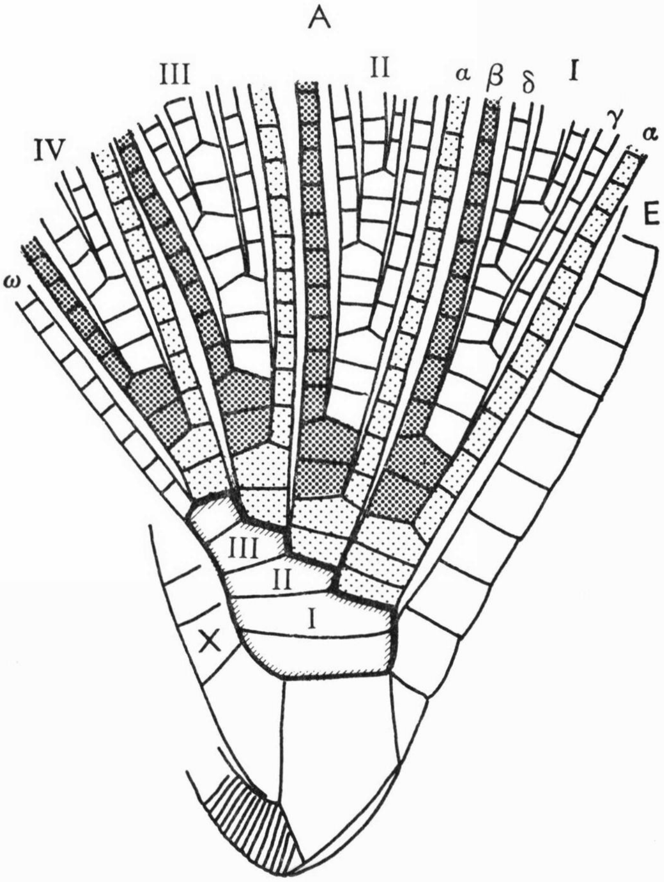


FIGURE 9. Anterior side of *Chirocrinus gotlandicus* (M. Sil.), type-species of the genus. The main-axil series is accented and alphabrachs with alpha-ramules and beta-brachs with beta-ramules are distinguished by patterns like those given in Figure 8.

a stout anal tube formed of uniserially arranged plates, instead of an arm, is an important but incidental feature. The proximal tube plate, next above the posterior superradial, is anal X.

The inferradial of the C-ray in calceocrinid genera has been considered by BATHER (1893, p. 61; 1900, p. 148) to be a radianal, which normally is an extra plate at the proximal extremity of the C-ray unmatched by similar extra plates in other rays. MOORE & LAUDON (1943, p. 27) classed this plate as an inferradianal. Primitively, in some cladid inadunates and flexible crinoids, the radianal may occur directly below the C-radial, with little or no left-lateral offset from it; generally, however, the radianal occurs obliquely leftward beneath the radial and in evolution tends to migrate upward to a position between the C- and D-radials, ultimately moving even above them out of the cup or becoming resorbed. It is true that the inferradial of the C-ray in calceocrinids occupies the position of a primitive radianal, but in my opinion the fact that it differs in no way from other inferradials and shows no tendency toward a special kind of evolutionary modification of the sort seen in typical radianals warrants rejection of designating it as a radianal or inferradianal. If this judgment is accepted, the occurrence of radianals as an element of dorsal-cup structure is limited to the Hybocrinida and Cladida, among inadunate crinoids, and to the Flexibilia. Seemingly, this may have significance in study of phylogenetic relationships of main groups of the Crinoidea.

ANAL TUBE

The anal tube of calceocrinids, as in homocrinids and numerous other inadunates, is an elongate, segmented, armlike structure that undoubtedly represents an evolutionary modification of an arm branch of the C-ray (Fig. 6,*1,4*). Not only is the tube similar to an undivided arm in appearance, but all morphologic evidence points to its antecedent true arm-branch nature. It extends upward to the summit of the crown, being equal in length to the arms or even exceeding them slightly. The uniserially arranged plates of the tube are massive and crescentic in shape transversely, the hollowed side facing ventrally inward; they closely resemble brachials except for their larger size and greater width of the ventral furrow, which in exceptionally well-preserved specimens is seen to be enclosed by a saclike covering of small, irregularly arranged plates.

Among calceocrinid genera the anal tube is the sole appendage borne by the radial plate to which it is joined. In *Cremacrinus* and *Senariocrinus* this is the superradial of the C-ray (Fig. 5), but in all other genera it is a fused superradial formed by lateral union of the B- and C-superradials, designated by most authors as the subanal plate.

ARM STRUCTURES

The median arm (borne by the E-superradial) may be undivided—the most common condition—or it may bifurcate one or more times and the branching of this ray, whenever present, is initially isotomous but subsequent divisions tend to be heterotomous (Fig. 7).

The arms of the lateral rays are invariably multiple. In each such ray of a typical calceocrinid (e.g., *Halysiocrinus*, Figs. 1, 8) a proximal group of brachials, mostly axillaries, is more or less clearly differentiated as the so-called **main-axil**. Arms (including their branches) articulating with main-axil brachials are termed **axil-arms.** The axil-arm borne by the axillary primibrach is the **primaxil-arm**, that supported by the axillary secundibrach is the **secundaxil-arm,** and so on. Normally, each second, third, or fourth brachial of an axil-arm is an axillary plate. Brachials of the first (lowest) axil series of any axil-arm are known as **alphabrachs**, those of the next series, as **betabrachs**, of the third as **gammabrachs**, and so on. The axillary alphabrach of each axil-arm invariably carries an unbranched ramule on its abanal side, this ramule being distinguished as the **alpha-ramule**, therefore. The axillary betabrach bears the **beta-ramule** on its adanal side and the gammabrach series gives rise to the **gamma-ramule** on its abanal facet. In this manner heterotomous branching extends throughout the axil-arm, with the gamma-ramule on the abanal side, delta-ramule on the adanal side, and so on (Fig. 8).

The terminal (adanal) axillary plate of each main-axil carries a branching axil-arm on its abanal side and an unbranched ramule on its adanal side. This arrangement seems to constitute an exception to the rule, but actually is not, because the adanally directed ramule is borne by a plate of the main-axil, rather than an axil-arm. Also, this ramule (for convenience designated as the **omega-ramule**) is interpretable ontogenetically as a continuation of the main-axil series in the position of a not-yet-developed additional axillary and axil-arm.

The classification and mode of designating lateral arm elements just described are based on BATHER'S

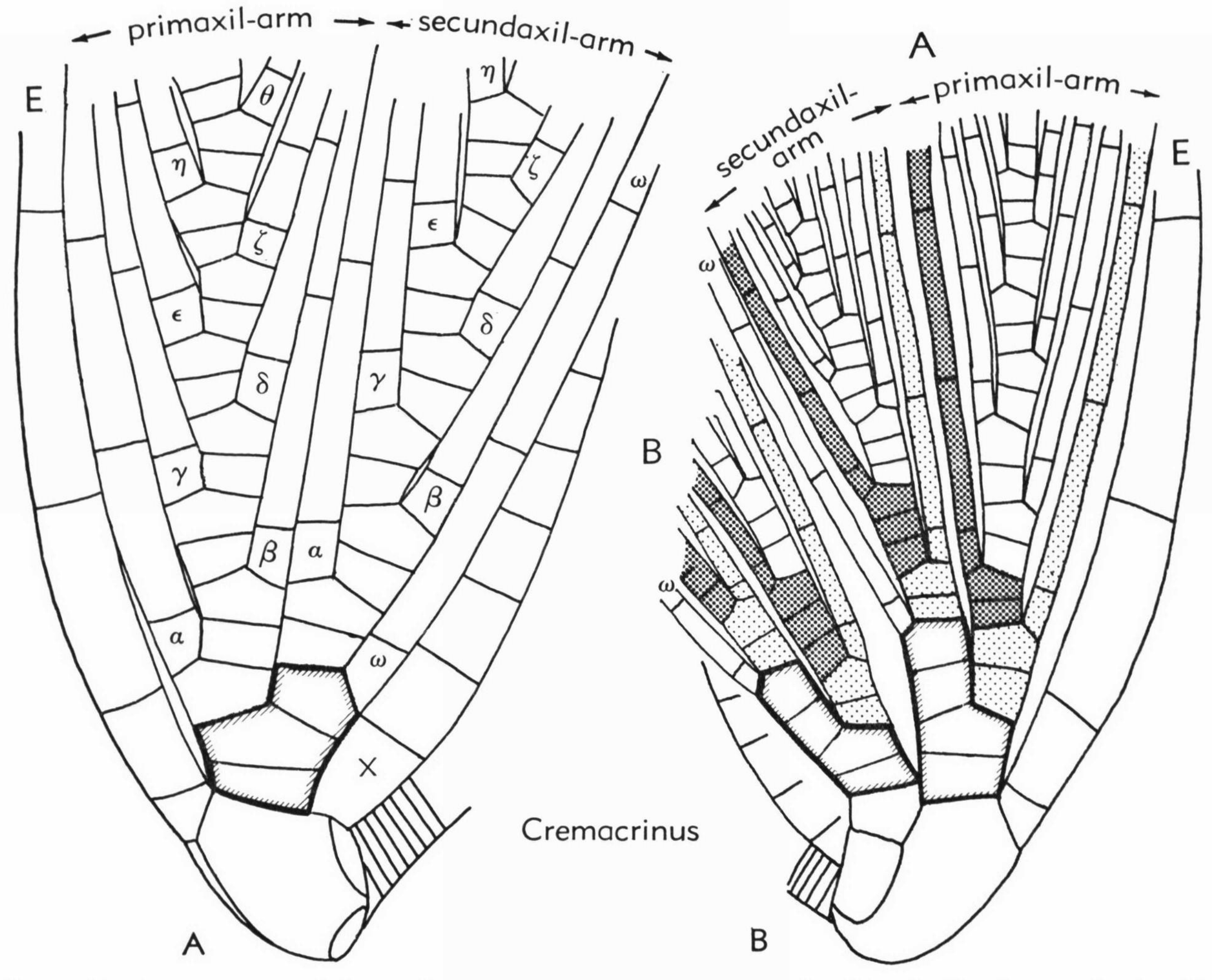


FIGURE 10. Arm structures of *Cremacrinus tubuliferus* (M.Sil.), left posterior (D-ray) side of crown in *A,* with anal tube at right, opposite (A- and B-rays) side in *B.* Limits of the main-axil series are accented and patterns for alphabrachs, alpha-ramules, betabrachs, and beta-ramules corresponding to those given in Figure 8 are shown in *B.* The ramules are identified by Greek letters in *A.*

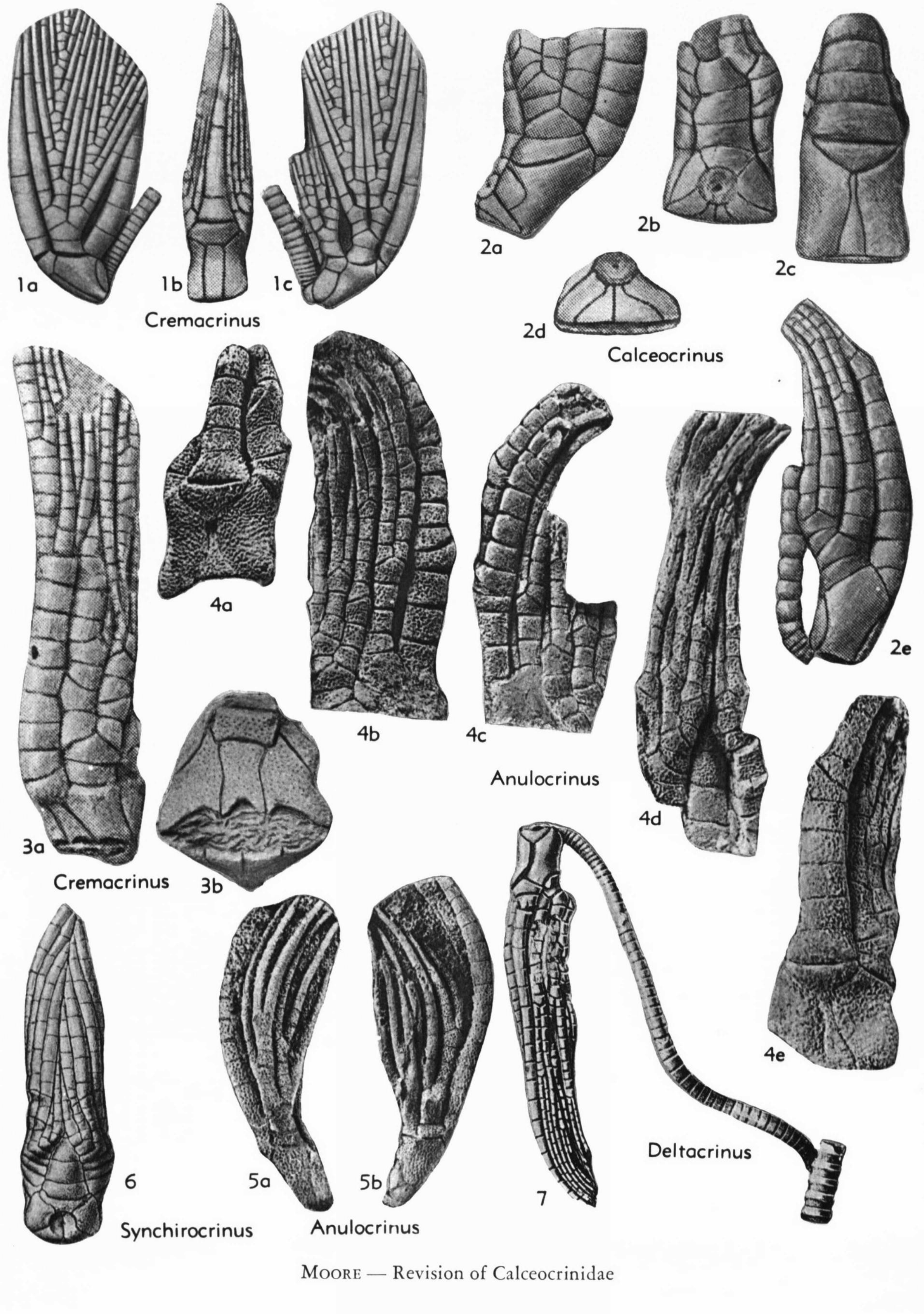
(1893) study of Gotland calceocrinids, especially *Chirocrinus gotlandicus* (Fig. 9) and species now assigned to *Synchirocrinus,* but designations for the ramules (e.g., alpha-ramule, beta-ramule, gamma-ramule) are added to his terminology. Examination of Figure 8, in which the brachials and ramules of the axil-arms classified according to Greek-letter designations are distinguished by various patterns, should make clear the utility of Bather's system of nomenclature for analysis and description of calceocrinid species. It may be noted that the primaxil-arm alphabrachs are actually secundibrachs (IIBrr), whereas the secundaxil-arm alphabrachs are tertibrachs (IIIBrr), and the tertaxil-arm alphabrachs are quartibrachs (IVBrr). The alpha-ramules of any axil-arm are invariably located on the abanal side of the axil-arm. The omega-ramule, borne by the axillary plate at the adanal extremity of the main-axil (VIIIBr in Fig. 8), is invariably directed adanally.

