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RAY STRUCTURES OF SOME INADUNATE CRINOIDS

By Raymond C. Moore

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By Raymond C. Moore

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CONTENTS

ILLUSTRATIONS

ABSTRACT

Terminology judged to be best suited for designation of skeletal elements belonging to the rays of inadunate crinoids, both in the dorsal cup and above the cup, is discussed and the evolutionary significance of various ray structures considered. The inadunates studied are divided into five groups, based on the number of multiple radials found in the cup (5, 3, 2, 1, or 0). Crinoids with five multiple radials include a few monocyclic forms (disparids) and a single known dicyclic form; those having only three or two such radials are all disparids. The occurrence of a radianal plate, which is inferradial in origin, in association with the C-ray radial (superradial in origin), is the basis for differentiating genera characterized by a single multiple radial. Crinoids that lack a radianal have no multiple radials. The conclusion is reached that no disparid inadunate possesses a radianal, whereas this plate is found in all hybocrinids (monocyclic) and in very numerous dicyclic forms (cladids and flexibles).

The term "brachianal," originally proposed for anal-X but never accepted, is newly introduced for designating the axillary C-ray plate in a half-dozen (or possibly nine) genera, all but one of which are disparids. Also, the usefulness and significance of the term "aniradial" is discussed, leading to the judgment that this name should not displace radial of the C-ray.

The nomenclature of brachial plates is reviewed. These are broadly divisible into two unequal groups: fixed-brachials (or brachs) and free-brachials (or brachs). Fixed-brachs are characteristic of camerate crinoids, common in flexible crinoids, and uncommon in inadunates. Free-brachs belong to parts of rays above the dorsal cup and are classifiable in various ways: according to the brach-series in which they occur (primibrach, secundibrach, etc.), according to their structural nature (axillary or axil, nonaxil, etc.), and according to the arm part to which they belong (main-axil-brach, axil-arm-brach, ramule-brach, etc.). The term "subaxil" is introduced and the need for it explained.

The description of selected genera, accompanied by a statement of characters of families to which they belong, comprises the latter part of the paper. New genera named *Peniculocrinus, Grenprisia,* and *Crinobrachiatus* are introduced in this section. Previously described genera discussed here include *Eustenocrinus, Ristnacrinus, Ottawacrinus, Myelodactylus, Eomyelodactylus, Herpetocrinus,* and *Brachiocrinus.*

INTRODUCTION

A subject of special interest in connection with the comparative morphology of several groups of Paleozoic inadunate crinoids is the nature of structural patterns of the skeleton that may be identified as antecedent to others derived from them. Effort to distinguish origins naturally must take account of the placements in geologic time of fossils considered and of the feasability of developing modified new structural arrangements by evolution of pre-existing ones. For example, separate ossicles belonging to an early type of crinoid may become fused together in a later one, but oppositely, consolidated skeletal elements resulting from evolution may not be expected to form independent new structures.

PURPOSE OF PRESENT PAPER

The objective of this article is two-fold, first to deal with problems of morphology encountered in a study of several inadunate-crinoid groups and the terminology thought to be best suited for description of them, and second, the introduction of some new genera. Both of the stated aims are correlated with preparation of the volume of the *Treatise on Invertebrate Paleontology* allotted to the Crinoidea.

PREVIOUS WORK

It is unnecessary and inappropriate to prepare a lengthy statement concerning studies made by previous authors on morphology of inadunate crinoids. Because the present paper is directed mainly to various questions of morphological terminology, it is sufficient to take account of a relatively small number of earlier publications that provide a background and lead up to discussions that follow.

WACHSMUTH & SPRINGER (1880-1886), in their extensive *Revision of the Palaeocrinoidea,* made a comprehensive review of morphological and taxonomic work on inadunates, as well as other crinoids, up to the time of their publication. They introduced the name Inadunata (1885, p. 305) and described most of their distinguishing structural features. Their observations and conclusions are of much value, though morphological terminology used by them has been superseded in considerable part.

It is BATHER who may be recognized as the chief contributor to definition of inadunate skeletal structures in modern terms and to interpretation of their significance, generally in a penetrating manner. A series of his papers (1890, 1892, 1893, 1898, 1899), and his chapter on the Crinoidea in the volume on *The Echinoderma* (1900), of which he was author, are indispensable references for later investigators of these fossils. Portions of his writing are impaired by their controversial nature, for misunderstanding and conflict marked his relations with WACHSMUTH & SPRINGER and to some extent with others.

SPRINGER (1920, 1926) has made very important additions to knowledge and interpretation of inadunate groups specially considered in this and the accompanying paper prepared by me on calceocrinids. The value of SPRINGER's work in acquiring study materials and in describing and illustrating them can hardly be overestimated.

ULRICH (1925) advanced knowledge of several monocyclic inadunates very appreciably in his paper that introduced *Eustenocrinus, Daedalocrinus,* and other new genera.

MOORE & LAUDON (1943) undertook to synthesize and coordinate accumulated information relating to Paleozoic crinoid genera, including inadunates. They sought especially to recognize homologous structural elements in many inadunate genera and to designate them consistently in the same way. This inevitably called for conclusions as to the nature of evolutionary changes and their products. Also, the validity of extending to monocyclic disparids distinction of plates identified as radianals, or infer- and superradianals was insufficiently explored. Though in part the identification of these named elements accorded with designations by BATHER, my present judgment does not support the morphological terminology applied to the plates mentioned. MOORE (1948) accepted the views of MOORE & LAUDON (1943) but went further in classing as a radial plate the first primibrach of the right posterior (C) ray in *Synbathocrinus,* for example, and the fixed primibrach of the same ray in *Ectenocrinus.* Even the brachial next following the axillary primibrach of *Iocrinus* (in the present paper designated as brachianal) was classified as a radial plate. As now viewed, the terminology previously used by MOORE & LAUDON leads to confusion and calls for restudy.

ACKNOWLEDGMENTS

Assistance in preparing some of the drawings, mostly made by me, has been given by ROGER B. WILLIAMS. Photographs of fossil specimens were made by J. S. VAN SANT and J. E. SORAUF. DORIS E. N. ZELLER helped in organizing the list of references and in editorial checking of the typescript. I express appreciation to these members of my *Treatise* staff. In addition, I am happy to acknowledge the financial support of the United States National Science Foundation for advancing publication of the *Treatise,* toward which this paper contributes.

MORPHOLOGICAL TERMINOLOGY

INTRODUCTORY GENERAL STATEMENT

Inadunate crinoids are disinguished from other groups by the relatively simple structure of their dorsal cups, composed of close-sutured plates that lack incorporated interradial elements, and by arms that (with minor exceptions in some primitive forms) are free above the proximal plates of each ray. These proximal ray plates are designated as radials. A large majority of the recognized genera possess two circlets of plates (basals, infrabasals) below the radials and hence are termed dicyclic. The remainder are monocyclic, having only basals between the radials and topmost columnal of the stem.

For purposes of description, the crown is oriented with the arms directed upward because this is the normal living position of crinoids, or if arms are lacking (generally owing to their separation from the dorsal cup before or after fossilization but in some genera as result of an armless state during life) the dorsal cup is placed similarly, with the oral (ventral) side up and the aboral (dorsal) side down. A few inadunate crinoids exhibit perfect pentamerous symmetry, such a state being interpretable almost invariably as a product of prolonged evolutionary development which has led to suppression of structural features that introduce bilateral symmetry. In perfectly pentamerous crinoids any one ray or interray cannot be distinguished from others. On the other hand, the oral or aboral or both of these parts of a particular interray is found in nearly all inadunates to be clearly distinguishable from the others in various ways. It may be noticeably wider, may contain an extra plate or plates, and may be marked by the presence of an eccentrically located anal vent. The ventral side may have in this interray an oral plate larger than the others, with or without a hydropore or madreporite. The unique interray furnishes a firmly identifiable area of reference, which, according to convention, is designated as posterior. The ray opposite the posterior interray is then defined as anterior, and with the oral side of the crinoid held upward and the anterior ray away from an observer, left and right sides can be differentiated in orientation corresponding to his own. In viewing the aboral side of a dorsal cup, it is necessary to point the anterior ray toward the observer if left and right positions as just described are maintained. Although orientation in this manner has been common practice, it gives rise to infelicities of topsy-turvy arrangement adopted for many illustrations and is called for only by the really unnatural set of directional designations that incorporates lefts and rights.

An alternative method of defining individual rays and interrays of the crinoid skeleton has been adopted for use in the *Treatise on Invertebrate Paleontology* and accepted in the present paper. This method, introduced by P. H. CARPENTER (1884), assigns the letter A to the anterior ray, distinguished in the previously described manner, and B, C, D, and E to other rays in clockwise succession, viewing the oral side, or in counter-clockwise succession, viewing the aboral side. The interrays can be indicated precisely as AB (between the A- and B-rays), BC, CD, DE, and EA. Such designations are explicit, concise, and easy to use, regardless of the orientation of the crinoid or the point of view from any side. In addition to choosing the Carpenter system, a uniform orientation of side views of crinoids with the oral surface upward and of oral and aboral views or diagrams with the anterior ray directed upward is judged to be a desirable convention. The oral and aboral sides are then invariably shown with the anterior (A) ray in 12 o'clock position and the posterior (CD) interray in 6 o'clock position.

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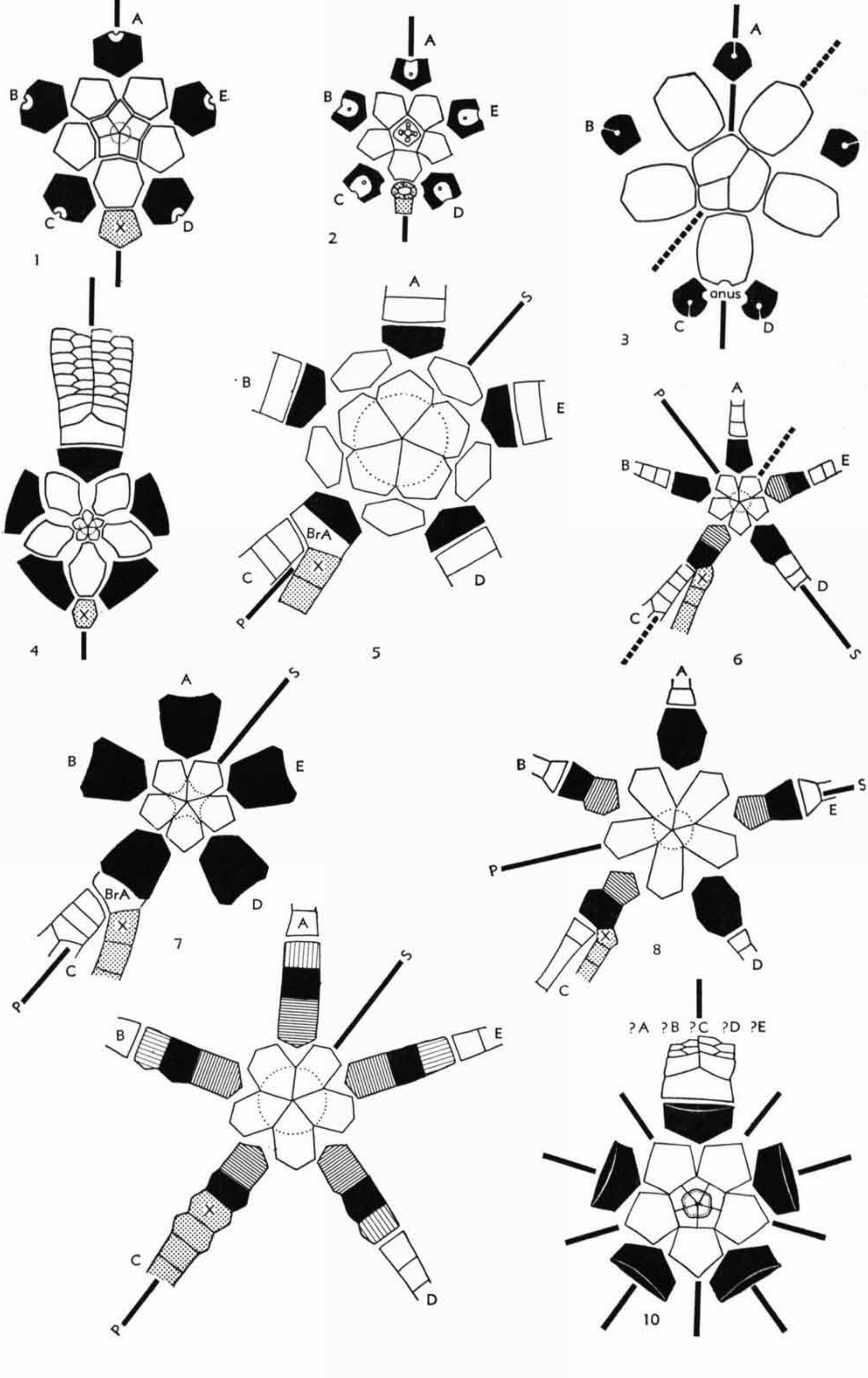
FIG. 1. Orientation of bilateral symmetry in inadunate crinoids (not to scale).

1-4. Crinoidal plane, through A-ray and CD-interray: *1, Cyathocrinites* (Sil.-Perm.); *2, Gasterocoma* (M.Dev.); *3, Lecythiocrinus* (Penn.); *4, Delocrinus* (Penn.-Perm.). —*5, 7, 9.* Eustenocrinoidal plane, through C-ray and AE-interray: *5, Merocrinus* (M.Ord.); *7, Iocrinus* (?L.Ord., M.Ord.-U.Ord.); *9, Eustenocrinus* (M.Ord.).—*6.* Heterocrinoidal plane, through D-ray and AB-interray: *Heterocrinus* (M. Ord. - U. Ord.).—*8.* Homocrinoidal plane, through E-ray and BC-interray: *Homocrinus* (M.Sil.-L. Dev.).—*10.* Encrinoidal planes, through all rays and interrays: *Sinocrinus* (U.Carb.). [Explanation: P-S indicates plane of bilateral symmetry. Rays are identified by letter symbols of the Carpenter system. Some categories of plates are indicated by patterns: inferradials ruled transversely to ray; radials and superradials, solid black; fixed-brachs ruled parallel to ray axis; anal plates stippled. BrA, brachianal; X, anal-X plate.]



A
B
C
D
E
X
1
2
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4
BrA
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?A ?B ?C ?D ?E
10

STRUCTURAL ELEMENTS AND THEIR ARRANGEMENT IN RAYS OF INADUNATE CRINOIDS

STRUCTURAL ELEMENTS

Similarities and differences of the ray structures observed in inadunate crinoids, both as pertains to the five separate rays of individual specimens and to corresponding rays in different genera, are important in a study of the origin and evolution of each skeletal element, in a study of the suitability of morphological terms generally used for each element, and in a study of inadunate crinoid taxonomy. I have just noted the methods adopted in the *Treatise* and in this paper for designating respective rays and orienting them in illustrations. It is desirable next to enumerate the kinds of structural features that need to be considered and make a brief advance survey of the basic patterns in which these features are arranged.

Structural elements of the proximal, medial, and distal parts of inadunate crinoid rays consist of relatively large to very diminutive plates which are widely varied in shape, placement with respect to adjoining or neighboring plates, function, and nature of movable or immovable contacts with other parts of the skeleton. They include plates that universally have come to be known as radials and brachials, and associated with one of the rays or interrays, there are in addition few or many plates called anals. Questions of morphological terminology arise in connection with particular elements in each of these groups. They are to be discussed later.

Whether a ray plate forms part of the dorsal cup or belongs above the cup in a free arm or one of its branches makes a difference for purposes of morphological classification. The presence or absence of branching in a ray is an important character. If branching occurs, many details of its pattern must be considered for purposes of classification and interpretation of evolution. After morphological analysis of any given crinoid has been made—or rather, in the course of making it—terminology used to designate each kind of structural element or each of several individual elements needs to be as simple and unambiguously objective as possible. This statement is made because the literature on inadunate crinoids is especially burdened by mophological designations that depend on homologies based on inference or supposed evolutionary origins. Thus, not only may the same plate be differently named by different authors, but it may be differently named by the same author at different dates. In this paper I seek to reject morphological terms that depend on subjective judgments for their acceptance and in this way to remove discordant nomenclature as far as possible.

BILATERAL SYMMETRIES

A broad survey of the arrangement of structures present in the rays (and to some extent in the CD-interray) of inadunate crinoids indicates the existence of five different types of bilateral symmetry, developed in varying degrees of perfection by genera belonging to each symmetry group. Of course, the bilateral symmetry is superposed on the fundamental pentamerous arrangement of the crinoid skeleton, and with the notable exception of the monocyclic family named Calceocrinidae, bilateral symmetry is subordinant. The first four groups distinguished by the nature of their bilateral symmetry display a single dominant plane of such symmetry, oriented so as to coincide with a particular ray, but this may be combined with less evident bilateral symmetry affecting certain parts of the skeleton only. The fifth group has five planes of bilateral symmetry, one coinciding with each ray.

(1) The so-called **crinoidal plane** of bilateral symmetry is perfectly developed in *Cyathocrinites* (Fig. 1,*1*), *Gasterocoma* (Fig. 1,*2*), *Delocrinus* (Fig. 1,*4*), and numerous other inadunates, but less perfectly in *Lecythiocrinus* (Fig. 1,*3*) and still others. The plane of symmetry coincides in position with the A-ray and bisects the posterior (CD) interray, which generally contains one or more anal plates.

(2) The **homocrinoidal plane** of bilateral symmetry (*Homocrinus,* Fig. 1,*8*) is mainly defined by the undivided radials of the A- and D-rays combined with placement of compound radials in the B-, C-, and E-rays. The plane of symmetry coincides with the E-ray.

(3) The **heterocrinoidal plane** of bilateral symmetry (*Heterocrinus,* Fig. 1,*6*) is chiefly based on distribution of three undivided radials and two compound radials; the plane of symmetry coincides with the D-ray.

(4) The **eustenocrinoidal plane** of bilateral symmetry (*Eustenocrinus,* Fig. 1,*9*; *Iocrinus,* Fig. 1,*7*; *Merocrinus,* Fig. 1,*5*) is represented by inadunates having four or five compound radials (*Eustenocrinus, Ristnacrinus, Peniculocrinus*) or only one such radial (actually simple radial plus large radianal, as developed in the Hybocrinidae and Cornucrinidae). The plane of symmetry coincides with the C-ray, as most clearly seen in *Eustenocrinus,* with anal tube and no