Among little-advanced Ordovician calceocrinids (e.g., *Cremacrinus, Calceocrinus, Anulocrinus*) branching of the proximal parts of the lateral rays just above the large radials is isotomous or nearly so, and therefore the arrangement of axillary primibrachs, secundibrachs, and in some species tertibrachs and quartibrachs, offers little or no suggestion of a main-axil series (Figs. 10-14). Only by recognition of homologous elements based on comparison with genera having well-developed main-axils (e.g., *Chirocrinus, Synchirocrinus, Halysiocrinus, Chiropinna*) can the beginning of a main-axil pattern be discerned (Figs. 9, 15, 16). *Deltacrinus* has a definite but ill-developed main-axil series (Fig. 17). Heterotomy may be strikingly prominent in most of the axil-arms (e.g., *Cre-*

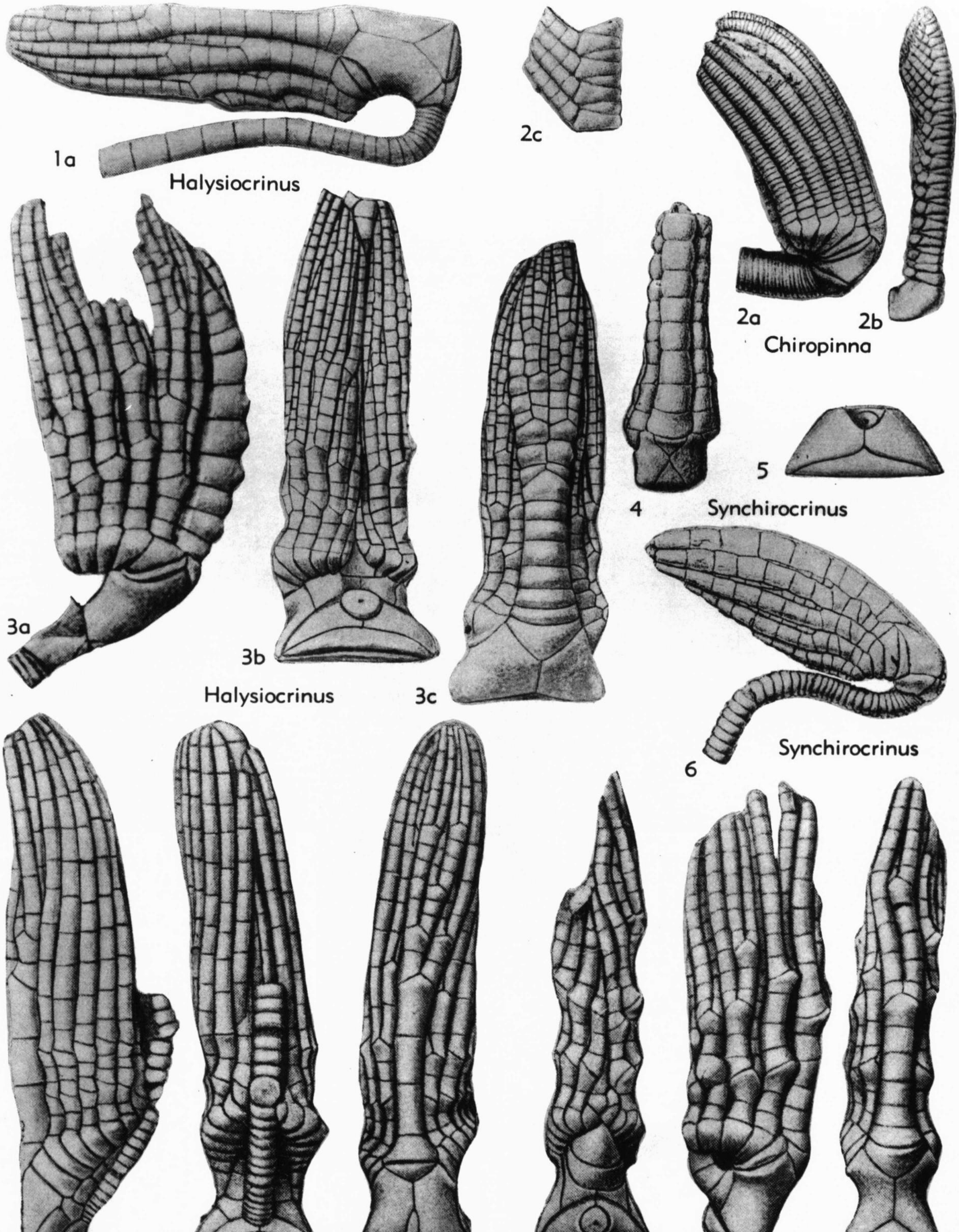
EXPLANATION OF PLATE 1

Figure Page

1. *Cremacrinus tubuliferus* Springer, Middle Silurian, Beech River Formation, Decatur County, Tennessee; *1a,c,* lateral views of lectotype (U.S.N.M., no. S2159a), herein designated, from D- and A+B-ray sides, showing unbranched E-arm in profile, stout anal tube parallel to stem, ×2.5; *1b,* median view of paralectotype (U.S.N.M., no. S2159b) showing tall, narrow inferradial and short, wide superradial of E-ray, flanked by parts of large, undivided lateral radials, ×2.5 (all after Springer, 1926).... 20
2. *Calceocrinus chrysalis* (Hall), Middle Silurian, Rochester Shale, Niagara Group, New York; *2a,* lateral view of A-ray side, showing very robust E-arm at right and profile of anal tube at left, B-arm vanished, ×2.5; *2b,* posterior view showing placement of stem impression impinging on basals and radial plates of cup, ×2.5; *2c,* median (E-ray) view of dorsal cup and proximal part of E-arm, ×2.5; *2d,* basal circlet with stem impression, ×2.5; *2e,* crown (U.S.N.M., no. S2165) from anterior (A-ray) side (holotype of *Proclivocrinus radiculus* Ringueberg, type-species of this genus), ×2.5 (all after Springer, 1926) 18
3. *Cremacrinus punctatus* Ulrich, Middle Ordovician, Decorah Shale (Blackriveran), Minneapolis, Minnesota; *3a,* crown (holotype, U.S.N.M., no. 89879) from left posterior (D-ray) side, showing E-arm at left, ×2.5; *3b,* dorsal cup of another specimen (U.S.N.M., no. S2156) from hinge side, with numerous small "supplementary" plates in space between denticulate margins of hinge area, ×2.5 (both after Springer, 1926) 20
4. *Anulocrinus thraivensis* Ramsbottom, Upper Ordovician, Ashgillian, near Girvan, Scotland; *4a,e,* two paratypes from left anterior (E-ray) side, showing characters of radial circlet and proximal part of stout median E-arm, ×3.5; *4b,c,* holotype from A- and D-ray sides, with median (E) arm at right margin in *4b* and at extreme left in *4c,* ×3.5; *4d,* a paratype from right posterior side, showing part of anal tube and adanal parts of D-arms at left and B-arms at right, ×3.5 (all after Ramsbottom, 1961) 21
5. *Anulocrinus drummuckensis* Ramsbottom, Upper Ordovician, Ashgillian, near Girvan, Scotland; *5a,b,* holotype from left posterior (D) and anterior sides, latter showing E-arm at right, A-arms in middle, and B-arms at left, ×3.5 (after Ramsbottom, 1961) 21
6. *Synchirocrinus tenax* (Bather), Middle Silurian, Wenlockian, Gotland, Sweden; posterior view of crown, showing large stem impression located almost entirely on lateral basals (AB, CD) but barely impinging on median basal (DE+EA) below and fused BC-superradial above, large C- and B-inferradials at left and right of stem impression, anal-X broadest and shortest plate of anal tube, which is bordered by curved adanal parts of main-axil series terminating in axillary that bears axil-arm with stout beta-ramule on abanal side and omega-ramule on adanal side, ×2 (after Bather, 1893) 27
7. *Deltacrinus clarus* (Hall), Middle Devonian, Hamilton, New York; holotype specimen of type-species of genus, showing widely separated E-ray infer- and superradial, relatively stout and unbranched median arm, ill-defined main-axil of anterior (A) ray obliquely at right from dorsal cup, and small number of axil-arms with long ramules, ×1.3 (after Goldring, 1923) 27



MOORE — Revision of Calceocrinidae


1a
Halysiocrinus
2c
2a
2b
Chiropinna
3a
3b
Halysiocrinus
3c
4
5
Synchirocrinus
6
Synchirocrinus
7a
7b
Synchirocrinus
7c
1b
1c
1d
Halysiocrinus

macrinus tubuliferus, Fig. 10) or in varying degree obscure (e.g., *Calceocrinus,* Fig. 11; *Anulocrinus,* Figs. 12-14). Heterotomous branching expressed by the development of ramules is found in all calceocrinids except *Senariocrinus,* in which the axil-arms are undivided, and *Chiropinna,* which bears abundant pinnules. The manner in which basic features of the pattern of heterotomy remain unchanged from genus to genus in the Calceocrinidae is not indicated in descriptive discussions published by Ulrich (1886), Ringueberg (1889), Bather (1893), or Ramsbottom (1952), but in spite of conditions that obscure it in some forms (notably species assigned to *Synchirocrinus*), Springer (1926) recognized it clearly, though he failed to emphasize it.

The new genus here named *Chiropinna* (Fig. 18) calls for special notice, because one might assert that the arms supported by its lateral radials do not branch at all, thus differing radically from all other calceocrinids. Such an assertion is true, if the numerous branchlets on each side of the axil-arms are classified as pinnules, but not true if the branchlets are defined as ramules on the basis of their homology with the ramules of other calceocrinid genera. To classify the branchlets as ramules and all brachials of the axil-arms as axillaries is specious, (1) because the whole axil-arm structure precisely corresponds to that of a normal uniserial pinnulate arm, as seen in *Decadocrinus* and many other inadunates, and (2) because the

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EXPLANATION OF PLATE 2

Figure Page

1. *Halysiocrinus dactylus* (Hall), Lower Mississippian, Osagian, upper part of Burlington Limestone, Burlington, Iowa; *1a,* holotype specimen (Harvard Mus. Comp. Zool.) of type-species of genus, showing nature of stem, dorsal cup, and arms, median (E-ray) arm at top and axil-arms of A-ray below, ×2; *1b-d,* posterior, anterior, and E-ray sides of another nearly complete crown (U.S.N.M., no. S2193), alpha-ramule of secundaxil-arm visible in *1c* but not in other axil-arms, ×2 (all after Springer, 1926) 31
2. *Chiropinna pinnulata* (Bather), Middle Silurian, Wenlockian, Gotland, Sweden; *2a,* holotype specimen of type-species of *Chiropinna* Moore, n. gen., showing unusually thick stem composed of thin columnals, well-developed main-axil series of A-ray, and its accompanying five axil-arms in adjoined parallel position with no pinnules visible, E-ray arms in profile at right and anal tube at left of crown, ×1.3; *2b,* side view of single axil-arm of anterior ray, showing stout pinnules borne by successive brachials in alternation on opposite sides, double row of these pinnules with food grooves on inner (ventral) sides visible near distal extremity of axil-arm, ×2; *2c,* detail of axil-arm with pinnules, emphasizing cuneate nature of brachials, which are thickest at pinnule sockets, ×4 (all after Bather, 1893) 28
3. *Halysiocrinus nodosus* (Hall), Lower Mississippian, Osagian, Borden Group (Keokuk), Indian Creek, near Crawfordsville, Indiana; *3a,* nearly complete crown (U.S.N.M., no. S2203) from anterior side, showing maximum close apposition of dorsal-cup plates along hinge (seen in edge view on lower side of cup not far from stem) and wide gape on adanal side of cup, median arm (at right) being brought almost into line with stem by this rotation along hinge, ×2; *3b,c,* posterior and left anterior (E-ray) views of another crown (U.S.N.M., no. S2203), showing basal circlet rotated to position tightly against posterior (B+C) inferradials (visible in adjoined location just above proximal columnal of stem in *3b*), and in *3c* showing heterotomous branching of E-ray arms above the isotomous division on axillary IBr_7, ×1.3 (all after Springer, 1926) 31
4. *Synchirocrinus nitidus* (Bather), Middle Silurian, Wenlockian, Gotland, Sweden; left anterior (E-ray) view of incomplete crown, ×2 (after Bather, 1893) 27
5. *Synchirocrinus? halli* (Ringueberg), Middle Silurian, Niagaran, Rochester Shale, New York; holotype specimen of species erroneously considered by some authors to be type-species of *Calceocrinus,* basal circlet showing broad, low median basal (DE+EA), which forms one margin of hinge, ×1.3 (after Springer, 1926) 27
6. *Synchirocrinus tucanus* (Bather), Middle Silurian, Wenlockian, Gotland, Sweden; view of crown and attached stem seen from anterior side with unbranched E-arm in profile at top, alpha-ramules of axil-arms invisible, ramule-like branches of axil-arms seen on abanal side of each actually consisting of heterotomous main "stem" of axil-arm, whereas prominent unbranched parts of arms are very robust beta-ramules, ×2 (after Bather, 1893) 27
7. *Synchirocrinus bifurcatus* (Springer), Middle Silurian, Beech River Formation, Decatur County, Tennessee; *7a-c,* holotype specimen (U.S.N.M., no. S2170) viewed from left posterior (D), posterior, and left anterior (E) sides, closely parallel robust beta-ramules which match lower parts of axil-arms (alphabrachs, betabrachs) in size of segments being especially well shown in *7a,* ×2 (all after Springer, 1926) 27

most proximal brachial of each arm differs from the axillary alphabrach of normal calceocrinids in supporting its branchlet (pinnule, not ramule) on the adanal side, rather than the abanal side. Therefore, *Chiropinna* must be excluded from the generalization as to the pattern of heterotomy typical of calceocrinids.

CLASSIFICATION

The classification of calceocrinid genera is not a difficult problem, for it can be guided by distinctive structural characters of the dorsal cup and arms, which display significant evolutionary changes along divergent lines. Questions of generic nomenclature are another matter, in some instances involving numerous complexities. Important revisions in the application of two or three well-known generic names are required, since in treating the Calceocrinidae it is proposed to conform with stipulations of the Rules, rather than to seek abrogation of them by the International Commission on Zoological Nomenclature through use of its plenary powers. Chiefly concerned are the nominal genera *Calceocrinus* and *Eucheirocrinus* as explained in discussing them later.

SYSTEMATIC DESCRIPTIONS AND DISCUSSION

Family CALCEOCRINIDAE Meek & Worthen, 1869

[=Chirocrinidae Angelin, 1878; Cheirocrinidae Zittel, 1879; Cremacrinidae Ulrich, 1886; Castocrinidae Jaekel, 1918; Calceocrinites Jaekel, 1918 (suborder) *(partim)*]

Crown pendent or recumbent on stem, with imperfect to completely perfect bilateral symmetry developed in the plane of the E-ray and BC-interray. Dorsal cup monocyclic; basal circlet subtriangular in outline, consisting of 4, 3, or 1 plates which bear all or part of stem impression at apex of triangle, circlet muscularly hinged with radial plates along base of triangle; median (E) radial compound, with inferradial forming middle part or all of hinge contact with basals and superradial connected broadly to narrowly with inferradial or disconnected by intervention of adjoined edges of large lateral (A and D) radials; B- and C-radials compound, in some genera with infer- and superradial elements of each distinct, but in others with superradials fused together and in one genus (*Senariocrinus*) with inferradials fused in accompaniment with unfused superradials; lateral radials (A and D) large and undivided, oppositely placed with respect to the plane of bilateral symmetry. Median (E-ray) arm unbranched or isotomously divided; lateral arms multiple, characterized by conjoined proximal axillary brachials that form main-axil series and more or less numerous axil-arms with heterotomously developed unbranched ramules produced alternately from abanal and adanal sides of the axil-arms. Anal tube composed of stout transversely crescentic plates arranged uniserially with inner (ventral) side covered by irregular, thin, small plates. Stem formed of moderately thin, discoidal columnals, which in some genera diminish in size distally. *M.Ord.-L.Miss.*

This family was introduced provisionally (Meek & Worthen, 1869, p. 73) to include crinoids which then were assigned uncertainly to *Calceocrinus* because this nominal genus was involved in unsettled questions of synonymy with *Cheirocrinus* Eichwald, 1856. The family taxon is a valid one (provided that *Calceocrinus* is found to be recognizable and to have standing), with priority over later-published names based on synonyms or on other genera included in the assemblage.

Genus CALCEOCRINUS Hall, 1852 (p. 352)

Plate 1, figures *2a-e*; Text-figures 3,*2a,b*; 5,*3*; 7,*C-G*; 11

[Type-species, **Cheirocrinus chrysalis* Hall, 1860 (p. 123) subseq. desig. Wachsmuth & Springer, 1886 (p. 281)] [=*Cheirocrinus* Hall, 1860 (p. 122), type-sp., **C. chrysalis* Hall, 1860, subseq. desig. Bassler & Moodey, 1943 (p. 468); *Eucheirocrinus* Meek & Worthen, 1869 (p. 73), type-sp., **Cheirocrinus chrysalis* Hall, 1860, subseq. desig. Springer, 1926, (p. 111) (also Bather, 1893, see below); *Proclivocrinus* Ringueberg, 1889 (p. 396), type-sp., **Calceocrinus radiculus* Ringueberg, 1882, orig. desig. (=**C. chrysalis* Hall, 1860); *Euchirocrinus* Bather, 1893 (p. 65), type-sp., **Cheirocrinus chrysalis* Hall, 1860, orig. desig. (also fixes type-species of *Eucheirocrinus*, senior obj. syn.)] [*non Calceocrinus* auctt. (=*Chirocrinus* Angelin, 1878)]

Crown with complete but not strikingly evident bilateral symmetry, median arm (E-ray) generally branched dichotomously but may be unbranched (Fig. 7), two laterally placed arm systems (A- and D-rays) on opposite sides of crown composed of weakly developed main-axils, which commonly include nonaxillary plates alternating with successive axillaries that may have subequal distal facets, axil-arms relatively few and tending to have more numerous alphabrachs (up to eight) than in other calceocrinid genera, ramules few but developed in normal manner with alpha-ramules on abanal side of axil-arms and omega-ramule borne by adanal tip of main-axil (Fig. 11). Dorsal cup with four basals, each of which forms part of stem impression, suture between two small median basals (DE, EA) tending to be obscure (Fig. 5); oppositely placed large radials of A- and D-rays undivided, superradial of E-ray mostly connected narrowly with inferradial, which widens proximally, inferradials of B- and C-rays small and spear-shaped, well separated from each other by basals and fused superradial situated obliquely above them, this superradial forming subanal plate that supports anal-X plate and anal tube adjoined by stem in median plane of bilateral symmetry. *M. Ord.-U. Sil.,* North America-Europe (England-Sweden).

HALL's original description and illustrations of *Calceocrinus* were unaccompanied by a specific name, and therefore, when RINGUEBERG (1889, p. 403) redescribed and figured a fragmentary fossil reported to be HALL's original specimen of *Calceocrinus,* naming it *C. halli,* various authors, including BASSLER (1938, p. 56), BASSLER & MOODEY (1943, p. 345), and RAMSBOTTOM (1952, p. 34), judged that the failure by HALL to publish a specific name for his single known representative of the genus had been rectified by RINGUEBERG. Accordingly, they cited *C. halli* RINGUEBERG as the type-species of *Calceocrinus.* RINGUEBERG, however, did not consider the very incomplete type specimen named *C. halli* adequate to serve for delineating characters of the genus and he therefore published description and illustrations of a crown which he named *C. typus.* RINGUEBERG (1889, p. 402) explicitly designated *C. typus* as the type-species of *Calceocrinus* and this action was accepted by BATHER (1893, p. 65), SPRINGER (1926, p. 115), and others as valid.