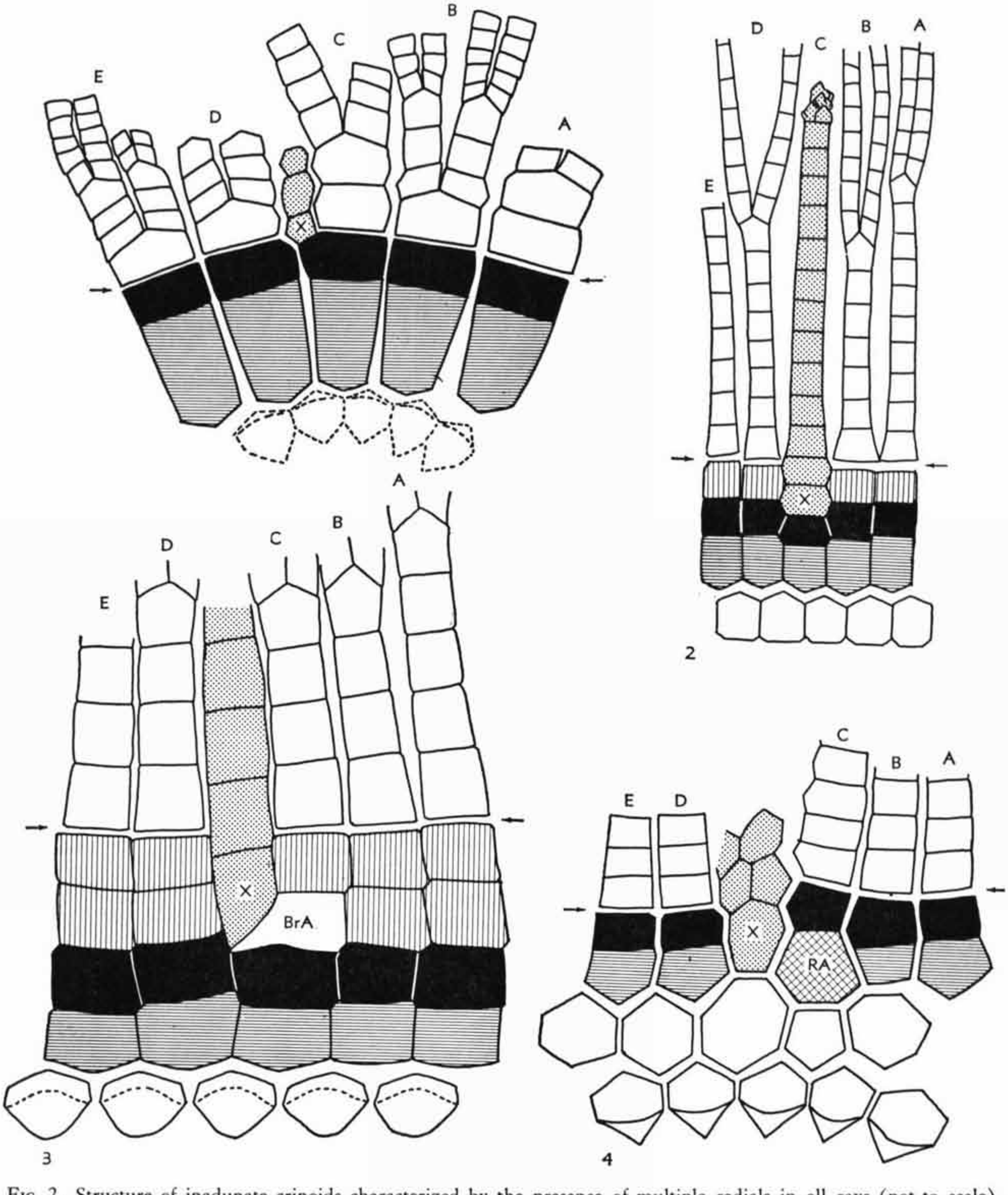

Fig. 2. Structure of inadunate crinoids characterized by the presence of multiple radials in all rays (not to scale).

1. Ristnacrinus Öpik (M.Ord., Estonia); plates interpreted as basals and radials, superposed without offset in rays, are here considered to be infer- and superradials, respectively.—*2. Eustenocrinus* Ulrich (M.Ord., Kentucky-Ontario); distinguished by long anal tube and absence of arm in C-ray, a fixed-brach followed by free-brachs in all other rays.—*3. Peniculocrinus* Moore, n.gen. (M.Ord., Kentucky); C-ray with large brachianal which supports normal-sized arm at right and anal tube at left, dorsal cup with two fixed-brachs in each ray.—*4. Ottawacrinus* W. R. Billings (M.Ord., Ontario); with radianal in primitive position, directly below C-radial, these plates together unquestionably corresponding to compound radials in other rays. [Explanation: Letter symbols and patterns as in Figure 1, with addition of RA for radianal, indicated by oblique cross-ruled pattern; top of dorsal cup marked by small arrows.]

accompanying arm above the C-radial, and in the five-armed hybocrinids *(Hybocrinus, Hoplocrinus)*.

(5) The **encrinoidal type** of bilateral symmetry (*Sinocrinus,* Fig. 1,*10*) accompanies perfect pentameral symmetry and is illustrated by several inadunates in which none of the rays can be identified by CARPENTER letters and all rays coincide with planes of bilateral symmetry.

RADIALS

Paleontologists acquainted with the general morphology of crinoids are likely to suppose that one of the least debatable constituents of the dorsal cup or calyx (theca) are the proximal ray plates termed radials. In a general way such a supposition is well supported, for in most crinoids, regardless of the subclass and order to which they belong, the identity of plates agreed to be radials is all but self-evident. This is because they are seen to be located at the lowermost extremities of the rays, alternating in position with the interradially disposed basals. Also, very commonly, though not universally, they are distinctly larger than the next higher ray plates (whether nonaxillary or axillary) that occur in series above the radials. Among inadunate crinoids the radial plates bear articular facets on their distal margins for varyingly mobile connection with the free arms and these facets differ obviously from the close sutures occurring along the proximal and lateral margins of the radials. Observations of this sort are trustworthy as applied to most crinoids, but not to all—or at least problems of interpretation are encountered.

A survey of divergent conclusions as to what are radial plates published by various authors shows that two sorts of structural conditions found in many monocyclic inadunate crinoids and in a very few dicyclic inadunates have given rise to different morphological treatments. These conditions are (1) serial arrangement of two or more plates (up to four) within the dorsal cup in five, three, or two rays, and (2) special structures of different kinds that distinguish the C-ray, all of which are related to introduction of an anal tube or sac in the posterior (CD) interray. The two types of variations will be considered separately, giving attention first to crinoids having multiple plates in two or more rays.

DORSAL CUPS WITH MULTIPLE RADIALS IN FIVE RAYS

The heading given for this section of the discussion of radial plates is not intended to prejudice a definition of what plate or plates in any ray should be identified as the structural element called radial. Four genera are cited for examination—*Ottawacrinus* BILLINGS and *Ristnacrinus* ÖPIK, with a pair of sequent plates in each ray of the cup; *Eustenocrinus* ULRICH, with three such plates in all rays except the C-ray, which has four; and *Peniculocrinus* MOORE, n.gen., which has four serially arranged plates in each ray beneath the upper limit of the dorsal cup (Fig. 2). All of the named genera come from Middle Ordovician rocks. *Ottawacrinus* is dicyclic and the others are monocyclic. What nomenclature is judged to be most suitable for these ray plates in the A-, B-, D-, and E-rays, if consideration of problems relating to the C-ray is postponed momentarily?

A possibility that might be accepted as logical is designation of the single plate at the proximal extremity of each ray as a radial. Such procedure would be objective and simple to apply. Question is immediately introduced, then, concerning nomenclature appropriate for the next following plate and with respect to homologies of either or both of these ray plates in other crinoid genera. The penultimate ray plates

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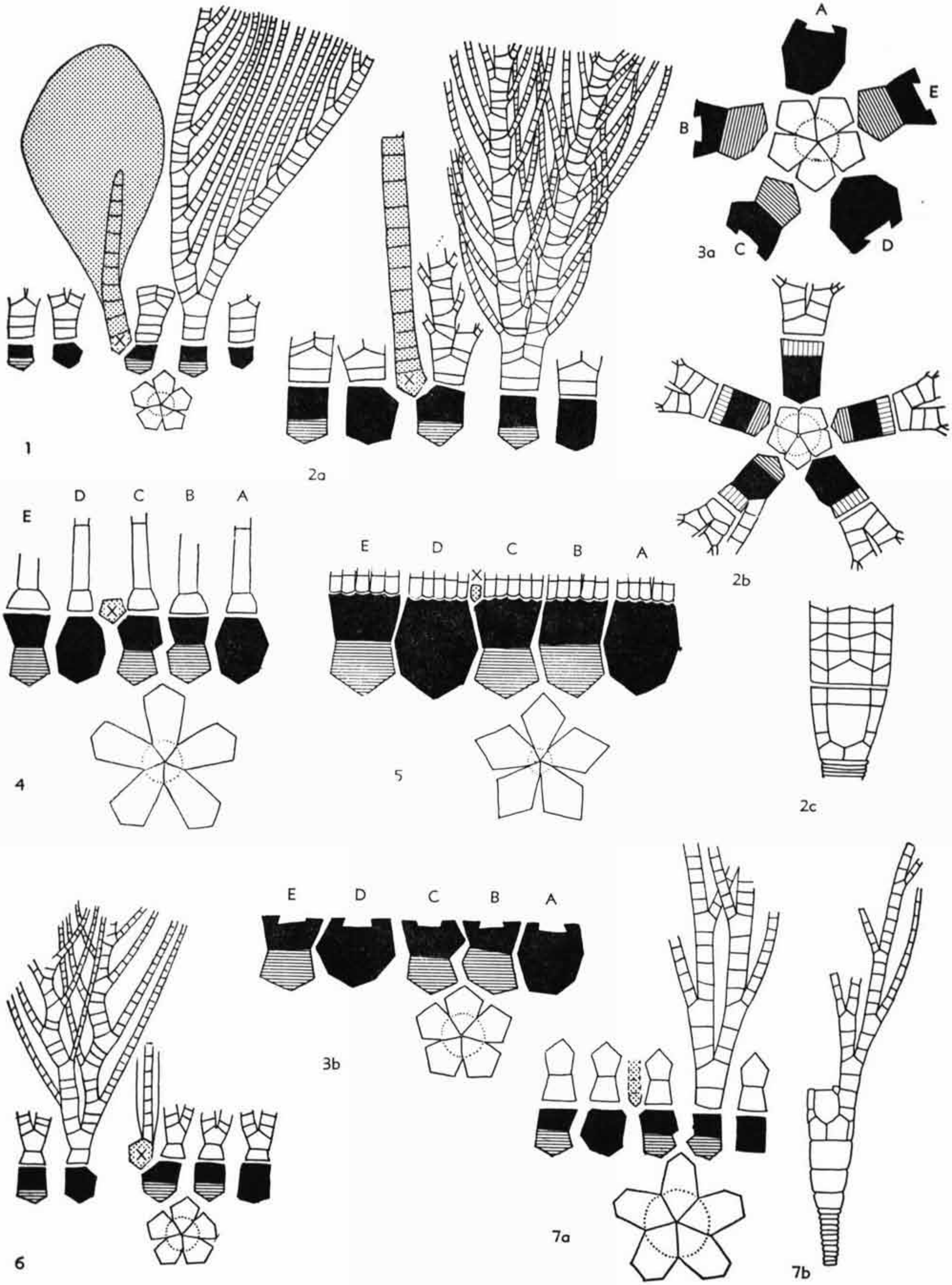
FIG. 3. Structure of inadunate crinoids characterized by the presence of multiple radials in three rays only (B,C,E) (not to scale). All genera illustrated belong to families of the monocyclic order Disparida.

1. Daedalocrinus ULRICH (M.Ord., Ontario), Homocrinidae; branching of arms distinctive.—*2. Ectenocrinus* S. A. MILLER (M.Ord.-U.Ord., USA-Canada), Homocrinidae; *2a,* arms with regularly spaced ramules that resemble pinnules, nonaxil-brachs alternating with subaxils; *2b,c,* diagram and A-ray view of *E. canadensis* (BILLINGS) (M.Ord., Ontario), showing circlet of fixed-brachs and illustrating bilateral symmetry in homocrinoidal plane.—*3. Haplocrinites* STEININGER (M.Sil.-L.Carb., Europe-Africa-North America), Haplocrinitidae; *3a,* diagram showing bilateral symmetry; *3b,* radials arranged horizontally.—*4. Homocrinus* HALL (M.Sil.-L.Dev., USA-Canada-Germany), Homocrinidae; slender arms unbranched.—*5. Anamesocrinus* GOLDRING (U.Dev., New York), Anamesocrinidae; five threadlike arms directly borne by each radial.—*6. Drymocrinus* ULRICH (U.Ord., USA-Canada), Homocrinidae; geniculate arms with ramules.—*7. Sygcaulocrinus* ULRICH (U.Ord., Iowa), Homocrinidae; *7a,b,* diagram of structure and D-ray view showing expanded proximal stem segments. [Explanation: Letter symbols and patterns as in Figure 1.]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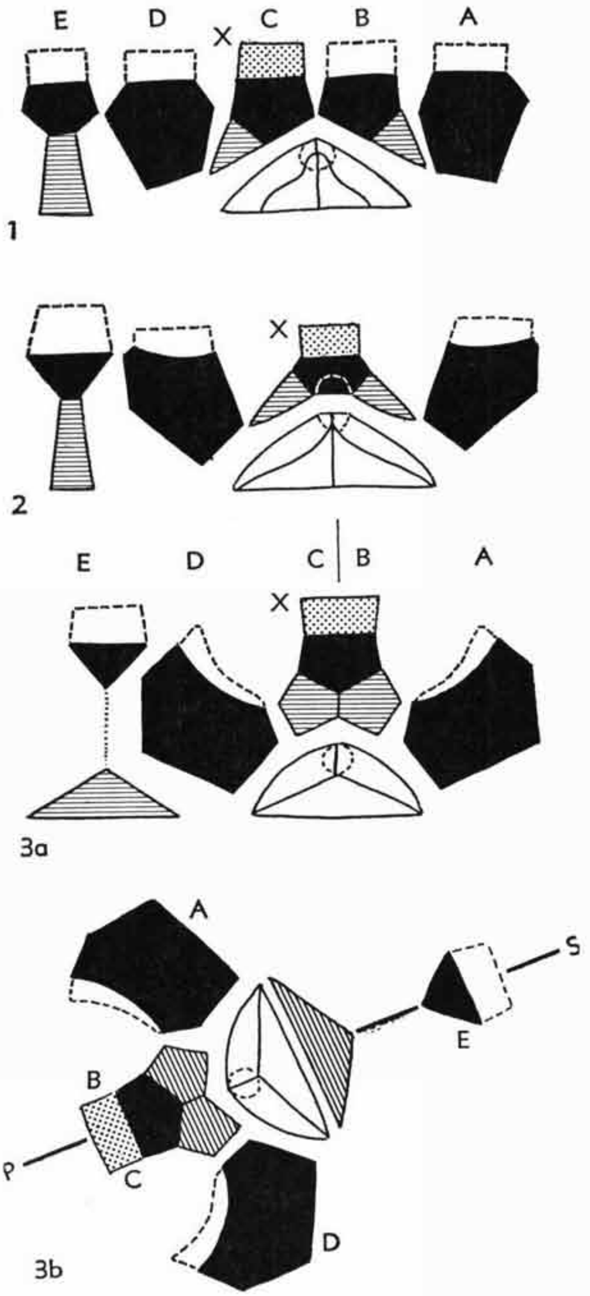

FIG. 4. Structure of calceocrinid dorsal cups and plates next above cup. *1. Cremacrinus* ULRICH (M.Ord.-U.Ord., USA-Canada); anal-X borne by C-superradial.—*2. Calceocrinus* HALL (M.Ord.-M.Sil., USA-Canada-England; anal-X supported by fused B+C superradial (subanal plate).—*3a,b. Halysiocrinus* ULRICH (M.Dev.-L.Miss., USA); resembling *Calceocrinus* except for separation of E-ray infer- and superradial, adjoined B- and C-inferradials, and 3-plate basal circlet; *3b,* showing P-S, plane of bilateral symmetry through E-ray and BC-interray. [Explanation: Letter symbols and patterns as in Figure 1.]

seem rather surely to correspond to the superradial elements of the so-called compound radials of homocrinids, heterocrinids, and some other disparid inadunate families, especially where the cup includes only ray-plate pairs, as in *Ottawacrinus* and *Ristnacrinus*. Even if one should grant that no *a priori* basis exists for rejecting classification of these plates as fixed-brachials, such treatment has little or nothing to recommend it (and as observed in later consideration of the C-ray of *Ottawacrinus,* the proximal plate here surely is distinguishable as a primitive radianal and therefore the next following plate is identifiable as the radial of this ray). I conclude that the bottommost two plates of each ray in the four crinoid genera here considered are best defined as infer- and superradial elements of compound radials, and as a corollary one may judge these crinoids to belong near the point of origin of ray structural evolution, being characterized by compound radials in every ray.

Eustenocrinus and *Peniculocrinus* are even more primitive than *Ottawacrinus* in having brachial plates incorporated in the dorsal cup. The demarcation between dorsal cup and free arms in these crinoids is not a matter of guesswork, for it is indicated clearly by the interlocking and close sutures of the cup plates and narrowing of the rays where the separate free arms begin. Accordingly, the dorsal cup of *Eustenocrinus* can be described as consisting of compound radials in each ray, followed by a single fixed-brachial in each ray. *Peniculocrinus* differs in having two fixed-brachials in each ray, as well as in characters of the C-ray and CD-interray.

DORSAL CUPS WITH MULTIPLE RADIALS IN THREE RAYS ONLY

Nearly 20 genera of disparid inadunates belonging to the families Homocrinidae, Calceocrinidae, Anamesocrinidae, and Haplocrinitidae are characterized by the presence of compound radials in three rays (B, C, E), whereas large undivided radials occur in the other two rays (A, D) (Figs. 3, 4). Again passing over special questions relating to the C-ray and CD-interray, no problems are encountered in defining dorsal-cup elements that are classed as radial, simple or compound. Only in primitive (Middle Ordovician) species of *Ectenocrinus* (Fig. 3,*2b,c*) are fixed-brachials observed as parts of the rays included in the dorsal cup. [See also Pl. 1.]

The Calceocrinidae are a remarkably specialized family having infer- and superradials in three rays MOORE, 1962). All but one or two primitive genera

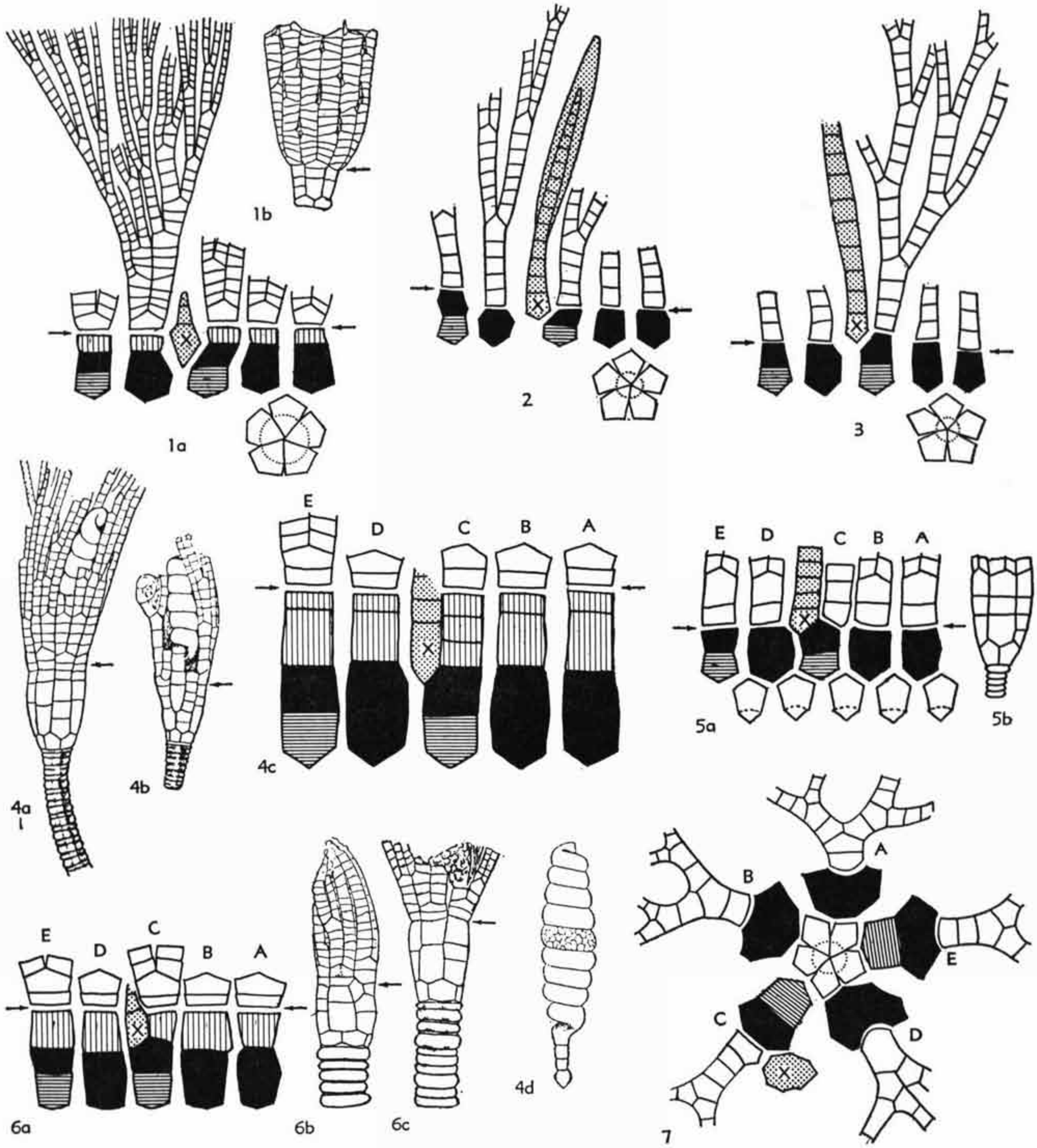

FIG. 5. Structure of inadunate crinoids characterized by the presence of multiple radials in two rays only (C,E) (not to scale). All genera illustrated belong to families of the monocyclic order Disparida.