Actually, neither *Calceocrinus halli* nor *C. typus* is eligible under the Rules to be the type-species of the genus, for this must be either (1) the first species with valid "indication" assigned definitely to *Calceocrinus* by a subsequent author, if only one such species was so assigned, or (2) a species selected from a group of definitely referred species, if two or more were so referred at the same time, this selection being made either by the author who first assigned them to the genus or, if no selection then was made, by the first subsequent author who made a choice from the assigned group (all other species being excluded from consideration). Search of the literature shows that no species were unequivocally placed in *Calceocrinus* until 1877 when S. A. MILLER (p. 72-73) listed 12 validly established species as belonging to this genus;[1] each of these had previously been referred to *Cheirocrinus* HALL, 1860 (*non* EICHWALD, 1856) or recorded as assigned questionably to *Calceocrinus.* MILLER's list included species originally named *Cheirocrinus chrysalis, C. dactylus, C. lamellosus, C. nodosus, C. tunicatus, C. ventricosus* (all HALL, 1860); *C. clarus* HALL, 1862; *C. stigmatus* HALL, 1863; *C. perplexus* SHUMARD, 1866; and *Calceocrinus? bradleyi, C.? wachsmuthi* MEEK & WORTHEN, 1869; and *C.? barrisi* WORTHEN, 1875. The type-species of *Calceocrinus* must be one of these—not some later-described species, such as RINGUEBERG's *C. halli, C. typus,* or others. MILLER failed to name any of the species assigned by him to *Calceocrinus* as type-species of the genus, and therefore none was fixed in 1877. WACHSMUTH & SPRINGER, in 1886 (p. 281) were first to do this when they explicitly designated *Cheirocrinus chrysalis* (one of the group named by MILLER) as type-species of *Calceocrinus.* It follows that diagnosis of this genus must embrace characters observed in *C. chrysalis.*

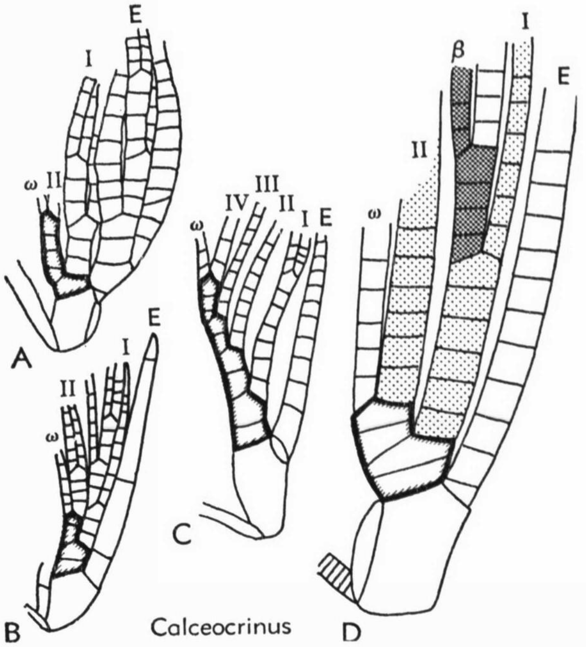

FIGURE 11. Arm structure of anterior (A) and left anterior (E) rays in various species of *Calceocrinus,* with outline of ill-defined main-axil series accented and elements of axil-arms identified by patterns in *D* corresponding to those given in Figure 8 (not to scale).—*A. C. anglicus* (M.Sil.).—*B. C. minor* (M.Sil.).—*C. C. barrandei* (M.Ord.), showing unusual number of axil-arms and nearly linear main-axil series.—*D. C. chrysalis* (M.Sil.).

Unhappily, we find that *Cheirocrinus chrysalis* has been cited universally (BATHER, 1893, p. 65; SPRINGER, 1926, p. 111; BASSLER, 1938, p. 97; BASSLER & MOODEY,

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[1] The fact that MEEK & WORTHEN (1873) cited *Calceocrinus wachsmuthi* and *C. bradleyi* without accompanying question marks in synomymic references (p. 444, 502) and in the index lacks significance because internal evidence plainly shows that omissions of the question marks are typographical errors.

1943, p. 468) as the type-species of *Eucheirocrinus* Meek & Worthen, 1869. How does this come about? Meek & Worthen introduced *Eucheirocrinus* provisionally without naming any species but plainly intending that the name should apply to forms incorrectly called *Cheirocrinus*. Contrary to statements by Springer (1926, p. 101), Meek & Worthen indicated no type-species for *Eucheirocrinus* and Hall (1860) designated no type-species for *Cheirocrinus* Hall (*non* Eichwald). Further, in writing "the form here under consideration might be called *Eucheirocrinus*," Meek & Worthen (1869, p. 73; repeated verbatim, Meek & Worthen, 1873, p. 443) introduced ambiguity as to species eligible to be named as type-species of the proposed genus, because it is uncertain whether Hall's described species of *Cheirocrinus* or the new species *Calceocrinus? bradleyi* and *C.? wachsmuthi* described by them constituted "the form here under consideration." Decision resolving this doubt may be accepted on the first-subsequent-reviser principle, for Bather (1893) acted on the premise that *Cheirocrinus chrysalis* was legally choosable as the type-species of *Euchirocrinus (=Eucheirocrinus)*. Therefore, Meek & Worthen's genus acquired a type-species when Bather (1893), who invalidly altered *Eucheirocrinus* to *Euchirocrinus* (p. 59), chose *Cheirocrinus chrysalis* as the type-species of *Euchirocrinus* (thus automatically fixing the type-species of *Eucheirocrinus*, its senior objective synonym). Therefore, again, both nominal genera must be recognized as junior objective synonyms of *Calceocrinus*.

Previous usage of authors has been erroneous in employing *Calceocrinus* as the name of crinoids considered congeneric with *C. halli* and *C. typus* and in using *Eucheirocrinus* for crinoids judged to be congeneric with *C. chrysalis*. If the Rules are followed, as proposed to be in the *Treatise*, *Calceocrinus* (which of course remains as type-genus of the family Calceocrinidae) takes over for *Eucheirocrinus* of general former usage. Then, question arises concerning nomenclature applicable to species previously classed as belonging to *Calceocrinus* but clearly not congeneric with *C. chrysalis*. Some 20 such species are found in the literature. Study of them has led to assignments among three genera—*Chirocrinus* Angelin, 1879, *Synchirocrinus* Jaekel, 1918, and *Chiropinna* Moore, n. gen. This does not take account of various species originally referred to *Calceocrinus* which have been transferred firmly to *Cremacrinus* or *Halysiocrinus*.

Six species of *Calceocrinus* now are known, one (*C. barrandei* Walcott, Figs. 7,*D*; 11,*C*) from Middle Ordovician (Trenton Limestone) rocks of New York, and five from Lower to Upper Silurian of North America (N.Y.-Ind.-Tenn.-Ont.) and Europe (Eng., Pl. 1, figs. 2a-e). The American species are **C. chrysalis* (Hall) (Figs. 7,*E*; 11,*D*), *C. indianensis* S. A. Miller, *C. minor* (Springer) (Fig. 7,*C*; 11*B*), and *C. ontario* (Springer) (Fig. 7,*G*). The English species is *C. anglicus* (Springer) (Figs. 7,*F*; 11,*A*).

Genus CREMACRINUS Ulrich, 1886 (p. 107)

Plate 1, figures 1a-c, 3a,b; Text-figures, 3,*1*; 5,*1*; 6; 7,*A*; 10

[Type-species, **C. punctatus* Ulrich, 1886, orig. desig.] [=*Castocrinus* Ringueberg, 1889 (p. 396), type-sp., **Calceocrinus furcillatus* W. R. Billings, 1887, orig. desig.; *Castrocrinus* Wachsmuth & Springer, 1890, p. 387 *(nom. null.)*]

Bilateral symmetry of crown imperfectly developed, calyx asymmetrical, arm-bearing rays four, stem not in plane of anal tube. Median (E) ray typically unbranched but in some species bifurcating distally, quadrilateral inferradial rather broadly in contact with superradial. Lateral arms three, those of A- and B-rays on one side and of D-ray alone on opposite side, each arm with ill-defined but definite main-axil series consisting of two primibrachs (axillary with subequal distal facets) and one or two secundibrachs; axil-arms few, generally two borne by each main-axil but may be only one in B-ray, ramules numerous, strictly conforming to calceocrinid pattern of heterotomy, with alpha-ramules on abanal side of axil-arms and well-developed omega-ramule given off at adanal extremity of main-axil series. Anal tube supported by C-superradial, B-superradial supporting arm that generally is distinctly smaller than that borne by adjoining A-ray; B- and C-inferradials spear-shaped, separated from one another by basals and superradials. Basals four, all partly covered by stem impression. *M. Ord.-M. Sil.*, North America.

Cremacrinus contains the oldest and unquestionably the most primitive known members of the calceocrinid family. Morphological comparison with *Ectenocrinus* and *Homocrinus* supports judgment that *Cremacrinus* and later bent-crown crinoids were derived from a homocrinid stock, even though *Cremacrinus* is found in slightly older deposits (Blackriveran) than beds (Trentonian) containing the oldest known species of any homocrinid genus. No problems of classification and nomenclature concern *Cremacrinus*.

Eight Middle Ordovician species of *Cremacrinus* and three Middle Silurian species are known, all from North America. The Ordovician forms include five from the Ottawa and Kirkfield areas of Ontario;

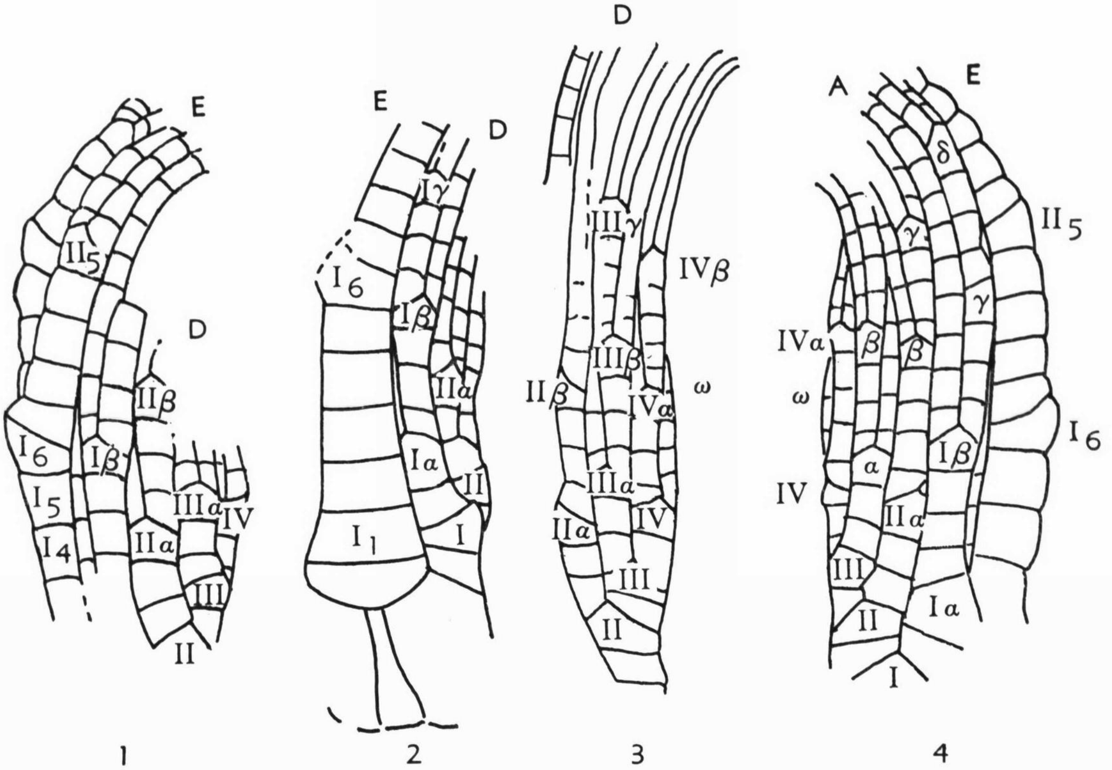

Figure 12. Arm structure of *Anulocrinus thraivensis* (×4) based on photographs reproduced on Plate 1, figures *4b* (=*4* of this figure), *4c* (=*1* of this figure), *4d* (=*3* of this figure), and *4e* (=*2* of this figure), with notation of individual brachials and ramules of axil-arms. This figure is intended to serve for documentation of the diagrams of arm structure given in Figure 13 (after Ramsbottom, 1960).

these are *C. articulosus* (Billings), *C. billingsianus* (Ringueberg), *C. furcillatus* (W. R. Billings), *C. inaequalis* (Billings), and *C. rugosus* (W. R. Billings), among which *C. articulosus* is recorded also from Kentucky, *C. furcillatus* from northern Michigan, and *C. inaequalis* from Wisconsin. **C. punctatus* (Pl. 1, figs. 4a,b), the type-species, has been found in Minnesota and northern Michigan, *C. arctus* in Minnesota, and *C. kentuckiensis* (Fig. 7,*A*) in Kentucky. The Silurian species, all described by Springer from Tennessee, are *C. decatur, C. tubuliferus* (Pl. 1, figs. 1a-c; Fig. 10), and *C. ulrichi*.

The fact that *Cremacrinus*, the least specialized genus of the Calceocrinidae, is so well represented in North America but unknown elsewhere strongly indicates that the origin of the calceocrinids was in shallow-sea areas west of the Atlantic, probably not long before Blackriveran time. Until recently no Ordovician members of the family have been known from Europe, though 12 Silurian species, now classified in four genera, are known. The discovery of calceocrinids *(Anulocrinus)* with four arm-bearing rays in Upper Ordovician strata of Scotland now indicates that forms related to *Cremacrinus* migrated to the Old World from North America during Ordovician time. It is curious that no descendants of the presumed European migrants have been discovered in that continent in rocks younger than Early Devonian, whereas many species are fairly widespread in Devonian and Mississippian deposits of the United States.

Genus ANULOCRINUS Ramsbottom, 1960 (p. 8)

Plate 1, figures 4a-e, 5a,b; Plate 3, figure 5; Text-figures 12-14

[Type-species, **A. thraivensis* Ramsbottom, 1960; orig. desig.]

Crown pendent, subparallel to stem, like *Cremacrinus* in having four arm-bearing rays, E-arm unbranched or divided isotomously on about the sixth primibrach and fifth secundibrachs, lateral rays (A, B, D) with arms that branch isotomously or nearly so within the main-axil series but heterotomously in all axil-arms, axil-arms and ramules few to numerous, all arranged precisely in conformance with the normal calceocrinid pattern of heterotomy. Dorsal cup incompletely known in that nature of triangular basal circlet (presumably composed of four plates arranged as in *Cremacrinus*) is undetermined; superradial of E-ray wider than high, narrowly touching slender inferradial, which is slightly sinuous-sided and appreciably taller than wide; large undivided lateral radials of A- and D-rays forming most of opposite sides of dorsal cup, B-superradial small, subquadrangular, B- and C-inferradials spear-shaped, in type-species C-superradial (termed subanal plate) seemingly a wide, low, nearly median piece at proximal extremity of anal tube, visible part of which consists of large, stout plates with height of each about equal to width. Stem moderately slender, composed of discoid to barrel-shaped columnals, circular transversely, thinnest in proximal region near cup and thickening distally until height may appreciably exceed diameter. *U. Ord.-M. Sil.,* Europe and North America.

The discovery in Upper Ordovician rocks of the Girvan district in southwestern Scotland of several specimens on which definition of this genus is based is exceptionally interesting and it should contribute importantly to better understanding of calceocrinid evolution. The significance of the Scottish fossils seems not to have been fully appreciated by Ramsbottom, for his descriptions are unhappily lacking in detail and the illustrations (though they include excellent photographs) are inadequately explained in terms of morphological features actually shown. Interpretative line drawings are limited to two diagrams, one of which accurately shows structure of the isotomously branched median (E-ray) arm of *Anulocrinus thraivensis*. The other gives a composite, very incomplete indication of lateral-arm pattern, which my study of the photographic illustrations fails to confirm. *Anulocrinus* was interpreted by Ramsbottom to be characterized by isotomous branching exclusively in all rays, lateral (A, B, D) as well as median (E). On the contrary, Figs. 12 and 13, based on Ramsbottom's photographs (my Pl. 1, figs. 4a-e) indicates that all lateral arms of the type-species *(A. thraivensis)* exhibit heterotomous branching in the normal pattern of calceocrinid arm structure (Fig. 13). The same is true of the axil arms of the D-ray and of B-ray branching in *A. drummuckensis* (Pl. 1, figs. 5a,b; Fig. 14).