1. Dystactocrinus ULRICH (U.Ord., Ohio), Heterocrinidae; *1a,* arms beyond axillary primibrach heterotomously branched, some secondary arms isotomously branched; *1b,* B-ray view of proximal part of crown showing top of cup just below primaxils (after Ulrich).—*2. Isotomocrinus* ULRICH (M.Ord., Ontario), Heterocrinidae; arms isotomously branched.—*3. Heterocrinus* HALL (M.Ord.-U. Ord., USA-Canada), Heterocrinidae; arms isotomously branched on primaxils, secundibrach subaxils distributed at intervals giving off ramules on alternate sides.—*4. Ohiocrinus* ULRICH (M.Ord.-U.Ord., Ohio-Indiana-Kentucky), Heterocrinidae; *4a,b,d,* E- and C-ray views of crown and part of stem, and spirally coiled anal tube, top of dorsal cup indicated by arrow in *4a,b,* suture between infer- and superradial of C-radial indicated by broken line (omitted by ULRICH), ×3 (after Ulrich, 1925); *4c,* plate diagram showing fixed-brachs above radials.—*5. Columbicrinus* ULRICH (M.Ord., Tennessee), Heterocrinidae; *5a,b,* plate diagram and A-ray view of proximal part of crown.—*6. Atyphocrinus* ULRICH (U.Ord., Ohio), Heterocrinidae; *6a,* plate diagram showing fixed-brachs; *6b,c,* D-ray and AE-interray views of crown and large stem, ×1.5, ×1.8 (arrow indicates top of dorsal cup) (after Ulrich, 1925).—*7. Anomalocrinus* MEEK & WORTHEN (U. Ord., Ohio), Anomalocrinidae; plate diagram showing bilateral symmetry. [Explanation: Letter symbols and patterns as in Figure 1.]

developed perfect bilateral symmetry disposed in the plane of the E-ray and BC-interray (Fig. 4). A peculiarity is the fusion of superradials belonging to the B- and C-rays to form a single subanal piece that supported the anal tube adjacent to the stem.

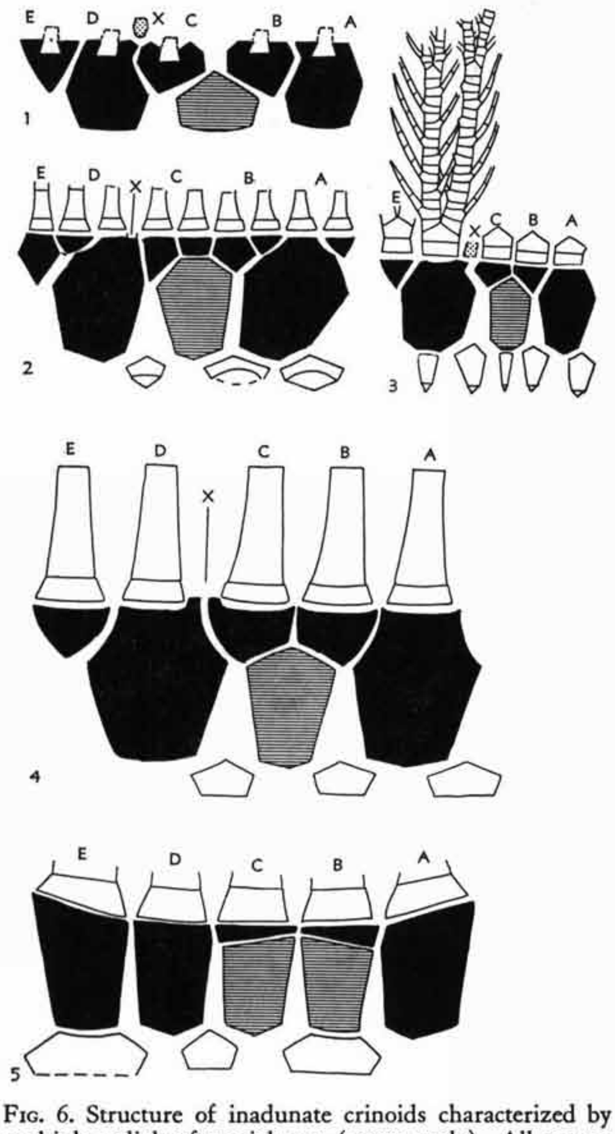

Fig. 6. Structure of inadunate crinoids characterized by multiple radials of special type (not to scale). All genera illustrated belong to the Pisocrinidae.—*1. Pisocrinus* de Koninck (M.Sil., North America-Europe-Australia); basals omitted.—*2. Calycanthocrinus* Follmann (L.Dev.-M.Dev., Germany); distinguished by pararadials (small superradial-type plates), all radial elements except B+C inferradial bearing slender, unbranched arm.—*3. Cicerocrinus* Sollas (M.Sil.-U.Sil., Europe); like *Pisocrinus* but having arms that branch isotomously on primaxil and at much higher level on secundaxil, arms composed of nonaxil-brachs and subaxils that bear short ramules (not pinnules).—*4. Triacrinus* Münster (M.Sil.-U.Dev., Germany-Sweden); basal circlet triangular.—*5. Quiniocrinus* Schmidt (M.Dev., Germany); B- and C-radials compound, E-radial large and undivided. [Explanation: Letter symbols and patterns as in Figure 1.]

DORSAL CUPS WITH MULTIPLE RADIALS IN TWO RAYS ONLY

The Heterocrinidae and Anomalocrinidae are disparid inadunate families in which only two rays (C, E) are differentiated by the presence of compound radials; large, undivided radials occur in the A-, B-, and D-rays (Fig. 5). In this group, as in the homocrinids and other families with three rays having compound radials, long-established usage satisfactorily determines morphological terminology applied to the radial plates. Mostly, the dorsal cups do not incorporate fixed-brachials, but they are found to occur in *Dystactocrinus* (Fig. 5,*1a,b*), *Ohiocrinus* (Fig. 5,*4a-c*), and *Atyphocrinus* (Fig. 5,*6a-c*). It is interesting to observe that in some species of *Ohiocrinus* and *Atyphocrinus* the fixed-brachials are larger than the superradials beneath them. [See also Pl. 1.]

DORSAL CUPS WITH MULTIPLE RADIALS OF SPECIAL TYPE

The pisocrinids (Fig. 6) are a family of disparid inadunates of a peculiar sort in that they might be characterized as having a composite two-ray (B+C) compound radial, with separate superradials above a single fused inferradial, and the superradial half of a compound radial in the E-ray without any trace of an accompanying inferradial. Because the large undivided radials occur in the A- and D-rays, the plane of bilateral symmetry of pisocrinid dorsal cups exactly corresponds to that of homocrinids and calceocrinids in its placement, coinciding with the E-ray and BC-interray (Fig. 7,*2*). The A- and D-ray plates of the radial circlet are obviously named as radials, whereas the plates that support the arms in the B-, C-, and E-rays are morphologically superradials and may as well be so designated. This leaves the combined B+C inferradial as the remaining element of the circlet. It has been classed as a radianal plate by Bather (1900, p. 149) and as an inferradianal by Moore & Laudon (1943, p. 27), both ill-advisedly in my present opinion. It is better classified as a unique sort of 2-ray fused inferradial.

DORSAL CUP WITH MULTIPLE RADIAL IN A SINGLE RAY

Very numerous inadunate crinoids, mostly dicyclic but including monocyclic genera of the order Hybocrinida (Figs. 7, 8), are distinguishable from others in having a multiple (i.e., divided) radial in a single ray. Invariably this is the C-ray and hence we are led to problems of morphological interpretation and terminology which have come to be applied to special plate elements and arrangements of them in the posterior interray area. For the moment, these matters may be put aside so that attention is directed strictly to the multiple nature of the plates belonging to the C-ray, with a lower (proximal) element, classed as radianal, that clearly corresponds to an inferradial in crinoids having two or more compound radials, and an upper (next-to-proximal) element that is equivalent to a superradial of other crinoids having compound radials. This is unequivocal and therefore has not been subject to debate. In *Cupulocrinus* (Fig. 9,*1*) and *Dendrocrinus* (Fig. 9,*5*), as well as in several genera of flexible crinoids, the inferradial element (radianal) directly underlies the superradial plate (radial) without offset, and this condition is interpreted as the most primitive or archaic. In a great majority of inadunate (and flexible) crinoids having a compound radial in the C-ray the inferradial element is displaced leftward more or less into the posterior interray and it then abuts against only the lower left margin of the superradial element (Figs. 7,*1*; 8,*1-4*; 9,*2-4,6-8*; 10,*1,3,5-7*) or it may come to lie laterally at the left of the superradial well above the proximal extremity of the superradial (Figs. 10,*2,4*; 13,*1c,e-j,4b*; 14,*3c-f*).

It is clear that crinoids having dorsal cups with a single multiple radial (as stated, invariably located in the C-ray and defined as radianal plus radial) constitute a distinct, though heterogeneous group. They are differentiated from more primitive crinoids that retain compound radials in two or more rays and are interpreted as less advanced in evolution than crinoids having no compound radials. Further discussion of C-ray plates of inadunate crinoids is given in considering plates called radianals and aniradials, discussed subsequently herein.

DORSAL CUPS WITH NO MULTIPLE RADIALS

Numerous genera of inadunate crinoids, both monocyclic and dicyclic, are characterized by possession of a radial circlet composed of essentially equal, undivided plates in each ray. These plates alternate in position with the plates of the next-lower (basal) circlet, and on their distal edges they articulate with free arms that are varyingly branched or unbranched and pinnulate or nonpinnulate. Some crinoids in this group are ancient and marked by other characters interpreted as primitive, whereas many are geological late-comers that surely are far advanced in evolution, though in part displaying regressive characters. Attention here is directed rather briefly to three groups: (1) simply constructed dorsal cups (here designated

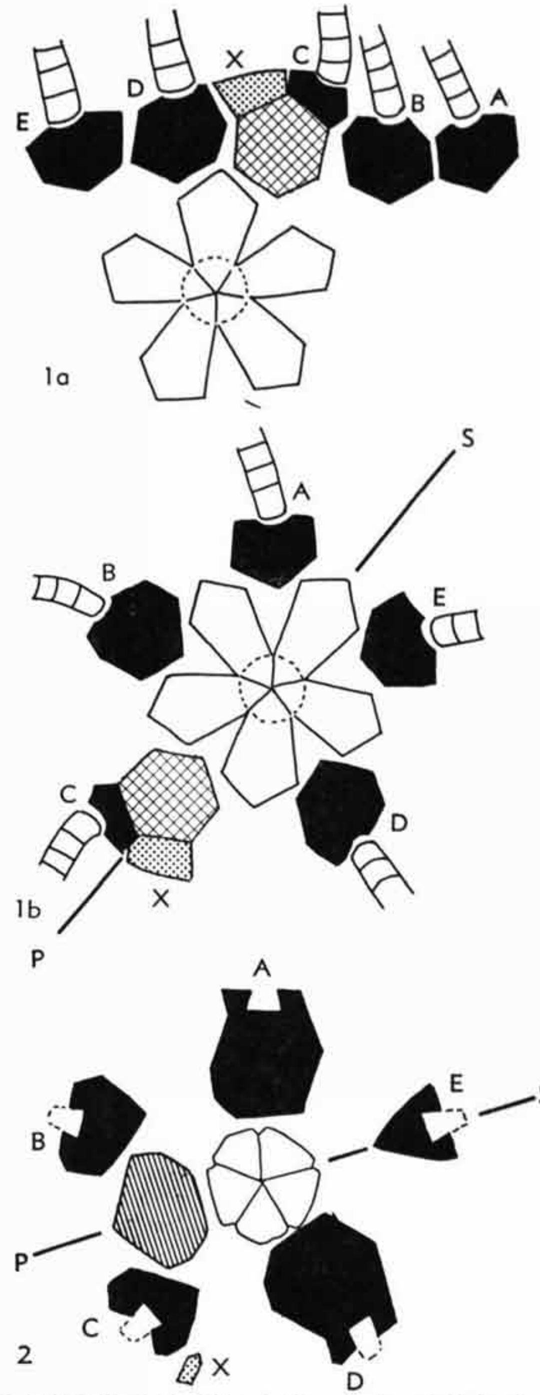

FIG. 7. Structure of hybocrinid and pisocrinid inadunate crinoids (not to scale).—*1. Hybocrinus* BILLINGS (M.Ord., USA-Canada), Hybocrinidae; *1a,* C-radial obliquely at right above large radianal, which is inferradial in origin, anal-X interrupting circlet of radials; *1b,* plates radially arranged to show bilateral symmetry in the eustenocrinoidal plane.—*2. Pisocrinus* DEKONINCK (M.Sil., Europe-North America-Australia); plates radially arranged to show bilateral symmetry in homocrinoidal plane. [Explanation: Letter symbols and patterns as in Figures 1 and 2; P-S indicates plane of bilateral symmetry.]

for convenience as the *Iocrinus* group) typified by *Iocrinus, Merocrinus,* and *Synbathocrinus* (Fig. 11) with single main arms borne by each radial and an anal tube developed as a left branch of the C-ray; (2) crinoids distinguished by undivided radials that bear multiple unbranched arms attached directly to the radials (Fig. 12) (designated as the *Allagecrinus* group); and (3) advanced types of inadunates with undivided radials or showing disappearance of radials (designated as the *Cyathocrinites* group).

CRINOIDS OF THE IOCRINUS GROUP

Iocrinus (?L.Ord.,M.Ord.-U.Ord) is a distinctive, moderately common monocyclic inadunate that is characterized by nearly perfect pentameral symmetry of the dorsal cup (Fig. 11,*1*). The statement as to pentameral symmetry just made depends on exclusion of all ray plates above the radials, defining the latter as the five subequal plates with wide, even summits that occur next above the basals, alternating with them. A need to define the radials explicitly in this way arises because some authors have classed the axillary plate next to the most proximal one of the C-ray as a radial (Bather, 1890, p. 329; Ubaghs, 1953, p. 679), superradial (Bather, 1900, p. 121), or superradianal (Moore, 1948, p. 31; Ramsbottom, 1961, p. 4), and the ray plate supported by the right-hand articular facet of this axillary has been designated as the C-radial (Moore & Laudon, 1943, p. 14; Moore, 1948, p. 31). Variations in nomenclature applied to the proximal part of the C-ray in *Iocrinus* are indicated in the following tabulation, which refers to Figure 11,*1b*.

It is clear that discrepancies in interpretation and nomenclature relate almost entirely to the ray plates numbered 1 and 2 in Figure 11,*1b*. The proximal plate of the anal tube is agreed to be the anal-X plate. Also, whatever the axillary ray plate on which it rests is called, it is agreed that this axil does not belong to the dorsal cup, (1) because it is definitely above the even summits of the five most proximal ray plates, and (2) because the distal edge of the most proximal C-ray plate is an articular facet exactly similar to those of other most-proximal ray plates, which surely are radials, since they differ markedly in size and shape from the succeeding uniserially arranged primibrachs.

The pattern of the five or six lowermost C-ray plates, including anal-X, as observed in *Iocrinus,* rather precisely match the arrangement of proximal C-ray plates seen in homocrinids, heterocrinids, and some other disparid families (Figs. 3, 5), but beyond this, resemblance vanishes. The inferred C-ray homologies, which account for the diversity of morphological terminology found in the literature, will be considered further in subsequent discussion of plates called radianal, aniradial, and brachianal. With respect to *Iocrinus,* it seems decidedly preferable to accept designations of plates that are as simply descriptive and as objective as possible, not mortgaged by conclusions that specified structural similarities denote actual homologies. Therefore, *Iocrinus* is classified as a crinoid having no multiple radials, each ray possessing a single large undivided radial, with that of the C-ray corresponding to others in shape and size. The only deviation from perfect pentameral symmetry of the dorsal cup is a generally observed slight greater-than-average height of the apposed parts of the C- and D-radials. This allows identification of the posterior (CD) interray.

Merocrinus (M.Ord.) is a smaller, more slender crinoid than *Iocrinus,* which differs in having a circlet of moderately large infrabasals beneath the ring of wide, low, hexagonal basals. The large stem is circular in section, instead of sharply pentagonal or pentastellate, as in *Iocrinus.* Otherwise, morphological features of these two genera are almost identical (Fig. 11,*2*) and considerations of terminology applicable to the C-ray are the same. The dorsal cup of *Merocrinus*

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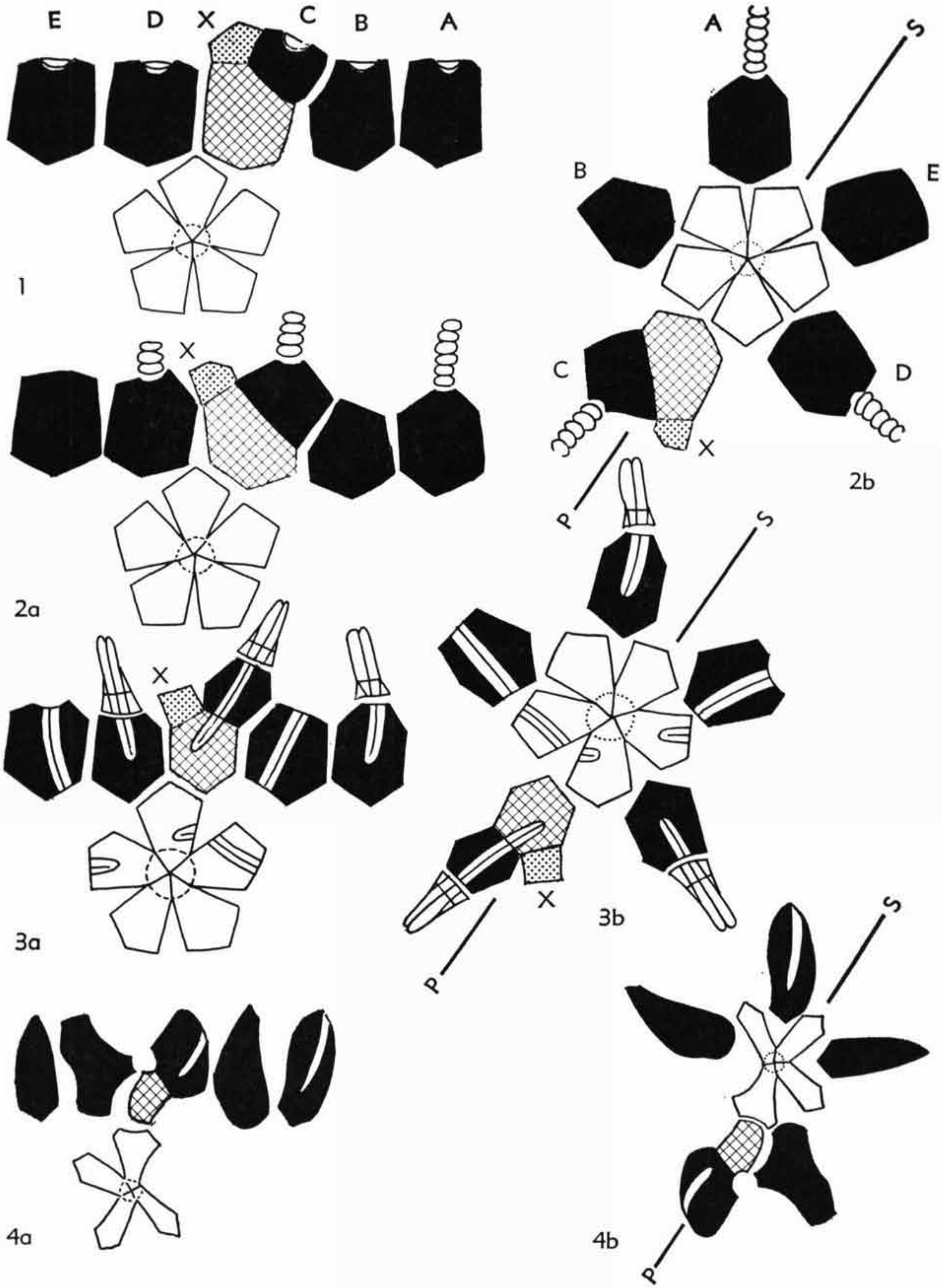
Fig. 8. Structure of inadunate crinoids characterized by a multiple radial (radial-and-radianal) in a single ray (not to scale). All genera illustrated belong to the monocyclic order Hybocrinida.