The lateral ray branching observed in *Anulocrinus thraivensis* now calls for examination in more detail. Characters of the A-ray will be noted first, and then the plan of the B- and D-rays. The diagrams of the A-ray (Fig. 13,*2a,b*) are based on Ramsbottom's photograph (his pl. 2, fig. 1) showing this ray and part of the E-ray at its right as seen in the holotype specimen (this paper, Pl. 1, fig. 4b). An outline drawing prepared by tracing features of the photograph on an acetate overlay provides a means for identifying individual brachials belonging to the main-axil and different axil-arms (Fig. 12,*4*). Thus, the interpretation of structural elements and pattern of branching indicated diagrammatically (Fig. 13,*2a,b*) is documented by the outline drawing of the photograph and by the photograph itself. The main-axil of the A-ray is composed of four axillary plates and five nonaxillary brachials, since the adanal group (quartibrachs) of the main-axil series happens to consist of three, instead of the normal two plates. The A-ray of *A. thraivensis* (holotype) contains four axil-arms, the primaxil-arm having alphabrach, betabrach, gammabrach, and deltabrach series (Fig. 13,*2b*). The alpha-ramule of this axil-arm is not visible in the photograph, although space for it appears on the abanal side of the arm distally from the axillary alphabrach of the primaxil-arm. The beta-ramule is clearly defined on the adanal side of this axil-arm and likewise the delta-ramule, but only a suggestion of the gamma-ramule. The secundaxil-arm closely resembles the primaxil-arm just described, with definitely identifiable beta-ramule and almost equally definite alpha-ramule and gamma-ramule indicated by presence of the axillary alphabrach and axillary gammabrach that support them. The tertaxil-arm exhibits the alphabrach series with alpha-ramule, betabrach series with beta-ramule, and an unbranched gamma-brach series. Finally, the quartaxil-arm is seen to have alphabrachs, the alpha-ramule, and unbranched betabrachs. The omega-ramule occurs in normal position joined to the quartaxil of the main-axil series.

The B-ray of *Anulocrinus thraivensis* has a short main-axil series composed of five plates and two axil-arms (Fig. 13,*1a,b*), of which only the secundaxil-arm is fairly well distinguishable in one of Ramsbottom's photographs (pl. 2, fig. 5). This arm shows the alphabrach series followed at left by unbranched betabrachs. The omega-ramule is clearly evident.

The D-ray of *Anulocrinus thraivensis* is rather difficult to decipher from the photographs because of need to supplement information obtainable from the holotype specimen (pl. 2, fig. 7; this paper, Pl. 1, figs. 4d,e, and Fig. 12,*2,3*) by determinations based on different views of various paratypes. When elements of the main-axil and axil-arms are properly integrated by study of the photographs, it is found that the structure of the D-ray is virtually a mirror image of the A-ray (Fig. 13,*4a,b*). The main-axil has one less nonaxillary brachial, but there are four axil-arms. In the primaxil-arm the gammabrach axillary is the highest one seen, whereas the A-ray shows a deltabrach axillary. In the secundaxil-arm the betabrach axillary is the highest determinable, as compared with a gammabrach axillary in this axil-arm of the A-ray. On the other hand, the tertaxil-arm of the D-ray shows the gammabrach

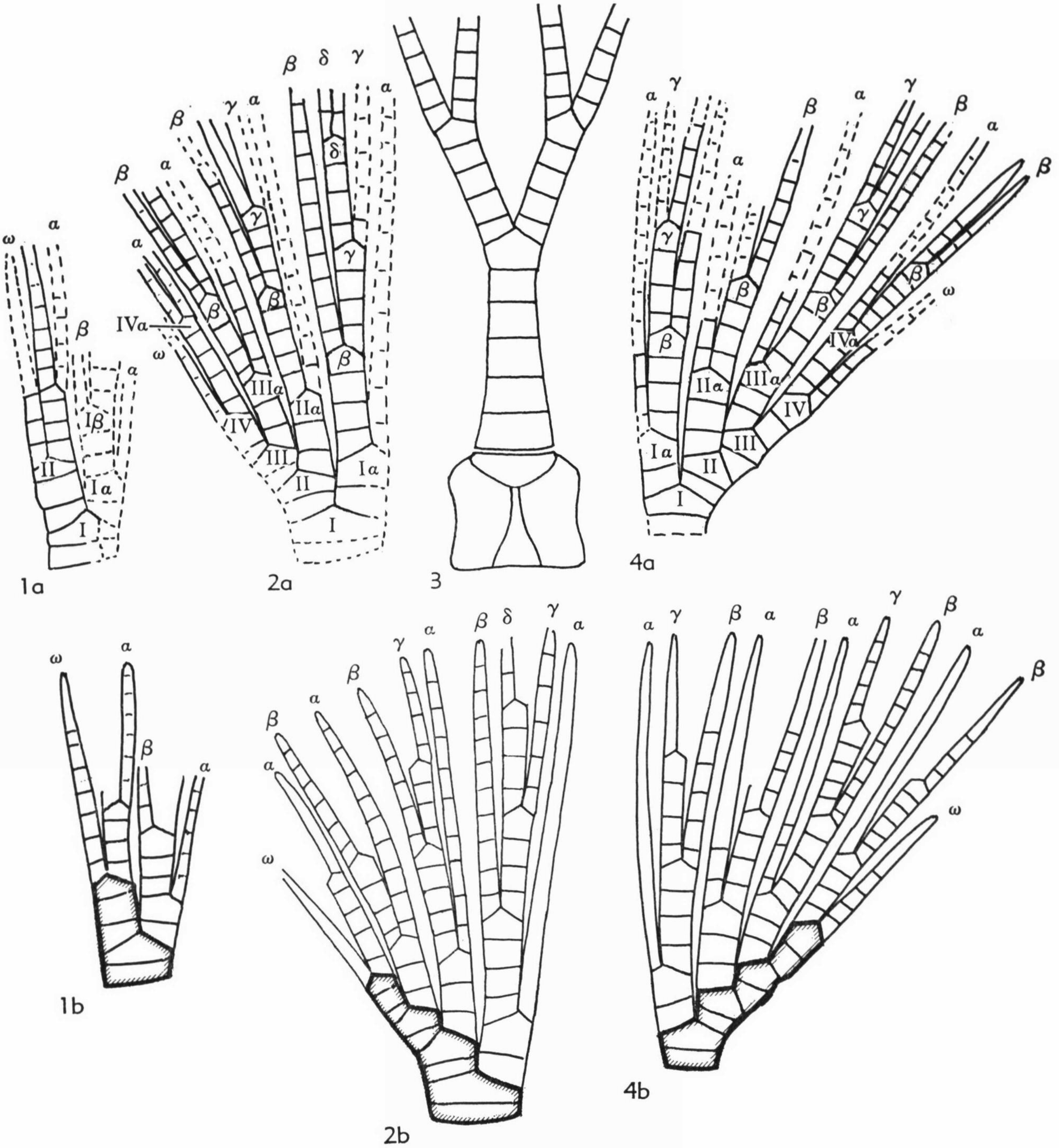

FIGURE 13. Arm structure of *Anulocrinus thraivensis* (diagrammatic) based on identification of elements as given in Figure 12. Parts not actually visible in the photographs are indicated by broken lines in *1a, 2a,* and *4a.* The main-axil series are accented in *1b, 2b,* and *4b,* and ramules are identified by Greek letters in these figures.

axillary and the quartaxil-arm the betabrach axillary, neither of which appear in preserved parts of the A-ray.

Attention is directed next to *Anulocrinus drummuckensis* Ramsbottom (1960, p. 9, pl. 2, figs. 9, 10), which is a somewhat smaller species than *A. thraivensis* and decidedly simpler in structural pattern. It is known from a single specimen, the holotype, obtained from the same horizon and locality as recorded for *A. thraivensis.* Reproduction of Ramsbottom's photographs of *A. drummuckensis* is given in Plate 1, figures 5a, b, and outline drawings that match the photographs are accompanied by diagrammatic representation of structure in Figure 14, *1a,b,2.* The dorsal cup is incompletely known but seems closely similar to that of *A. thraivensis.* The median (E) arm is long, relatively stout, and unbranched. Branching of the A-ray seems to be isotomous but in my view is correctly interpretable as showing three primibrach and two secundibrach elements of a primitive main-axil series, followed above by an alphabrach series with alpha-ramule and undivided betabrach series in the primaxil-arm, and by unbranched alphabrachs and the omega-ramule extending distally from the terminal (adanal) axillary of the main-axil. The B-ray has even simpler structure, with two unbranched series of brachials (alpha-ramule, betabrachs) beyond the axillary alphabrach, and the omega ramule on the adanal side of the three-plate "main axil."

The D-ray of *Anulocrinus drummuckensis* has best-developed heterotomy (Fig. 14,2), for above the main-axil the primaxil-arm is seen to have a well-differentiated alphabrach series and alpha-ramule, betabrach series and beta-ramule, and unbranched gammabrachs; the secundaxil-arm has alphabrachs, alpha-ramule, and unbranched betabrachs. The omega-ramule extends adanally from the tip of the main-axil series.

In addition to the two Scottish species of *Anulocrinus,* which have been considered, Ramsbottom has assigned to this genus a Middle Silurian species from Tennessee described by Springer (1926, p. 107) as *Cremacrinus simplex,* n. sp. (Pl. 3, fig. 5). In comparing *C. simplex* with other species of *Cremacrinus,* Springer called attention to "the small number of arm-branches [in this species] and their dichotomous bifurcation, which might well warrant a reference to a new genus." Nevertheless, examination of the illustrations given by Springer shows that the D-ray of *C. simplex* exhibits heterotomous branching precisely in accordance with the normal calceocrinid pattern, an alpha-ramule being produced from the axillary alphabrach of the primaxil-arm and an oppositely directed ramule (omega) from the adanal tip of the ill-developed main-axil (Fig. 14,*3a,4b*). In other words, *Anulocrinus simplex* (Springer) is entirely normal in its calceocrinid (or cremacrinid) type of lateral-arm branching. On the other hand, the A- and B-rays of this species lack heterotomy because they are developed only to the extent of a single branching of the arms (a primitive or juvenile, character) (Fig. 14,*3b,4a*). In my opinion, the holotype of this species (only known specimen) is a juvenile individual.

Review of the three species now assigned to *Anulocrinus—A. thraivensis* and *A. drummuckensis* from Upper Ordovician beds of the Girvan district in southwestern Scotland, and *A. simplex* from the Silurian of Tennessee—indicates that Ramsbottom was quite right in thinking that this genus represents an important connecting link (*anulus,* link of a chain) in evolutionary development leading from four-armed *Cremacrinus* to three-armed *"Eucheirocrinus"* (=*Calceocrinus*) and other calceocrinids. The lateral arms of *Cremacrinus* display obscure main-axil series (nevertheless quite definitely determinable by comparison with more advanced calceocrinids) and normally two axil-arms in each ray. The axil-arms are characterized by pronounced heterotomy, with stout ramules given off in zigzag fashion from opposite sides of the axil-arm (Fig. 10). Anticipated changes in evolution of arm-branching patterns should include increase in number of axil-arms accompanied by enlargement and accentuation of main-axils, and possibly by modifications in the plan of heterotomous branching. A replacement of heterotomy by isotomy in branching of the lateral rays is not reasonably expectable in the Calceocrinidae and in fact is not found (except in the main-axil series of some simple, presumably primitive or juvenile forms). *A priori* judgment, therefore, would suggest that Ramsbottom was mistaken in attributing a completely isotomous pattern of branching to *Anulocrinus* (in axil-arms, as well as main-axils) and in thinking that this constitutes an evolutionary step toward *"Eucheirocrinus."* It is erroneous to assert that *"Eucheirocrinus"* (=*Calceocrinus*) has isotomous, instead of heterotomous branching of the lateral rays, although axillaries of main-axils do show approximately equal distal facets (Fig. 11).

Genus CHIROCRINUS Angelin, 1878 (p. 22)

Plate 3, figure 7; Text-figures 5,*3a-c*; 7,*B*; 9

[Type-species, **C. gotlandicus* Angelin, 1878, by monotypy] [= *Calceocrinus* auctt. (*non* Hall, 1852); *non Cheirocrinus* Eichwald, 1856, *nec* Hall, 1852; *nec* Salter, 1873]

Crown with perfect bilateral symmetry; median (E) ray undivided, small inferradial generally separated from superradial; lateral rays (A and D) with large radials succeeded by two primibrachs, axillary primibrach with unequal distal facets, narrower one on abanal side supporting axil-arm and broader one bearing secundaxil of main-axil series, which, though definite, is not strongly distinguished or appreciably curved adanally; each axil-arm bearing moderately stout unbranched ramules that rise from axillaries separated by one or two quadrangular brachials, ramules of all series subequal in size. Dorsal cup showing moderately large spear-shaped inferradials of B- and C-rays well separated by basals and fused superradial beneath anal-X plate; basals reduced to three by fusion of DE and EA plates, which form low triangular basal that generally does not extend into stem facet. *L. Sil.,* North America; *M. Sil.,* Europe.

Nomenclatorially, *Chirocrinus* is entirely available as a generic name, even though it was published by

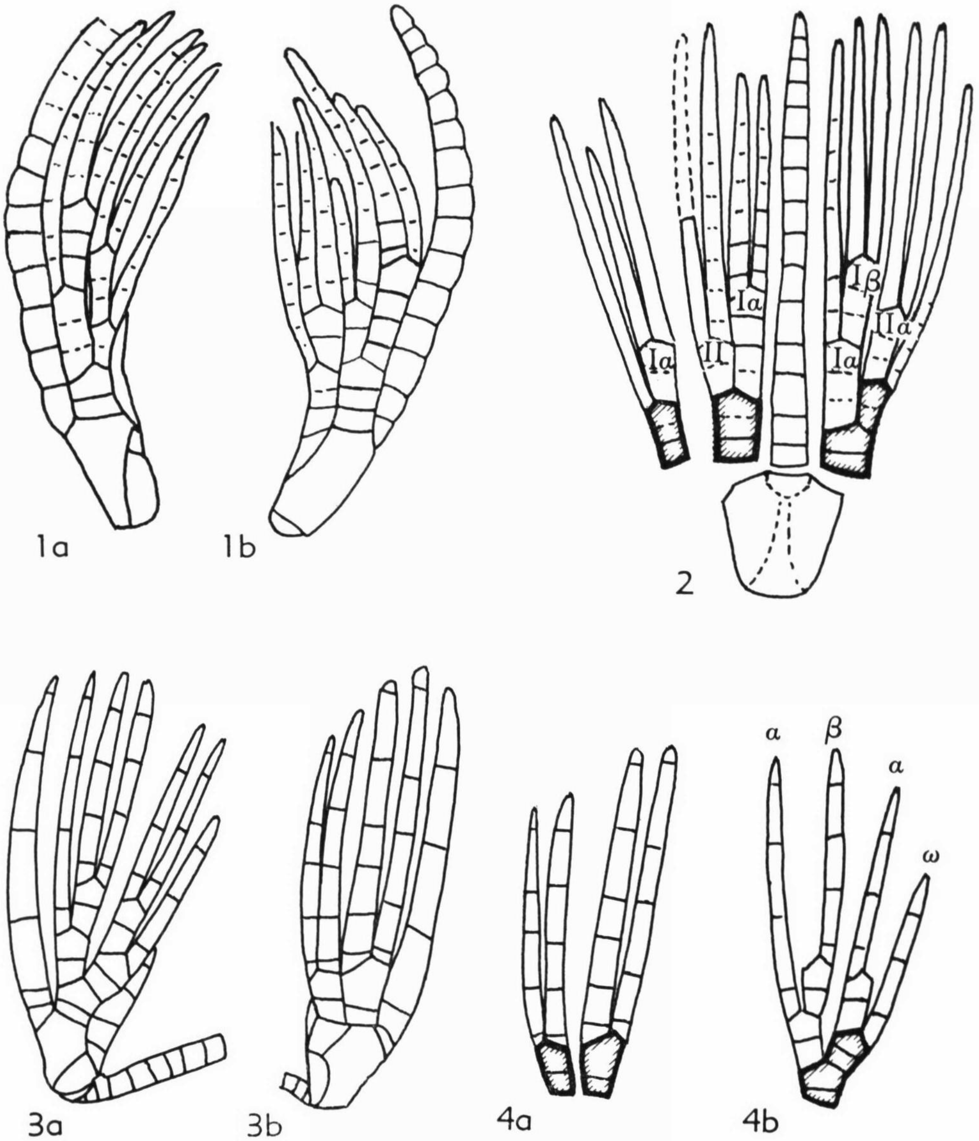

FIGURE 14. Arm structure of relatively simple, possibly juvenile crinoids classed as belonging to *Anulocrinus.*—*1a,b. A. drummuckensis* (U.Ord.), opposite sides of crown (holotype) based on photographs reproduced on Plate 1, figures *5a,b,* ×4 (after Ramsbottom, 1960).—*2.* Diagram of arm structure in *A. drummuckensis,* main-axils accented.—*3a,b.* Drawings of *A. simplex* (M.Sil.) with axil-arms spread slightly apart, left posterior (D-ray) and anterior (A-ray) sides, ×4 (after Springer, 1926).—*4a,b.* Diagrams of arm structure of *A. simplex,* main-axil series accented.