1. Hoplocrinus Grewingk (M.Ord., Estonia), Hybocrinidae; radianal very large, anal-X extending higher than D-radial.—*2. Baerocrinus* Volborth (M.Ord., Estonia-USSR), Hybocrinidae; *2a,* two radials armless; *2b,* plates radially arranged to show eustenocrinoidal plane of bilateral symmetry.—*3. Hybocystites* Wetherby (M.Ord., Kentucky-Ontario), Hybocrinidae; only three radials bearing armlike appendages that project above cup; *3a,* ambulacral grooves extending onto radianal and basals; *3b,* plates radially arranged to show eustenocrinoidal plane of bilateral symmetry.—*4. Cornucrinus* Regnéll (M. Ord., Sweden), Cornucrinidae; *4a,* food grooves on A- and C-radials, anal vent just above radianal, no anal-X plate; *4b,* plates radially arranged to show eustenocrinoidal plane of bilateral symmetry. [Explanation: Letter symbols and patterns as in Figures 1 and 2; P-S indicates plane of bilateral symmetry.]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4b
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shows not the slightest deviation from perfect pentameral symmetry, for within each of the three circlets every plate exactly duplicates the others. The C-ray is identifiable only in specimens consisting of crowns, in which several uniserially arranged primibrachs are seen to follow the radial directly in all rays except C; the C-radial supports a broad, low axillary plate (here termed brachianal), which bears the anal tube on its left side and a series of brachials (defined as primibrachs) on its right side. The anal-tube plates are somewhat narrower and taller than the primibrachs of this ray.

Another crinoid that is placed in the first group of no-multiple-radial inadunates is *Synbathocrinus,* and with it belong other genera of the Synbathocrinidae. It happens that *Synbathocrinus* has a low circlet of basals consisting of two large plates and a small one, the small basal being located in the EA-interray. The characters of this circlet lack special significance, since some other genera of the family have five basals. The important morphological feature is the subequal nature of the five plates of the radial circlet, accompanied by the presence of an anal tube joined to a narrow facet on the left shoulder of the C-radial (Fig. 11,*3*). The relations of this radial and anal-X are like those of a typical radianal with anal-X in such monocyclic inadunates as *Hybocrinus* (Fig. 7,*1*), *Hoplocrinus, Baerocrinus,* and *Hybocystites* (Fig. 8,*1-3*) and in very numerous dicyclic inadunates (Figs. 9, 10). For this reason, MOORE & LAUDON (1943, p. 27) and MOORE (1948, p. 31) designated the proximal C-ray plate as a radianal, describing *Synbathocrinus* as characterized by the presence of four radials and a large radianal of radial-like form horizontally in line with them. This is a curiously irrational sort of diagnosis unless agreement is had that a radianal may be defined as the most proximal plate of the C-ray, consisting either of the morphological equivalent of an inferradial or of an undivided radial. Such an agreement, particularly in reference to a plate interpretable as an undivided radial, has not been accepted and seems unlikely to find acceptance in the future by specialists in the study of crinoids, because (except in case of atrophy or lateral fusion of one or more plates of the radial circlet) all crinoids normally possess five radials. Moreover, the well-established tendency of undoubted radianal plates to shift laterally leftward, and in varying degree also upward, leads to placement of this plate in positions that are by no means unequivocally determinable as marking the proximal extremity of the C-ray. I advance the conclusion that designation of the proximal C-ray plate in *Synbathocrinus* and other synbathocrinid genera as a radianal is ill advised. Therefore, this plate is classed as a radial, homologous with others of the circlet in which it occurs.

The discussion just presented and conclusion expressed do not prevent differentiation of the C-radial as a special one, for which an individual supplementary designation may be considered useful. MOORE (1952, p. 616) introduced the name "aniradial" for it, because it is the radial that directly supports anal-X and the anal tube, but whether this term was intended as an exclusive one (replacing radial in the C-ray) or merely supplementary (not replacing radial) is uncertain. In advance of subsequent discussion, I state here that in my opinion an aniradial is best construed as a particular, special radial. It is then simply an individualized radial which occurs in some inadunates, and in describing such a crinoid one might write "with five subequal low radials, including an aniradial."

The occurrence in *Phimocrinus jouberti* (a Lower Devonian synbathocrinid from France) of traces of transverse sutures in the B-, C-, and E-radials (as noted by UBAGHS, 1953, p. 746) is extremely interesting

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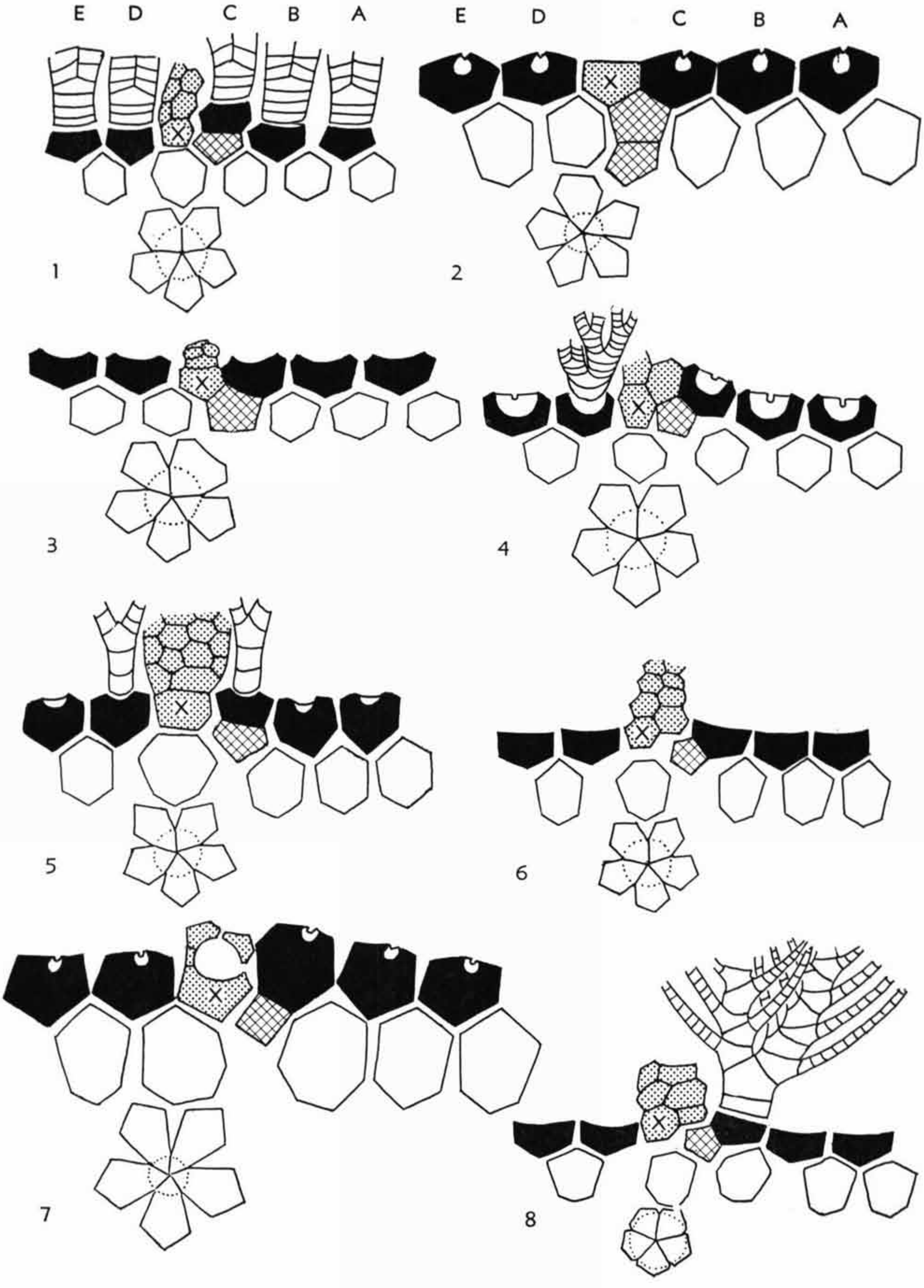
FIG. 9. Structure of inadunate crinoids characterized by the presence of a multiple radial (radianal plus radial) in a single ray (not to scale). All genera illustrated belong to the dicyclic order Cladida.

1. Cupulocrinus D'ORBIGNY (M.Ord.-U.Ord.,USA-Canada), Cupulocrinidae; radianal directly below C-radial, anal-X on truncate posterior basal.—*2. Carabocrinus* BILLINGS (M.Ord.-U.Ord., USA-Canada-Estonia), Carabocrinidae; only known crinoid with infer- and superradianal, together interrupting circlet of basals.—*3. Thenarocrinus* BATHER (M.Sil., England), Thenarocrinidae; undivided radianal almost directly below C-radial, interrupting circlet of basals as in *Carabocrinus*.—*4. Euspirocrinus* ANGELIN (M.Ord., Ontario-Sweden), Ampheristocrinidae.—*5. Dendrocrinus* HALL (M.Ord.-M.Sil., USA-Canada), Dendrocrinidae; radianal directly below C-radial, narrow articular facets on radials.—*6. Blothrocrinus* KIRK (L.Miss., Iowa-Illinois), Blothrocrinidae.—*7. Palaeocrinus* BILLINGS (M.Ord., Ontario), Palaeocrinidae; anal vent above large anal-X.—*8. Decadocrinus* WACHSMUTH & SPRINGER (U.Dev.-M.Penn., USA-Canada-Scotland), Scytalocrinidae; arms pinnulate. [Explanation: Letter symbols and patterns as in Figures 1 and 2.]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as an indication of relationship of the Synbathocrinidae to the Homocrinidae. The structural features of synbathocrinids can be explained very simply by fusion of the infer- and superradial components of the compound radials in the three rays mentioned. The suggested derivation of the synbathocrinids from homocrinid ancestors has no bearing on morphological terminology applicable to either group. In one assemblage (Synbathocrinidae) the radials are all undivided, that of the C-radial in *Synbathocrinus* having special characters which allow classification of it as an aniradial. In the other assemblage (Homocrinidae) three radials are compound, the superradial of the C-ray also having aniradial characters. The structural features displayed by the crinoid originally designated as *Phimocrinus jouberti* are judged to warrant distinction of this species as the type of a new genus, which is herein named *Theloreus* (p. 44).