Angelin (1878) as intended equivalent of *Cheirocrinus* Salter, 1859. The fact that Angelin's *Chirocrinus* is an unjustified emendation of Salter's nominal genus, which was a *nomen nudum* as of the date (1859) cited by Angelin, according to the new Rules, establishes it as a junior objective synonym that "has status in nomenclature with its own author and date" (Art. 33,a,ii). Also, *Chirocrinus* "remains available even though it becomes a junior synonym. . . . if the synonymy is judged to be erroneous, or if the senior synonym is found to be invalid or unavailable (Art. 17,1), even "if the difference between the two genus-group names is due to only one letter" (Art. 56,a). *Cheirocrinus* Salter, 1859, is invalid. *Cheirocrinus* Hall, 1860 (type-species, *C. chrysalis* Hall, 1860, subseq. desig. Bassler & Moodey, 1943) and *Cheirocrinus* Salter, 1873 (type-species, *C. serialis* Salter, 1873, subseq. desig. Moore, herein) are both junior homonyms, since they apply to fossils obviously very different from the cystoids named *Cheirocrinus* by Eichwald, 1856. Also, they are not congeneric with *Chirocrinus* Angelin.

Chirocrinus, as here described, is clearly and rather easily distinguished from other calceocrinid genera by the combined characters of its somewhat weakly defined main-axil series and the presence of numerous axil-arms, which commonly are spread well out like a fan so as to reveal the nearly uniform-sized ramules (Fig. 9). The median arm is undivided in known species. The infer- and superradial beneath this arm are variable in shape and in being either separated from one another or in contact along a moderately narrow suture.

In addition to the type-species, **Chirocrinus gotlandicus* (Fig. 9), known only from Gotland, and *C. fletcheri* (Pl. 3, Fig. 7; Fig. 5,*3c*), from upper Wenlock strata of England, the Lower Silurian (Brassfield) species described by Foerste (1936) from Ohio as *Calceocrinus? incertus* (Fig. 7,*B*) is assignable to *Chirocrinus.*

Morphological features typical of *Chirocrinus* point to a distinctly more advanced evolutionary stage than those represented by *Cremacrinus, Anulocrinus,* and *Calceocrinus,* but evidence indicating that *Chirocrinus* developed out of *Calceocrinus,* rather than from another (unknown) lineage connecting it with *Cremacrinus,* is lacking. Like *Calceocrinus,* species of *Chirocrinus* display perfect bilateral sym-

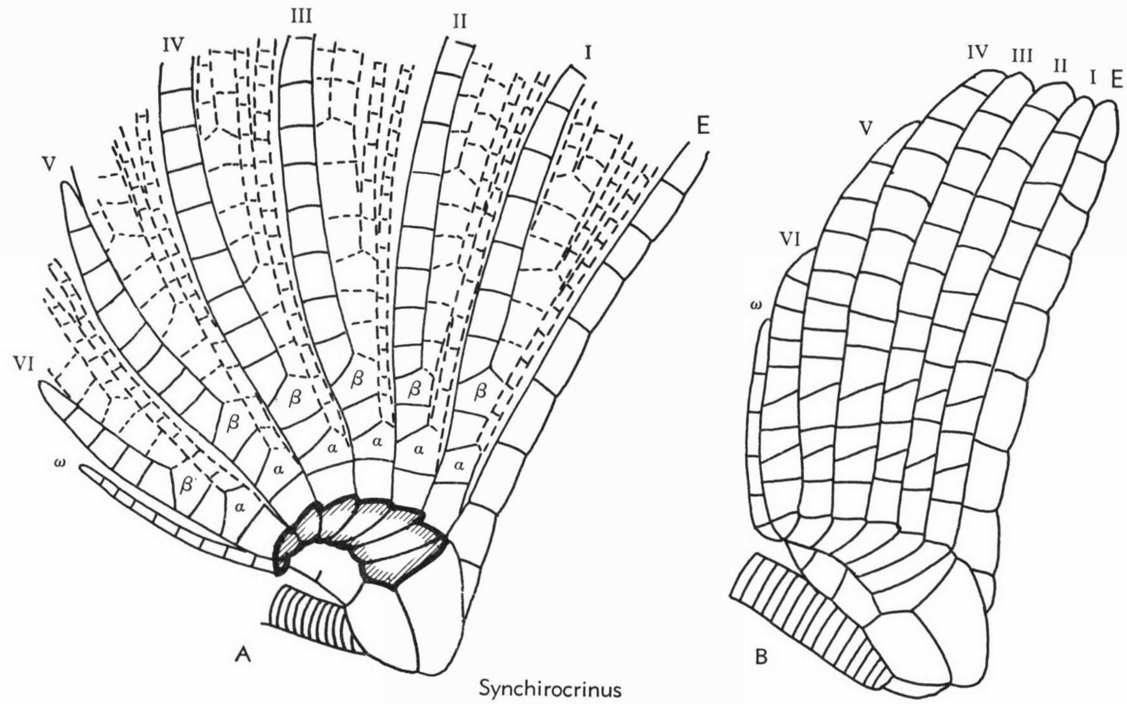

Figure 15. Diagrammatic representation *(A)* of main-axil and axil-arm structure of *Synchirocrinus foerstei* (M.Sil.) with axil-arms spread apart to allow broken-line indication of concealed brachials and ramules. At right *(B)* is an outline drawing of this species showing the alphabrachs and betabrachs (lowermost four brachials of each axil-arm) and stout beta-ramules above them, all in normal closely appressed position as seen on the anterior (A-ray) side of the crown, ×2 (after Springer, 1926).

metry but are distinguished by better-defined main-axils of the lateral rays, more numerous axil-arms, and a reduction in number of basals from four to three by fusion of the small median basal plate (DE, EA). Absence of a bifurcation even in a distal part of the E-ray in known species of *Chirocrinus* is interpreted as a primitive character, which is matched in various species of *Calceocrinus* but strongly in contrast with the four successive branchings of this ray observed in *Calceocrinus anglicus*. If this feature has evolutionary significance, it is nearly as well developed in *C. anglicus* as in *Halysiocrinus nodosus,* which is certainly an advanced calceocrinid and one of the last representatives (Mississippian) of the family. In both crinoids branching above the axillary primibrach is heterotomous.

Genus SYNCHIROCRINUS Jaekel, 1918 (p. 86)

Plate 1, figure 6; Plate 2, figures 4-7; Plate 3, figures 2-4, 8; Text-figures 2; 3,*3a,b*; 5,*4a,b*; 15; 16

[Type-species, *S. *anglicus* Jaekel, 1918 (p. 86) orig. desig. (= **Calceocrinus nitidus* Bather, 1893, p. 91)] [=*Cheirocrinus* Salter, 1859 *(nom. nud.)*; *Cheirocrinus* Salter, 1873, p. 118, *non* Eichwald, 1856, *nec* Hall 1860, (type-sp., **C. serialis* Salter, 1873, subseq. desig. Moore, herein); *Pendulocrinus* Salter, 1859 *(nom. nud.)*]

Crown with perfect bilateral symmetry, resembling *Chirocrinus* except in having strongly marked main-axil series in lateral rays and axil-arms that in side view of most specimens seem to consist of parallel rows of subequal brachials, whereas in fact they are chiefly composed of exceptionally robust beta-ramules. *L. Sil.,* North America (Ohio); *M. Sil.,* Europe (Sweden-England)-North America (Tennessee-New York); *L. Dev.,* North America (Iowa).

Synchirocrinus is one of the most distinctive, and therefore easily recognized of all calceocrinid genera. Also, it is one of the most common. It differs from *Deltacrinus* in its well-marked main-axils, which generally curve distinctly and diminish to a pointed extremity adanally; also, *Synchirocrinus* has much more numerous axil-arms, which bear specialized beta-ramules. *Halysiocrinus* is judged to be more closely related to *Synchirocrinus* than any other calceocrinid, mainly because it also tends to have differentiated robust beta-ramules. The two genera correspond to one another closely in nature of the basal "circlet" and prominent arcuate main-axil, but differ in the less dominant beta-ramules, greater separation of the E-ray infer- and superradials, and laterally adjoined positions of the B- and C-inferradials observed in *Halysiocrinus*.

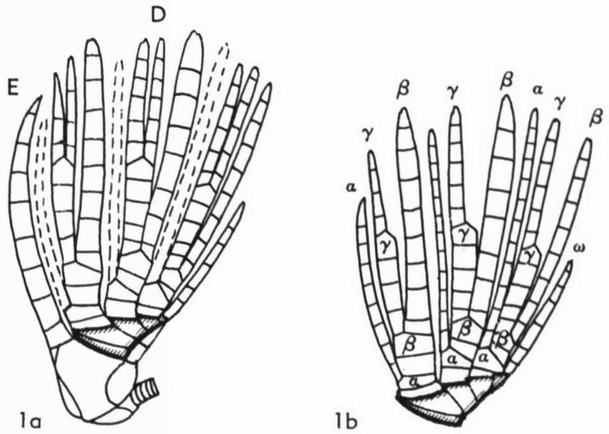

Figure 16. Main-axil series and axil-arm structures of *Synchirocrinus pugil* (M.Sil.), axil-arms being spread enough apart to allow space for showing the alpha-ramules (broken lines) (based on figures by Bather, 1893, and Springer, 1926).

Judgment that *Synchirocrinus* was derived from *Chirocrinus* or a closely similar stock is plausible, in spite of the fact that no species of *Chirocrinus* is known to antedate the appearance of *Synchirocrinus*. As presently interpreted, both genera are represented by Lower Silurian species from Ohio and are best known from Middle Silurian species of North America and Europe. *Synchirocrinus,* unlike *Chirocrinus,* according to records now available, persisted into the Devonian (three species, of which one is Middle Devonian). *Halysiocrinus* probably comprises descendants of the ancestors of *Synchirocrinus*.

Species assigned by me to *Synchirocrinus* are 17 in number, of which nine are North American and eight European. The American species include: (1) Lower Silurian, *S. centervillensis* (Foerste), from Ohio; (2) Middle Silurian, *S. bassleri* (Springer), *S. bifurcatus* (Springer) (Pl. 2, figs. 7a-c), and *S. foerstei* (Springer) (Pl. 3, fig. 8; Fig. 15), all from Tennessee, and *S.? halli* (Ringueberg) (Pl. 2, fig. 5) and *S. typus* (Ringueberg), from New York; (3) Lower Devonian, *S. keyserensis* (Springer) and *S. marylandensis* (Springer), from West Virginia and Maryland, respectively; (4) Middle Devonian, *S. barrisi* (Worthen), from Iowa. The European species referred to *Synchirocrinus* are all from Middle-to-Upper Silurian rocks of England and Sweden (Gotland), as follows: (1) occurring in both regions, **S. nitidus* (Bather) (Pl. 2, fig. 4; Pl. 3, fig. 4; Fig. 2), the type-species, and *S. pugil* (Bather) (Fig. 16); (2) reported only from Sweden, *S. interpres* (Bather), *S. tenax* (Bather) (Pl. 1, fig. 6), and *S. tucanus*

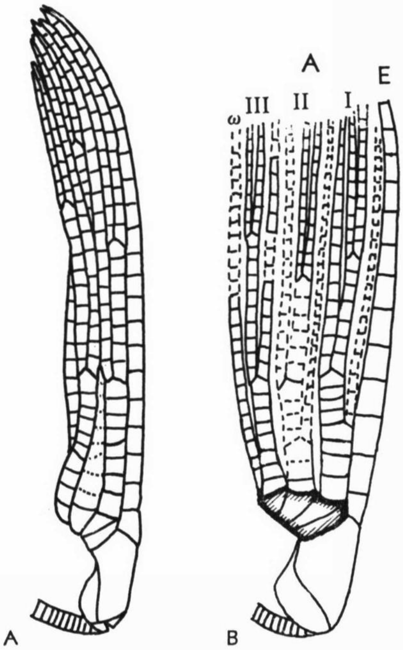

Figure 17. *A*. Anterior (A-ray) side of crown of *Deltacrinus clarus* (×2) based on photograph of holotype (Pl. 1, fig. 7). *B*. Diagram of main-axil and axil-arm structures with identification of ramules in each of the three axil-arms.

(Bather) (Pl. 2, fig. 6); (3) known only from England, *S. gradatus* (Salter) (Pl. 3, fig. 3), *S. inclinus* (Ramsbottom), and *S. serialis* (Salter) (Pl. 3, fig. 2).

Genus DELTACRINUS Ulrich, 1886 (p. 100)

Plate 1, figure 7; Text-figures 5, 6a,b; 17

[Type-species, **Cheirocrinus clarus* Hall, 1862, orig. desig.]

Crown slender and elongate, with perfect bilateral symmetry, median (E) ray undivided, lateral rays with very ill-defined main-axils and relatively few axil-arms which lack evident differentiation of alpha-, beta-, and gamma-ramules; inferradial of median ray triangular (delta-shaped) and widely separated from superradial by adjoined lateral radials; basals three, closely resembling those of *Chirocrinus*. *L. Sil.*, North America (Missouri); *M. Sil.*, North America (Indiana-New York); *M. Dev.*, North America (New York).

Deltacrinus is distinguishable from other calceocrinid genera by relatively advanced characters of the dorsal cup combined with unspecialized—not to say primitive—features of the main-axils and axil-arms. The arms are longer and more slender, with much wider spacing of axillaries than in other calceocrinids. For example, in *D. clarus* (Fig. 17) the alphabrach series of different axil-arms appears to range from two to five, betabrachs four to ten; and gammabrachs six to seven.

Features of the dorsal cup resemble those of *Halysiocrinus*. The three basal plates and large lateral radials broadly in contact with each other along the midline of the median ray, widely separating the infer- and superradial of this ray, are the same as in *Halysiocrinus*, except for the angular (rather than arcuate) stemward margin of the basal that forms the posterior part of the hinge articulating with the E-ray inferradial and excepting the generally greater width of the contact of the large lateral radials with each other in *Deltacrinus* (Fig. 5,*6a,b*). The inferradials of the B- and C-rays of *Deltacrinus* occur on either side of the fused superradial belonging to these rays and do not touch one another, whereas in *Halysiocrinus* these inferradials adjoin laterally beneath the superradial. The nearly uniform size of ramules given off by the axil-arms is a character suggestive of *Chirocrinus* but their number in *Deltacrinus* is fewer (commonly only three to each axil-arm) and the axillary plates supporting them are separated by four to nine brachials instead of only one or two, as in *Chirocrinus*.

The phylogenetic relationships of *Deltacrinus* are difficult to interpret. The genus may mark an independent line of development from *Cremacrinus* or possibly it branched off from an early member of the *Calceocrinus* group. Surely it cannot have descended from ancestors classifiable as belonging to *Synchirocrinus*, because of the numerous specialized betaramules that characterize this genus. Derivation from *Chirocrinus* seems hardly more possible, since this would call for retrogressive modifications of the main-axils and axil-arms associated with accelerated change of the dorsal cup in the direction of *Halysiocrinus*.

Five species are considered referable to *Deltacrinus*, although with reservations concerning some owing to incompleteness of information. The fossils are distributed from Lower Silurian to Middle Devonian, as follows: *D. alleni* (Rowley), Lower Silurian of Missouri; *D. contractus* (Ringueberg) and *D. stigmatus* (Hall), Middle Silurian of New York and Indiana, respectively; *D. secundus* (Hall), Lower Devonian, New York; and the type-species, **D. clarus* (Hall), (Pl. 1, fig. 7; Fig. 17), Middle Devonian, New York.

Genus CHIROPINNA Moore, n. gen.

Plate 2, figures 2a-c; Text-figures 5,*5a,b*; 18

[Type-species, **Calceocrinus pinnulatus* Bather, 1893 (p. 96), herein designated]

Crown compactly subcylindrical, dorsal cup of normal type, surmounted by pinnulate axil-arms in lateral rays and pinnulate dichotomous branches of median (E) ray, main-axils well developed. *M. Sil.*, Sweden (Gotland).

This crinoid is not only a unique sort of calceocrinid but it stands alone among all disparid (monocyclic) crinoids in having pinnulate arm structure.[1] Compared with all other calceocrinids, with which this genus unquestionably belongs, the unbranched offshoots of brachials on alternating sides are not different from ramules, except for the fact that every brachial plate of each axil-arm is in axillary, giving off a branchlet (pinnule) to left or right (Pl. 2, figs. 2b,c; Fig. 18,*B*). Thus the axil-arm structure of *Chiropinna* differs in no way from the pinnulate arms of such cladid inadunate genera as *Decadocrinus* and numerous others. These branchlets are undeniably pinnules, as judged by their attachment on alternate sides to each successive brachial, and in addition, whatever its significance may be, pinnulate arm-axils of *Chiropinna* give rise to first pinnules on the adanal side, rather than the abanal side of the main branch as characterizes the ramules in other genera of calceocrinids.

The median (E) ray of *Chiropinna* is unique among calceocrinids in showing a dichotomous divi-

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[1] This statement must be qualified at least to the extent of considering pinnules to be relatively diminutive unbranched appendages of crinoid arms given off on opposie sides of the arm in alternation and borne by successive brachials, as is the almost universal rule in pinnulate cladid inadunates (e.g., *Decadocrinus*, with uniserial brachials; *Eupachycrinus*, with biserial brachials), camerates (e.g., *Reteocrinus*, with uniserial brachals; *Batocrinus*, with biserial brachials), and articulates (e.g., *Pentacrinus*, *Comatula*, with uniserial brachials). In some homocrinids (e.g., *Ectenocrinus*, *Drymocrinus*, *Sygcaulocrinus*) and pisocrinids (e.g., *Cicerocrinus*) pinnulelike branchlets diverge from the opposite sides of arms in alternation at intervals of two to six brachials. Because these branchlets are undivided and display a regular heterotomous pattern, some authors have called them pinnules. In my opinion this is undesirable, since distinction is then obliterated between pinnules and unbranched ramules (as in *Dendrocrinus*, *Ottawacrinus*, *Daedalocrinus*, and many others, which no paleontologist considers to be pinnulate). If the alternating side branches of axil-arms observed in such calceocrinid genera as *Cremacrinus*, *Chirocrinus*, and *Halysiocrinus* were classifiable as pinnules, all of the Calceocrinidae (except *Senariocrinus*) would be describable as pinnulate. This is entirely unacceptable. Therefore, the statement that *Chiropinna* is the only known monocyclic inadunate crinoid with pinnules may be allowed to stand.

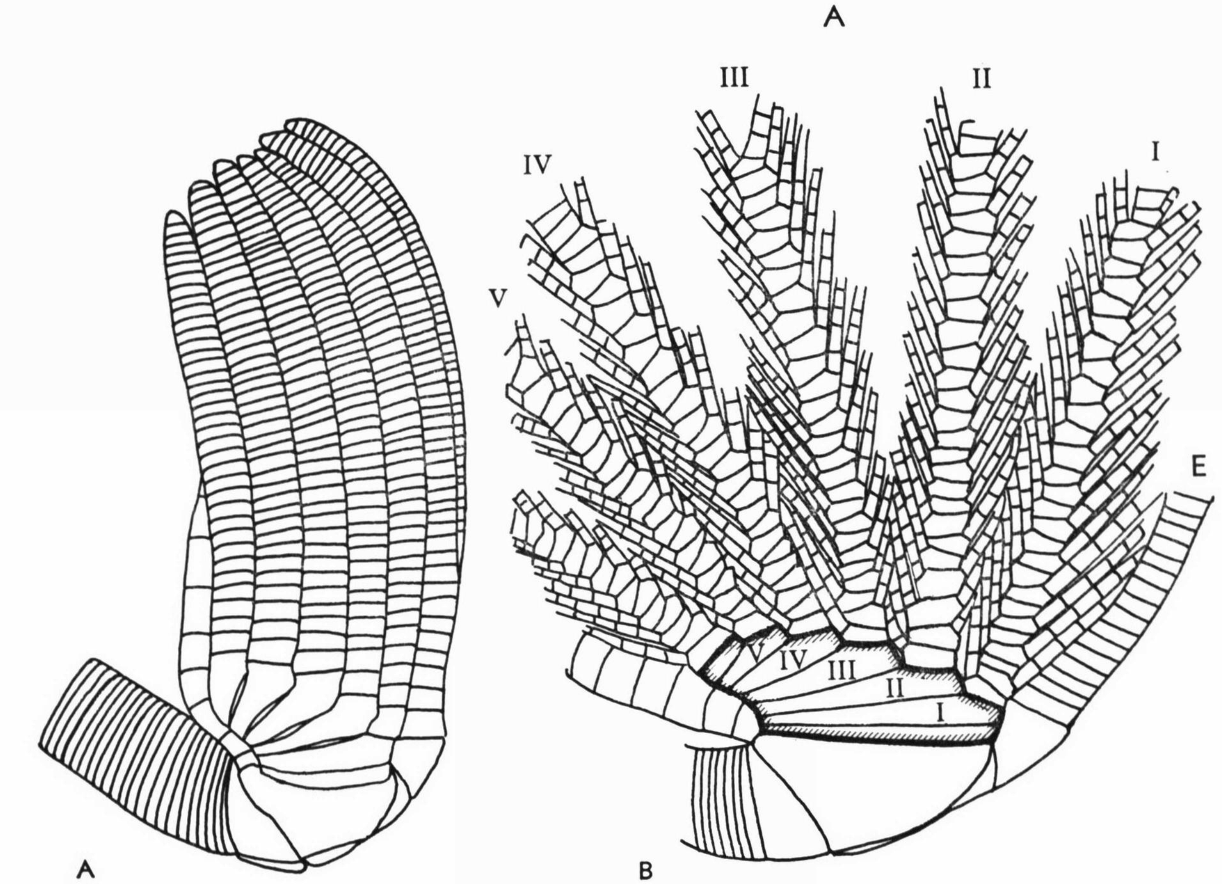


FIGURE 18. *A*. Anterior side of holotype of *Chiropinna pinnulata* (×2.7) showing well-developed main-axil series and closely appressed axil-arms composed of very numerous short brachials, anal tube and thick stem at left (after Bather, 1893). *B*. Arm structure of *Chiropinna pinnulata*, axil-arms being spread apart to show pinnules attached to each brachial (cuneate shape exaggerated); main-axil series distorted by arbitrary spread of axil-arms.

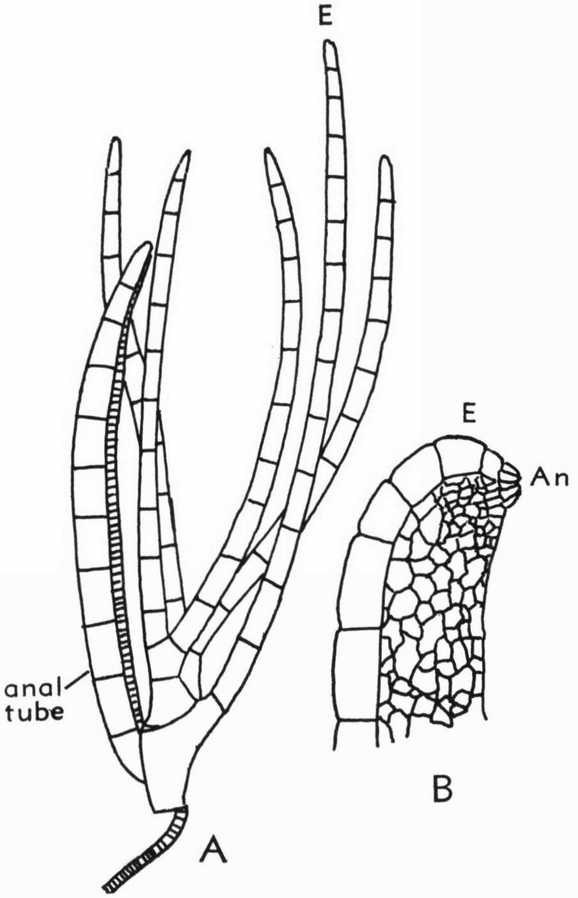


FIGURE 19. Crown of *Senariocrinus maucheri (A)* and enlargement of distal part of anal tube showing small anal pyramid at tip *(B)* (after Schmidt, 1934).

sion into two arms that are unbranched (except for abundant pinnules) above the single axillary primibrach which bears them (Fig. 5, *5b*). The first pinnules of the median arms are given off from the adanal side of the second brachials above the axillary primibrach. The branching of the E-ray arms on IBr, seems to be interpretable as an advanced evolutionary character, if one may compare *Chiropinna* with cladid crinoids. In *Calceocrinus anglicus* the median arm also bifurcates on the first primibrach, with additional heterotomous branchings higher up. The lowest bifurcation of this arm observed in other calceocrinids is on the third primibrach in *Calceocrinus ontario* and on the fourth primibrach in *Cremacrinus punctatus* and *Synchirocrinus bifurcatus*.

The dorsal cup of *Chiropinna* is unusual and distinct from those of other calceocrinids especially in characters of the compound radials, although the tripartite base is much the same as in *Deltacrinus, Chirocrinus, Synchirocrinus* and *Halysiocrinus*. The infer- and superradial of the median ray have an exceptionally broad contact with each other, considerably greater than in any other observed calceocrinid (Fig. 5, *5b*). If this is a primitive feature, as suggested by a general survey of the family and other disparid crinoids, then *Chiropinna* is at the bottom of the calceocrinid list of genera in this evolutionary character. On the other hand, the inferradials of the B- and C-rays, on the posterior side of the cup, are tiny, obliquely disposed plates with rectangular outline, widely separated from one another by the large subanal plate (Fig. 5, *5a*). Inferradials of this sort are not even approximately matched by corresponding plates in other calceocrinids, and they are interpreted as rather highly specialized.

On the whole, *Chiropinna* exhibits a very strange combination of peculiarities, the most distinctive and important of which is its remarkable development of abundant, quite typical pinnules. In the context of evolutionary differentiation of the calceocrinids, *Chiropinna* is isolated, standing alone and apart, without guessed-at origin and certainly without descendants. Its unique characters are without reasonably inferable sources in antecedent genera and without any known products of further evolution in later genera.

Only a single species of *Chiropinna* is known, the type-species, **C. pinnulata* (BATHER), from Middle Silurian rocks in two parts of Gotland. The holotype specimen comes from Faaroe, in southern Gotland.

Genus SENARIOCRINUS Schmidt, 1934 (p. 16)

Plate 3, figure 1; Text-figures 5,7; 19

[Type-species, **S. maucheri* SCHMIDT, 1934 (p. 16); monotypy]

Crown with strongly defined bilateral symmetry defined by the plane coinciding with the E-ray and BC-interray, distinguished by single dichotomous division of A- and D-arms, neither of which bear ramules, by long unbranched E-arm, and stout series of anal plates having U-shaped cross section and supporting fine-plated sac that arches over the grooved anal plates on the inner (ventral) side, small anal pyramid present at tip of anal series. Dorsal-cup plates doubly hinged on the homocrinoid (E-BC) axis of bilateral symmetry, one hinge between single triangular basal plate (presumably formed by coalescence of separate antecedent basals) and E-inferradial, and another hinge between fused BC-inferradials and B+C-superradials, which adjoin one another along oblique suture in such manner that C-superradial mainly supports anal X. Stem attached at extremity of basal opposite hinge; stem composed of small dis-

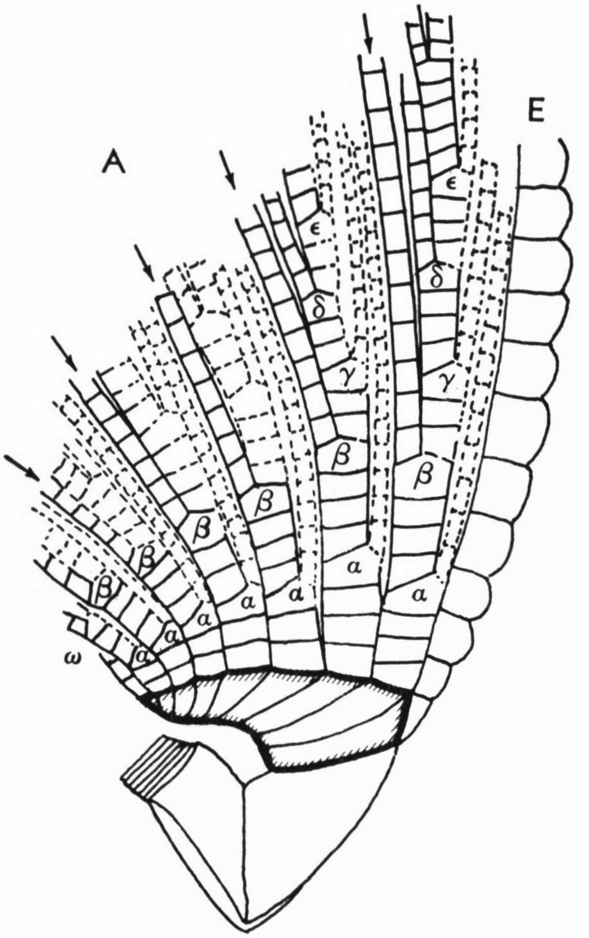


Figure 20. Main-axil and axil-arm structures of *Halysiocrinus,* the axil-arms being spread slightly apart in order to indicate some ramules and brachial series, which are concealed. Although the alpha-ramules, for example, are not exposed in some specimens, they are clearly observable in others (e.g., *H. dactylus,* Pl. 2, fig. *1a*; *H. nodosus,* Pl. 2, fig. *3a*) and their presence invariably is indicated by the discernible axillary nature of the most distal alphabrach.

coid columnals, thin, short, and tapering distally to a point. *L. Dev.,* West Germany.

This genus is represented only by the type-species, based on several well-preserved, fairly complete specimens, all collected from the Hunsrück Shale near Bundenbach, West Germany.

Senariocrinus unquestionably belongs to the Calceocrinidae but it is a very strange representative of the family, indeed. The genus is interpretable only as an unexpected sort of offshoot from the main stock which leads from Ordovician forms such as *Cremacrinus* and *Calceocrinus* to the Silurian *Chirocrinus* and *Synchirocrinus,* the Devonian *Deltacrinus,* and ultimately to the Mississippian *Halysiocrinus.* It is readily distinguished by the unbranched nature of its five arms, relatively stout anal tube, and double hingement of dorsal-cup plates (Figs. 5,7; 19). Two primibrachs are seen in the lateral rays (A, D) but no suggestion of main-axil structure.

Schmidt postulated that *Senariocrinus* was a free-swimming crinoid which was able to move through the water by sweeping motions of its lateral arms that alternated with forward-and-backward motions of the unpaired (E) arm and anal tube acting together. Thus he thought that the anal tube, derived by evolutionary modification of an arm, reverted in function to the swimming movements of an arm, though it continued to serve for discharge of waste and possibly for respiration instead of food gathering. The trailing slender stem, according to Schmidt, might have helped for steering, and for twisting about the stalks of other crinoids to provide temporary anchorage. Whether this guess as to the mode of life of *Senariocrinus* is approximately correct or not, the described crinoid is a unique form among calceocrinids. Its simplicity of arm structure, coupled with unusually specialized characters of the dorsal cup, suggests that the genus represents an advanced stage of evolution, mostly in a retrogressive direction. It is not primitive and not by any stretch of imagination can it be the ancestral stock from which other known calceocrinids could have descended. In retaining separate B- and C-superradials, the genus is more like *Cremacrinus* than any other member of the family. All in all, Schmidt's interpretation of *Senariocrinus* as end product of an evolutionary offshoot from *Cremacrinus* seems to be acceptable.

Genus HALYSIOCRINUS Ulrich, 1886 (p. 110)

Plate 2, figures 1a-d, 3a-c; Text-figures 1; 3,*4a,b*; 5,*8a,b*; 7,*H-K*; 8; 20

[Type-species, **Cheirocrinus dactylus* Hall, 1860 (p. 123); orig. desig.] [Bather's (1893, p. 63) designation of *Calceocrinus ventricosus* (=*Cheirocrinus ventricosus* Hall, 1860) as type-species of *Halysiocrinus* is invalid, whatever may be one's judgment as to the status of this species as a probable synonym of *Cheirocrinus dactylus,* as generally held, or as an independent species.]

Crown slender to moderately full in girth, perfectly symmetrical, median (E-ray) with infer- and superradial plates well separated by adjoined lateral radials between them and with isotomously to heterotomously branched medial and distal parts of median ray, lateral rays with large radials that support curved main-axils and numerous axil-arms which bear large but not dominant beta-ramules (Fig. 20), as in *Synchirocrinus*; dorsal cup composed of large lateral radials that adjoin one another between infer- and superradial of median radial, inferradials of B- and C-rays that adjoin above stem impression and beneath fused superradial of these rays, and a three-plate basal "circlet" in which the median element along the hinge is a low, arcuate plate. *M. Dev.*, North America (Iowa-Indiana); *L. Miss.*, North America (Indiana-Iowa-Kentucky-Tennessee).

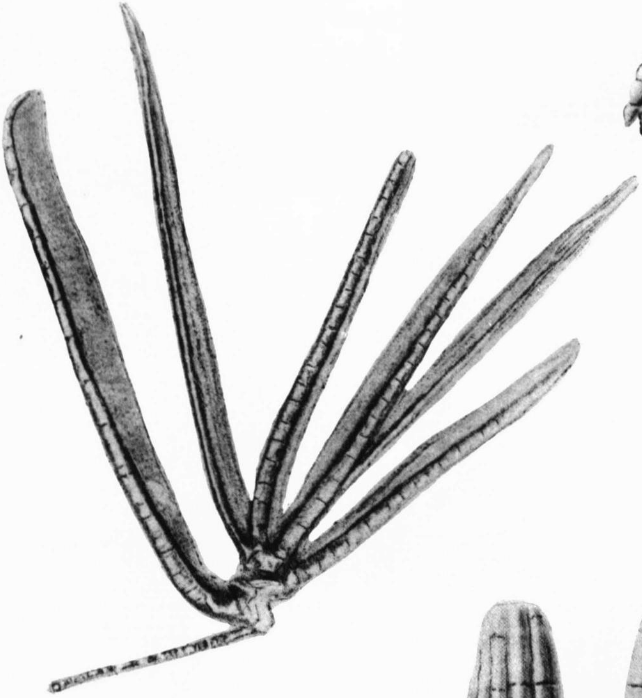
Halysiocrinus is a well-characterized calceocrinid which contains the geologically youngest representatives of the family. Species of the genus are distributed from Middle Devonian to Lower Mississippian, all from North America. Dorsal-cup characters resemble those of *Deltacrinus* in the broad contact of the lateral radials between the infer- and superradials of the median (E) ray and in characters of the basals, although the median basal of *Halysiocrinus* has an arcuate, rather than angular margin on the side toward the stem impression (away from the hinge) (Fig. 5, *8a,b*).

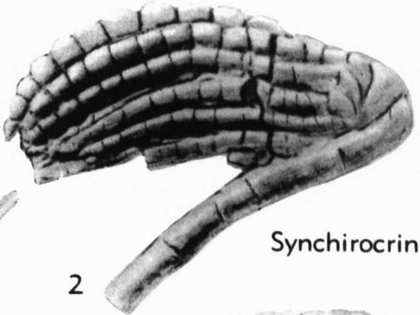
A feature that serves to distinguish *Halysiocrinus* from all other calceocrinids is occurrence of the inferradials of the B- and C-rays in contact with one another just above the stem impression (Figs. 3, *4b*; 5, *8a*). Except in *Halysiocrinus,* these plates are separated by the B- and C-superradials (*Cremacrinus*) or by the single plate (so-called subanal) formed by fusion of these superradials (*Calceocrinus, Chirocrinus, Synchirocrinus, Deltacrinus, Chiropinna*). Although these plates correspond precisely in shape and position to the superradials of these rays in *Cremacrinus,* they are unquestionably not superradials but identified as inferradials, (1) because such separate plates occur in all other calceocrinid genera except *Senariocrinus,* in which they are fused together, and (lacking good evidence) cannot be assumed to vanish abruptly in *Halysiocrinus,* and (2) because the reappearance of two superradials in place of the single fused superradial of other calceocrinid genera (so-called "T-piece" of BATHER or subanal of SPRINGER) would be an inexplicable backward step in evolution. Consequently, all authors have accepted the identification of these plates as inferradials.

Where, then, is the subanal? It should persist in *Halysiocrinus,* since it is found in all other calceocrinids except primitive *Cremacrinus* and in *Senariocri-*

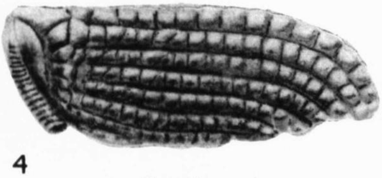
EXPLANATION OF PLATE 3

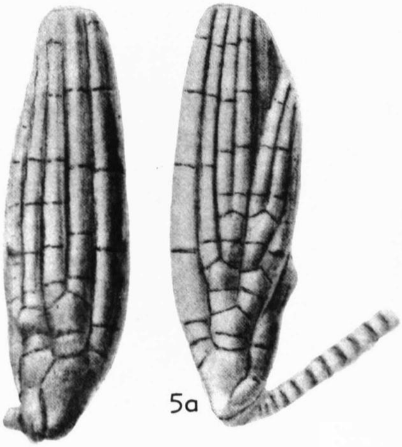
FIGURE		PAGE
1.	*Senariocrinus maucheri* SCHMIDT, Lower Devonian, Coblenzian, Hunsrück Shale, near Bundenbach, West Germany; holotype specimen of type-species of genus, crown from left posterior (D) side with part of very slender, distally tapering stem, anal tube with saclike cover at left and unbranched median (E-ray) arm at right, ×0.85 (after Schmidt, 1934)	30
2.	*Synchirocrinus serialis* (SALTER), Middle Silurian, Wenlockian, near Dudley, England; lectotype, anterior side, most of visible arms consisting of beta-ramules, ×1.3 (after Ramsbottom, 1952)	27
3.	*Synchirocrinus gradatus* (SALTER), Middle Silurian, Wenlockian, near Dudley, England; holotype, anterior side, ×1.3 (after Ramsbottom, 1952)	27
4.	*Synchirocrinus nitidus* (BATHER), Middle Silurian, Wenlockian, near Dudley, England; type-species of genus, a well-preserved complete crown recumbent on stem, left posterior (D-ray) view, long median arm at top, strong beta-ramules concealing distal parts of axil-arms, ×1.3 (after Springer, 1926)	27
5.	*Anulocrinus simplex* (SPRINGER), Middle Silurian, Niagaran, Beech River Formation, Decatur County, Tennessee; *5a,b,* holotype (U.S.N.M., no. S2158), left posterior (D-ray) and opposite (A- and B-ray) sides of crown, ×3 (after Springer, 1926)	21
6.	*Halysiocrinus perplexus* (SHUMARD), Lower Mississippian, Osagian, New Providence Shale, near Louisville, Kentucky; exterior of dorsal cup (U.S.N.M., no. S2196) showing grooved areas for muscle attachment along hinge, radial and basal circlets in fully extended position, ×1.3 (after Springer, 1926)	31
7.	*Chirocrinus fletcheri* (SALTER), Middle Silurian, Wenlockian, near Dudley, England; holotype, left posterior (D-ray) side, showing axil-arms spread out in fanlike manner with modest-sized ramules mostly visible, ×1.3 (after Ramsbottom, 1952)	24
8.	*Synchirocrinus foerstei* (SPRINGER), Middle Silurian, Niagaran, Beech River Formation, Decatur County, Tennessee; *8a,b,* lectotype (U.S.N.M., no. S2172a), herein designated, left posterior (D-ray) and left anterior (E-ray) sides, proximal four brachials of each axil-arm consisting of alphabrachs and betabrachs, succeeded upward (distally) by robust beta-ramules, which entirely conceal other parts of axil-arms with their small ramules, ×1.3 (after Springer, 1926)	27

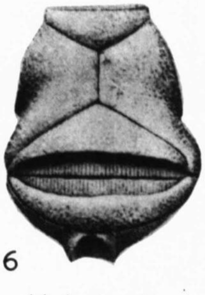

1 Senariocrinus

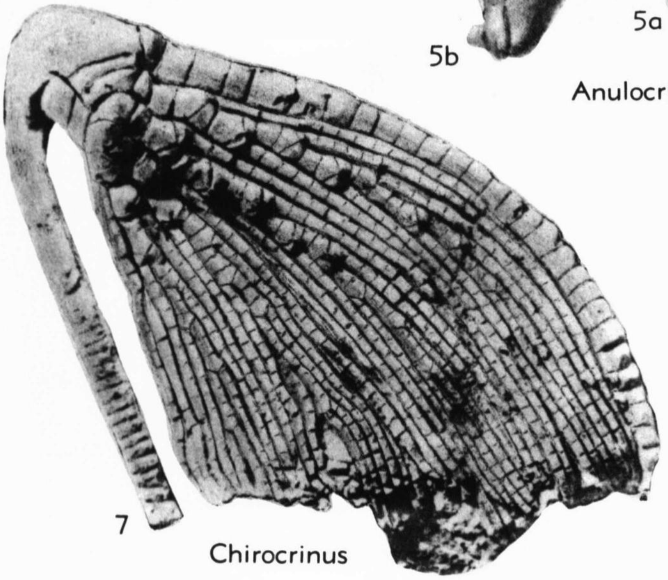

2 Synchirocrinus

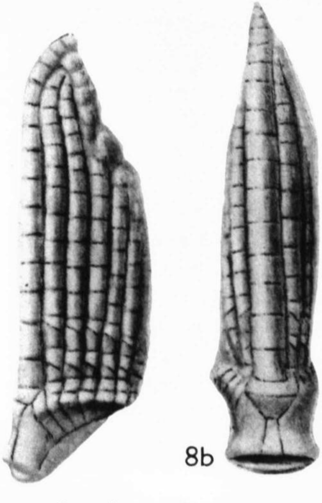

3 Synchirocrinus


4 Synchirocrinus


5a 5b Anulocrinus


6 Halysiocrinus


7 Chirocrinus


8a 8b Synchirocrinus

MOORE — Revision of Calceocrinidae

nus with their two superradials. BATHER (1893, p. 61) concluded that *Halysiocrinus* lacks a subanal plate, for he designated the plate next above the two inferradials as anal X, and his interpretation was accepted without comment by GOLDRING (1923, p. 337), SPRINGER (1926, p. 91), MOORE & LAUDON (1943, p. 27; 1944, p. 145), MOORE in MOORE, LALICKER & FISCHER (1952, p. 642), and UBAGHS (1953, p. 745). This, of course, signifies disappearance of the subanal in evolution of the single calceocrinid line comprised of the assemblage known as *Halysiocrinus*. In general discussion of the Calceocrinidae, SPRINGER (1926, p. 89), wrote: "later, the subanal piece atrophies, and the anal *x* or tube rests upon the corresponding inferradials." Concerning *Halysiocrinus*, he added (op. cit., p. 121): "Subanal piece atrophied or hidden, its place being taken by the posterior shifting of r.post. and r.ant. inferradials, which have met, supporting anal *x* directly." All this is based on tacit assumptions, which certainly are no more than that, since no actual evidence of vanishment of the subanal element is presented and possibility that the plate called anal X really may be the subanal piece was not even mentioned by BATHER, SPRINGER, or anyone else. In my view, it is much more logical to conclude that the alleged anal X of *Halysiocrinus* is in fact the subanal plate than to suppose that so persistent a structural element as the subanal should in this genus disappear. It was merely pushed upward by migration of the inferradials to their observed median position. To be sure, my interpretation also is based on assumptions, but they have the virtue of offering a better correlation of morphological features seen in *Halysiocrinus* with those of other calceocrinids than postulated atrophy of the subanal. Further, upward migration of the subanal seems to be a more expectable mark of a late stage in evolution of the posterior side of the dorsal cup in this group than vanishment. In other calceocrinids (e.g., *Calceocrinus, Chirocrinus, Synchirocrinus, Deltacrinus, Chiropinna*) the subanal plate, though definitely identifiable, may not differ greatly from anal X, and therefore, if both of these plates are pushed upward together, it is not surprising that the lower one (subanal) should have been misidentified as anal X.

The ancestral crinoids from which *Halysiocrinus* became differentiated might resemble *Deltacrinus*, as suggested by marked similarity of dorsal-cup features, or *Chirocrinus*, as indicated by characters of the lateral rays with strongly developed main-axils and numerous axil-arms, which in *Halysiocrinus* show enlargement of the beta-ramules less prominent than in *Synchirocrinus*. The evidence of similarity in arm structure is considered to be more significant than that furnished by features of the dorsal cup. Hence, *Halysiocrinus* is judged to be an offshoot of the *Chirocrinus* stock (Fig. 21).

Halysiocrinus, as presently known, contains two Middle Devonian species and nine Lower Mississippian species, all from the United States. The Devonian forms are *H. carinatus* SPRINGER and *H. elephantinus* LAUDON (Fig. 7, *H*), from northern Michigan and Iowa, respectively. Species from Burlington and Keokuk (Lower Mississippian) strata include the type-species, **H. dactylus* (HALL), (Pl. 2, figs. 1a-d; Fig. 7, *I*), *H. tunicatus* (HALL), *H. robustus* (WORTHEN), *H.? lamellosus* (HALL), and *H. wachsmuthi* (MEEK & WORTHEN), all from Iowa; *H. nodosus* (HALL), (Pl. 2, figs. 3a-c; Figs. 1; 7, *K*), from Iowa and Indiana; *H. bradleyi* (MEEK & WORTHEN) (Fig. 7,*J*), from Indiana; *H. granuliferus* (ROWLEY), from Kentucky; and *H. perplexus* (SHUMARD) (Pl. 3, fig. 6), from Indiana, Kentucky, and Tennessee.

SUMMARY OF CALCEOCRINID EVOLUTION

DEVELOPMENT OF BILATERAL SYMMETRY

The Calceocrinidae comprise a group of unusually distinctive monocyclic inadunate crinoids which are readily differentiated from others and which furnish among their members exceptionally well-defined evidence of evolutionary changes in morphology of the dorsal cup and arms. Their outstanding character is a remarkably emphasized bilateral symmetry in the plane that coincides with the E-ray and BC-interray, located at an angle of 72 degrees from the crinoid plane extending through the anterior (A) ray and posterior (CD) interray. The crinoid plane is dominant in most crinoids but in the calceocrinids it becomes entirely suppressed.

The structural plan of calceocrinids conforms to that of *Homocrinus* and other genera of the Homocrinidae in having large, undivided radial plates in the A- and D-rays and compound radials in the three remaining rays (Figs. 3, 4). The arrangement of simple and compound radials defines a plane of bilateral symmetry that coincides with the mid-line of the compound E-radial and the suture dividing the

B- and C-compound radials. The simple undivided radials are in lateral position on opposite sides. This arrangement is accentuated in calceocrinid genera by relative enlargement of the undivided lateral radials and diminution of the E- and B+C-compound radials (Fig. 3). In all but two genera (*Cremacrinus, Senariocrinus*), or possibly three (adding *Anulocrinus*), the superradials of the B- and C-rays are fused together so as to form the laterally extended subanal located exactly in the median plane of the crinoid. The anal tube supported by this plate is adjacent to the stem and parallels it. Bilateral symmetry is perfectly developed, and it characterizes all calceocrinids except *Cremacrinus* (and possibly *Anulocrinus*).

FEATURES OF THE DORSAL CUP

All genera of the Calceocrinidae display a movable hinge structure disposed perpendicular to the median plane of the dorsal cup and crown. It is located between the basals on one side (adjacent to the stem) and radials on the other (opposite to the stem). On the radial side the hinge abuts against the E-ray inferradial alone or it touches this plate in median position and edges of the A- and D-radials on either side of the E-inferradial (Fig. 5). This hinged arrangement, which is found in no other crinoids, seems to have been about as well developed in the oldest known representatives of the family (Middle Ordovician species of *Cremacrinus* and *Calceocrinus*) as in later ones, but differences are observed in the number and arrangement of plates that adjoin the hinge.

Cremacrinus, Calceocrinus, and probably *Anulocrinus,* are unlike other calceocrinids in having four basal plates, each of which forms part of one side of the hinge and is partly covered by the proximal columnal of the stem (Fig. 5,*1a,2a*). This pattern may be discriminated as the earliest and most primitive one known. On the opposite side of the hinge in these genera, the E-inferradial forms a narrow median portion and the large lateral radials make up the outer, larger extremities.

A seemingly more advanced evolutionary stage is represented by *Chirocrinus* and *Synchirocrinus,* because in these genera the basal "circlet" is reduced to three plates by fusion of the median ones (DE, EA) to form a wide, low triangular plate that along its base adjoins all or nearly all of the hinge (Fig. 5, *3a,4a*). In these two genera, as in *Cremacrinus, Calceocrinus, Anulocrinus,* and *Senariocrinus,* the radial side of the hinge is bordered by the narrow median E-inferradial and wider lateral divisions formed by edges of the A- and D-radials. *Senariocrinus* possesses a single basal plate of triangular form, which presumably represents the completely fused product of the three or four separate basals found in other calceocrinids (Fig. 5,*7*). If this is correct, *Senariocrinus* constitutes the most specialized (advanced) of all calceocrinids in this character, but it is combined with other features distinguished by extreme simplicity and seemingly interpretable as primitive. Possibly this indicates pronounced evolution in a regressive direction.

The dorsal cups of remaining calceocrinid genera (*Deltacrinus, Chiropinna, Halysiocrinus*) have three basals, of which the upper two meet one another along the mid-line and bear the stem impression (Fig. 5,*5a,6a,8a*); the lower basal is a very broad, low triangular or arcuate plate which extends all along the hinge to its extremities. The radial side of the hinge consists of the left anterior (E) inferradial only, without parts of the lateral radials touching the hinge. These characters, taken together, are inferred to mark a culmination of evolutionary trends affecting the dorsal cup in parts adjacent to the hinge. The extended sutural contact of the lateral radials with each other in *Deltacrinus* and *Halysiocrinus,* accompanied by wide separation of the infer- and superradials of the median (E) ray, is interpreted to be an advanced evolutionary feature, which contrasts with the exceptionally broad contact of the two parts of the median radial in *Chiropinna,* considered to be a primitive feature (Fig. 5, *5b,6b,8b*).

Finally, a review of dorsal-cup construction that seeks to distinguish signs of evolution must take account of the radial-plate elements of the B- and C-rays. These adjoin or are close to the basal plate (*Senariocrinus*) or plates (other calceocrinid genera) on sides away from the hinge upward and laterally. The inferradial plates of these rays are interpreted to be fused together in *Senariocrinus* but they are separate, generally spear-shaped components of the dorsal cup in other calceocrinids, and except in *Halysiocrinus* they do not touch each other (Fig. 5, *8a*). The B- and C-inferradials of *Halysiocrinus* are equidimensional pentagonal plates that meet along the mid-line just above the stem impression, indicating their inward-upward migration in the course of evolution. In *Chiropinna* they are symmetrically placed small quadrangular plates occurring obliquely below lateral extremities of the subanal (fused superradial element) (Fig. 5, *5a*). The subanal is a constant character of all calceocrinid genera (excepting *Cremacrinus, Senariocrinus,* and possibly *Anulocrinus,* in which the superradials are separate), but its shape is seen to vary considerably. The development of a subanal is certainly an evolutionary advancement from the separate superradials of *Cremacrinus,* and its migration upward to a position well separated from the stem impression, as seen in *Halysiocrinus,* distinguishes a terminal stage in evolution of the subanal.

The possibility that the C-inferradial of calceocrinids is equivalent to the radianal or inferradianal of some other inadunate crinoids has been considered under "Morphological Features" in discussing the structure of the dorsal cup. This possibility, which applies equally to all calceocrinids, is viewed adversely, mainly on the ground that no evidence has been found in any disparid crinoid (not including Hybocrinida) for differentiating the C-inferradial, C-superradial, or C-radial elements of the dorsal cup as specially distinct from other plates of the radial circlet in showing the functions and evolutionary trends of an undoubted radianal (and in the cladid crinoid *Carabocrinus,* an inferradianal) element and associated anal series. Likewise, identification of either the C-superradial of *Cremacrinus* and *Senariocrinus* or the subanal plate of other calceocrinids as a radianal is rejected, notwithstanding classification of the next higher plate as anal X, since it marks the proximal extremity of the anal tube. I conclude that the radianal and inferradianal are morphological elements quite foreign to calceocrinids.

ANAL TUBE

Distinguishing morphological features of the anal tube observed in all genera of the Calceocrinidae have been described in an early part of this paper. Relative massiveness of the uniserially arranged unbranched series of plates forming the anal tube is a chief character in addition to its constant occurrence above the C-superradial or B+C superradial (subanal) on the posterior side of the cup between the lateral radials. The only noteworthy modification that reflects a significant evolutionary change is a shift in position of the tube from its off-center placement above the C-ray in *Cremacrinus* (with the stem impression obliquely below it) to an exactly median location opposite the E-ray in other calceocrinids (with the stem impression directly beneath the proximal extremity of the tube). Once this step toward perfect bilateral symmetry was taken in evolution, little else happened.

The remarkable hingement between B+C inferradial and superradial elements in *Senariocrinus* is located only a little below anal X and this led SCHMIDT to postulate a forward-and-backward movement of the tube in conjunction with similar movement of the left anterior arm in rhythmic alternation with sweeping motions of the pair of lateral arms, working in unison so as to propel this crinoid in swimming. This would be a very unusual evolutionary attainment—one that seems to be highly conjectural. SCHMIDT's somewhat guarded conclusion that the anal tube of *Senariocrinus*—which is an undoubted product of evolution from an arm of the C-ray—reverted in its functions to those of an arm seems dubious, especially since the presence of a small anal pyramid at tip of the tube indicates that this supposed anal "arm" primarily served excretory purposes and not food-gathering.

STRUCTURE OF ARMS

Next to the evolutionary development in calceocrinids that produced unusual perfection of bilateral symmetry in the plane of the E-ray (Fig. 3), though actually comprising an essential part of this development, arm structures seen in genera of this family strikingly demonstrate certain common attributes which are coupled with indications of progressive evolution in various directions or of seemingly abrupt divergences along one line or another. The most important characters calling for comparison in seeking to classify developmental stages as primitive, intermediate, or advanced (specialized) are those of main-axil structure, on one hand, and of axil-arm pattern, on the other. In addition, the unbranched or branched nature of the arm borne by the E-superradial may be significant, (1) an unbranched arm being interpreted as primitive, (2) isotomous division well above the E-superradial being considered less advanced than near or at the proximal extremity of this arm, and (3) multiple heterotomous branching above the isotomous division being inferred to mark greatest observed specialization. As for main-axil structure, it is rather clear (4) that lack of evident distinction of main-axils in arm systems borne by the large undivided lateral radials is a primitive character, and commonly such ill-defined main-axils contain axillary brachials with subequal distal facets, which denote isotomous division within the main-axil series, are composed of very few brachials, commonly confined to primibrachs, secundibrachs, and possibly tertibrach, and include nonaxillary brachials in series higher than primibrachs (Fig. 11). Advanced main-axils (5) are composed of successive axillaries without interposed nonaxillary plates, (6) display axillaries with decidedly unequal distal facets, those bearing axil-arms being much the smaller, and (7) consist of relatively numerous axillaries, which taper and tend to curve adanally. The axil-arms are rather difficult to interpret in terms of evolutionary significance, partly because of the uniformity throughout the family in basic features of the heterotomous branching that gives rise to ramules on opposite sides of the axil-arms. The pattern of branching is remarkably constant, alpha-ramules being given off invariably on the abanal side of the axil-arms, beta-ramules on the adanal side, and so on. Presumably, few ramules given off at widely spaced intervals would represent a more primitive type of heterotomy than numerous ramules in somewhat closely spaced arrangement. The correctness of such an inference is doubtful, since *Deltacrinus* (Fig. 17) illustrates axil-arms with relatively few and widely spaced ramules, whereas *Cremacrinus* (Fig. 10), which certainly is a more primitive calceocrinid, has numerous, rather closely spaced ramules. The foregoing observations indicate that the number and spacing of ramules are indeterminate markers of evolutionary advancement in the Calceocrinidae. Absence of ramules, as in *Senariocrinus,* is interpreted as a sign of advanced regressive evolution. The presence of abundant pinnules in *Chiropinna* (Fig. 18,*B*) sets this genus apart from all other calceocrinids and is not explainable as an evolutionary development of the ramule-bearing axil-arms of other calceocrinids.

The main-axils of the lateral rays are an important distinguishing feature of calceocrinids taken as a group (Fig. 8), but they are very unequally developed in different genera belonging to the family. In *Senariocrinus* they are entirely lacking (Fig. 19). The main-axil structure is so ill developed in *Cremacrinus, Calceocrinus, Anulocrinus,* and *Deltacrinus* as to be hardly discernible (Figs. 10, 11, 13, 14, 17); it is moderately defined in *Chirocrinus* (Fig. 9) but lacking in prominence; in *Synchirocrinus, Chiropinna,* and *Halysiocrinus* the main-axil series is highly developed and very prominent as a feature of the lateral rays (Figs. 15, 16, 18, 20), generally it is accompanied by marked curvature of the abanal to adanal axillaries of the series. With little doubt, the indistinct main-axil pattern of *Cremacrinus, Calceocrinus, Anulocrinus,* and *Deltacrinus* represents an early stage in evolution of this character and *Chirocrinus* indicates an intermediate stage. Culmination in development of the main-axil arrangement of plates at the proximal extremity of axil-arms of the lateral rays is surely indicated by *Synchirocrinus, Chiropinna,* and *Halysiocrinus.* In other characters, however, the three last-mentioned genera are rather widely divergent.

Fewness of axil-arms accompanies weak development of main-axils and is interpreted as a primitive character. Their number is invariably two in each lateral ray of *Senariocrinus* (Fig. 19), generally two or rarely three in *Cremacrinus* and up to four in *Calceocrinus* (Figs. 10, 11), three or four in *Deltacrinus* (Fig. 17), and five to eight in *Anulocrinus, Chirocrinus, Synchirocrinus, Chiropinna,* and *Halysiocrinus* (Figs. 9, 13-16, 18, 20). In view of specialized dorsal-cup characters observed in *Senariocrinus* and its occurrence in the Devonian, the simplicity of arm structure in this genus may denote regressive evolution, but *Cremacrinus* and *Calceocrinus* surely represent an early stage in evolution of axil-arm structures. *Halysiocrinus* clearly shows a peak of development along this line, whereas other genera are intermediate.

Heterotomous branching of the axil-arms is discernible but not strikingly evident in *Calceocrinus, Anulocrinus, Deltacrinus,* and some species of *Cremacrinus.* Also, inspection of the visible part of the axil-arms belonging to most specimens of *Synchirocrinus* misleadingly suggests that heterotomy does not exist in this genus (Fig. 15,*B*), though actually it is both highly and peculiarly developed. As pointed out in previous description of *Synchirocrinus,* an exceptional robustness of the beta-ramules of each axil-arm, combined with their parallel arrangement on the outer face of the lateral rays, gives the appearance of simple, unbranched arms that arise from each axillary primibrach. Repeated heterotomous branching occurs along the concealed parts of the axil-arms, but the alpha-ramules, gamma-ramules, delta-ramules, and others are diminutive. Strongly marked heterotomy characterizes the axil-arms of some species of *Cremacrinus* (e.g., *C. tubuliferus,* Fig. 10) and virtually all crinoids assigned to *Chirocrinus* and *Halysiocrinus.* Together with *Synchirocrinus,* these genera are definable as advanced in accentuation of this character, even though basically it may be an archaic type of arm division.

The absence of ramules in *Senariocrinus* is puzzling in view of their prevalence in other calceocrinid genera (excluding *Chiropinna*). That the lacking ramules indicate loss during evolution from the ancestral stock of this genus, whatever relative of *Cremacrinus* it may have been, seems more probable than the postulate that the lineage of *Senariocrinus* failed to achieve heterotomy of the axil-arms.

Discussion of the arm structure of *Chiropinna* has already emphasized its inexplicably unique nature in possessing an abundance of typical pinnules (Fig. 18,*B*). One may well classify this genus as an amazing evolutionary freak, especially in view of the fact that no other monocyclic inadunate crinoid is known to have pinnules.[1] *Chiropinna* is a typical calceocrinid in all essential features of its dorsal cup and crown, including well-developed hinge between the median (DE+EA) basal and E-inferradial, and pendent position of the crown close to the large stem. It is a quite normal member of the family in having perfect bilateral symmetry defined by the plane that bisects the E-ray and BC-interray. The main-axils of the lateral rays are prominent, very well differentiated, and curved toward the adanal extremities. The two arms of the E-ray and numerous axil-arms of the lateral rays are the elements that obviously are very foreign to the Calceocrinidae. They are unallowable, yet not to be denied. Therefore, we can only treat *Chiropinna* as a highly aberrant, possibly precocious product of evolution which abruptly appeared "out of nowhere" and with equal abruptness vanished without trace as to lineage. In the context of its Silurian calceocrinid associates, it represents an evolutionary explosion presumably induced by far-reaching abrupt mutation of genes and is comparable to a short-lived "nova" star as observed by astronomers.

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[1] See footnote, p. 29.

PHYLOGENY OF CALCEOCRINIDAE

The origin of the family known as Calceocrinidae almost surely can be assigned to ancestors classifiable as belonging to the Homocrinidae, even though none of the latter are known to antedate the oldest yet discovered calceocrinids. Representatives of both of these families first appear in the Middle Ordovician but it is reasonably certain that source homocrinids antedate the earliest calceocrinids, since the latter are distinguished by such derived special characters as recumbent position of the crown accompanied by a unique hingement involving dorsal-cup plates. The homocrinid pattern of bilateral symmetry defined by arrangement of the large undivided radials of the A- and D-rays and compound radials of other rays was strongly accentuated in the calceocrinid stock by the tendency of the B- and C-rays to become suppressed.

Although *Cremacrinus* and *Calceocrinus* are represented by almost equally old species, the former is judged to be the genus having characters closest to their common homocrinid ancestors. This is because *Cremacrinus* lacks perfect bilateral symmetry, having four arm-bearing radials in addition to the fifth (C-ray) which gives rise to the anal series.

Anulocrinus is an Upper Ordovician to Middle Silurian genus that rather surely is interpretable as a direct descendant of *Cremacrinus,* as indicated by its four arm-bearing radials (Fig. 21). The type-species of *Anulocrinus* shows advancement over known representatives of *Cremacrinus* in having more numerous axil-arms, and the same is true of *Calceocrinus* except for the Middle Ordovician *C. barrandei.*

Senariocrinus seems to be an aberrant and tardy derivative of the *Cremacrinus* stock, possibly through *Anulocrinus,* as suggested by the observed dorsal-cup structures of *Senariocrinus,* combined with the simplicity of arms in some species of *Anulocrinus.* Also, *Anulocrinus* and *Senariocrinus* both occur in western Europe, whereas *Cremacrinus* is yet known only from localities in North America. The inferred phylogenetic relationships of these three genera are indicated graphically in Figure 21.

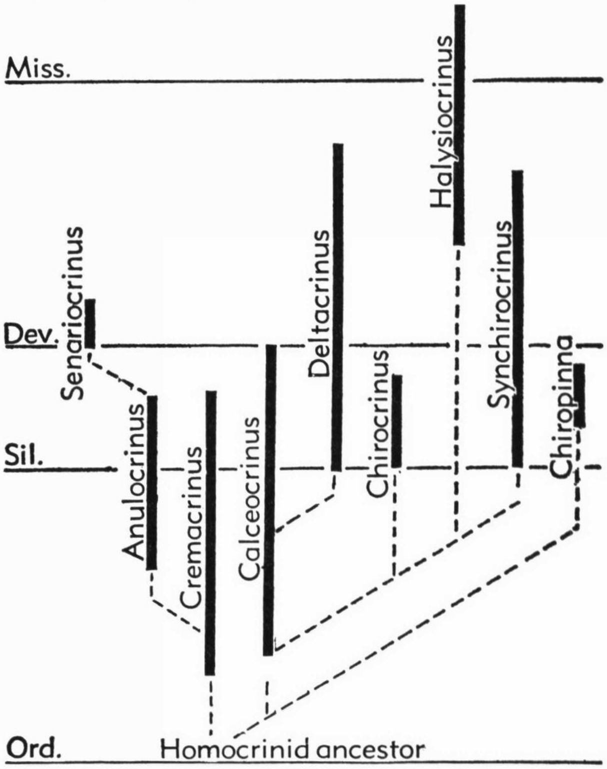

FIGURE 21. Stratigraphic distribution and inferred phylogenetic relationships of calceocrinid genera.

Deltacrinus which ranges from Early Silurian through Middle Devonian, is interpreted as a descendant of *Calceocrinus* (Fig. 21). It has perfect bilateral symmetry and possesses relatively advanced evolutionary characters of the dorsal cup, combined with little-developed main-axils and only a few axil-arms that give rise to widely spaced ramules.

Chirocrinus, Halysiocrinus, and *Synchirocrinus* may be considered together because of general resemblance to one another in main morphological characters. Each genus is well advanced in evolution, having large main-axils and relatively numerous axil-arms. *Chirocrinus,* which ranges from Early Silurian through Middle Silurian, has the most generalized structure and consequently may be regarded as closest to *Calceocrinus,* which probably gave rise to all three genera of this group (Fig. 21). *Synchirocrinus* is longer-ranging (Early Silurian to Middle Devonian) than *Chirocrinus* and is represented by more numerous species. In specialized features of the axil-arms of the lateral rays, particularly robustness and parallel arrangement of the beta-ramules, with accompanying concealment of brachials and ramules above the beta-brachs, *Synchirocrinus* is highly distinctive. It marks the culmination of evolutionary trends affecting heterotomy of the axil-arms. *Halysiocrinus* may be characterized as an entirely normal calceocrinid that possesses highly developed main-axils combined with axil-arms which are intermediate between those of *Chirocrinus* and *Synchirocrinus.* Its dorsal cup is of advanced type in all features, but especially in showing upward migration of the B- and C-inferradials to adjoined position just above the stem impression borne by the basals. If *Halysiocrinus* is correctly interpreted as a derivative of the lineage that gave rise to *Chirocrinus* and *Synchirocrinus,* but not of either one or the other of these genera, the inferred Late Ordovician, Silurian, and Early Devonian forerunners of *Halysiocrinus* are unknown (Fig. 21).

Discussion of *Chiropinna* has emphasized the uniqueness of its pinnule-bearing arms. In other features, including well-developed hingement in the dorsal cup and advanced type of main-axil series, this genus is a very typical calceocrinid. It appeared in the Middle Silurian crinoid assemblage of Gotland, persisted possibly into the early Late Silurian (Ludlovian), and then vanished. That *Chiropinna* could have been shaped out of ancestors assignable to any known calceocrinid genus is inconceivable. Therefore, its origin is guessed to belong near the beginning of the calceocrinid assemblage and evolutionary development of the necessarily once-existing antecedents of *Chiropinna* in Ordovician time is quite unknown (Fig. 21).

In conclusion, one may observe that very few groups of animals are as well circumscribed by morphological features as the crinoids of the Calceocrinidae. The taxonomic affinities of calceocrinid genera are beyond doubt. Modifications of different structures forming parts of the skeleton can be seen to develop divergently and at uneven evolutionary rates. Certain trends, such as progression toward perfect bilateral symmetry and increased complexity of lateral-ray structures, are distinguishable and interpretable with confidence, whereas others are not clear and are explainable only by speculation. The most interesting observation called to notice by a comparative survey of the calceocrinid genera, in my opinion, is the persistent pattern of heterotomous branching of axil-arms belonging to the lateral rays. This extends to constant arrangement of the ramules. Only *Senariocrinus* and *Chiropinna* constitute exceptions.

Surveying the nine genera now recognized as members of the Calceocrinidae, it may be noted that two (*Chiropinna, Senariocrinus*) are monotypic and these are the only genera restricted to Europe. Three genera (*Cremacrinus, Deltacrinus, Halysiocrinus*), together containing 27 species, are confined to North America in so far as known. The remaining four genera (*Calceocrinus, Anulocrinus, Synchirocrinus, Chirocrinus*) include 16 North American species and 13 European species, a total of 29. The distribution of calceocrinid species is indicated in the following tabulation.

Stratigraphic and Geographic Distribution ol Calceocrinid Species

Genus	North America				Europe			Total
	Ord.	Sil.	Dev.	Miss.	Ord.	Sil.	Dev.	
Calceocrinus	1	4	..	..	..	1	..	6
Cremacrinus	8	3	..	..	..	..	..	11
Anulocrinus	..	1	..	..	2	..	..	3
Chirocrinus	..	1	..	..	..	2	..	3
Synchirocrinus	..	6	3	..	..	8	..	17
Deltacrinus	..	3	2	..	..	..	..	5
Halysiocrinus	..	..	2	9	..	..	..	11
Senariocrinus	..	..	..	..	..	..	1	1
Chiropinna	..	..	..	..	..	1	..	1
Totals	9	18	7	9	2	12	1	58

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