CRINOIDS OF THE ALLAGECRINUS GROUP

The assemblage of genera considered here is characterized by undivided radial plates, which in two or more rays bear unbranched arms that arise directly from facets on the distal edges of the radials. These genera are all monocyclic inadunates belonging to the Allagecrinidae (Fig. 12). *Kallimorphocrinus,* a microcrinoid with only a single arm to each ray, is included in the family because study of ontogenetic series belonging to some members of the family shows that development proceeds from earliest *Kallimorphocrinus*-like calices to others having multiple-arm attachments to some of the radials *(Allagecrinus, Allocatillocrinus)* (Moore, 1940). The peculiarity of separate arms that rise from a series of facets located on the distal edge of individual radial plates, combined with absence of any compound radials in the dorsal cup, distinguishes the allagecrinid genera. *Anamesocrinus* (Fig. 3,*5*), which has five unbranched arms directly attached to each radial, differs in having three compound radials. In *Catillocrinus* (Fig. 12,*11*) the A-radial carries as many as 33 long, slender arms parallel to one another. The arms consist of uniserially arranged brachials which lack pinnules.

An anal tube composed of relatively stout U-shaped segments is borne by the C-radial. Most allagecrinids (Figs. 12,*2-4,6,7,9-11*), possess one arm in addition to the anal tube attached to the C-radial, thus matching the arrangement of appendages borne by the aniradial of *Synbathocrinus.* In *Wrightocrinus, Xenocatillocrinus,* and *Isocatillocrinus* (Fig. 12,*5,8,12*), two to four arms are carried by the C-radial in addition to the anal tube.

Bilateral symmetry is exhibited by all of the allagecrinids. In *Kallimorphocrinus* (Fig. 12,*1*) the plane of this symmetry coincides with the A-ray and CD-interray, which is known as the crinoidal plane, but in all others it is developed with varying distinctness in a differently oriented plane; this runs through the E-ray and BC-interray, which is the homocrinoidal plane, most strikingly emphasized in the Calceocrinidae. The homocrinoidal plane of bilateral symmetry is most clearly seen in *Mycocrinus, Paracatillocrinus, Eucatillocrinus,* and *Catillocrinus* (Fig. 12,*2,4,9,11*), in each of which the A- and D-radials are notably much larger than the other radials. Extremes are found in *Eucatillocrinus* and *Catillocrinus,* both of which especially well illustrate the disparate nature of dorsal cups classed in the Disparida.

It is not appropriate here to discuss at any length the inferred nature of evolutionary changes that need to be invoked to explain the development of such radial plates as occur in the Allagecrinidae. These plates, whether very large or relatively small, are undivided. Almost surely the multiple-arm-bearing radials are a product of fusion such as would yield solid radials if the large A- and D-radials of calceocrinids became fused with plates of the main-axil series, each of which bears an axil-arm. Calceocrinids, however, cannot be considered at all as antecedents in an evolutionary chain leading to the allagecrinids, even though they display the same sort of bilateral sym-

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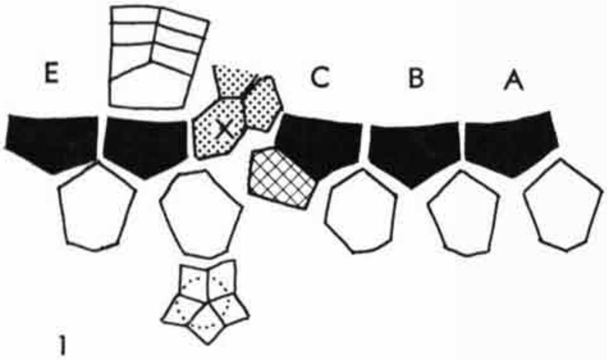
Fig. 10. Structure of inadunate crinoids characterized by th the presence of a multiple radial (radianal plus radial) in a single ray (not to scale). All genera illustrated belong to the dicyclic order Cladida.

1. Phanocrinus Kirk (U.Miss., USA, L.Carb., Scotland), Erisocrinidae.—*2. Cestocrinus* Kirk (L.Miss., Indiana), Lecythocrinidae; radianal even with and somewhat above C-radial.—*3. Ampheristocrinus* Hall (M.Sil., Illinois-Indiana-Tennessee), Ampheristocrinidae.—*4. Corynecrinus* Kirk (M.Dev., Indiana), Lecythocrinidae; small radianal left of but not below C-radial.—*5. Lasiocrinus* Kirk (L.Dev.-L.Miss., Iowa-New York-Germany), Dendrocrinidae.—*6. Cromyocrinus* Trautschold (L.Penn., USA; U.Carb., USSR), Cromyocrinidae.—*7. Poteriocrinites* Miller (M.Dev.-Perm., Europe-North America-East Indies), Poteriocrinitidae. [Explanation: Letter symbols and patterns as in Figures 1 and 2.]



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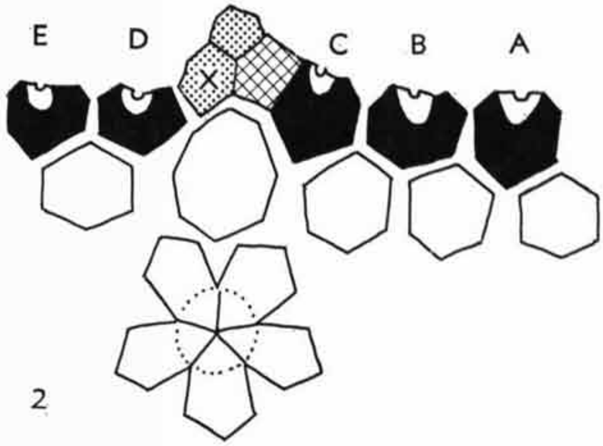

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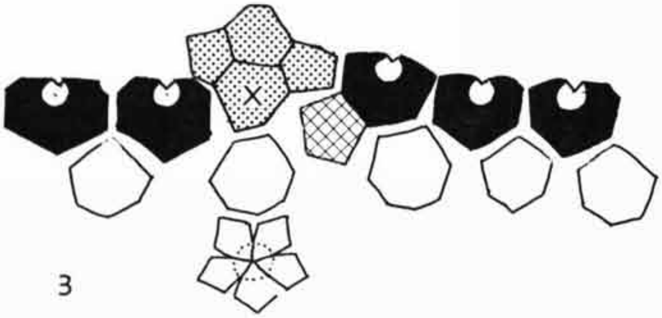

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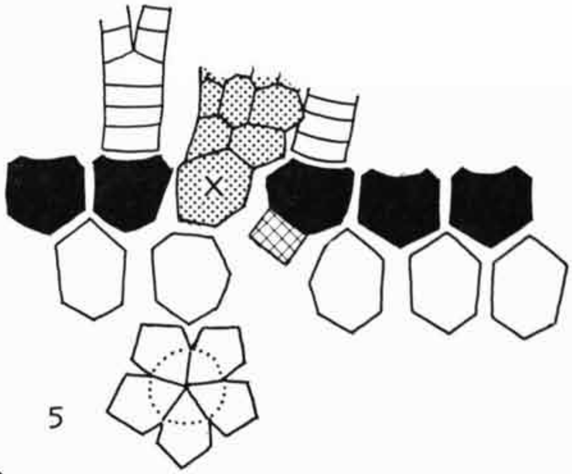

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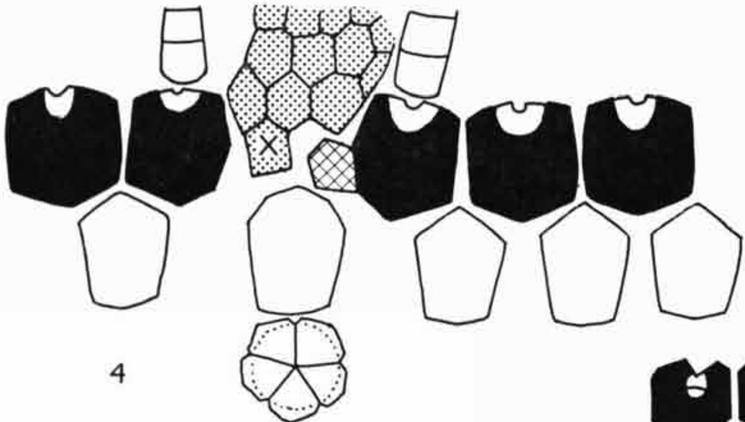

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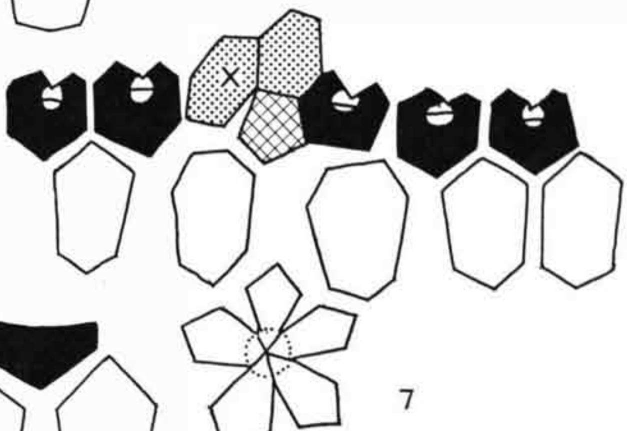

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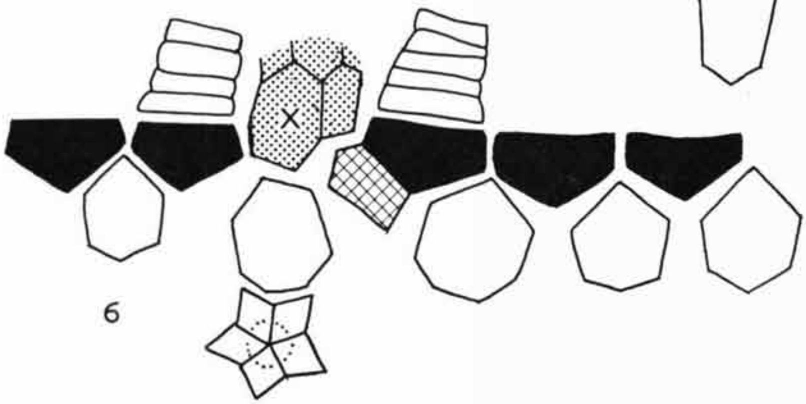

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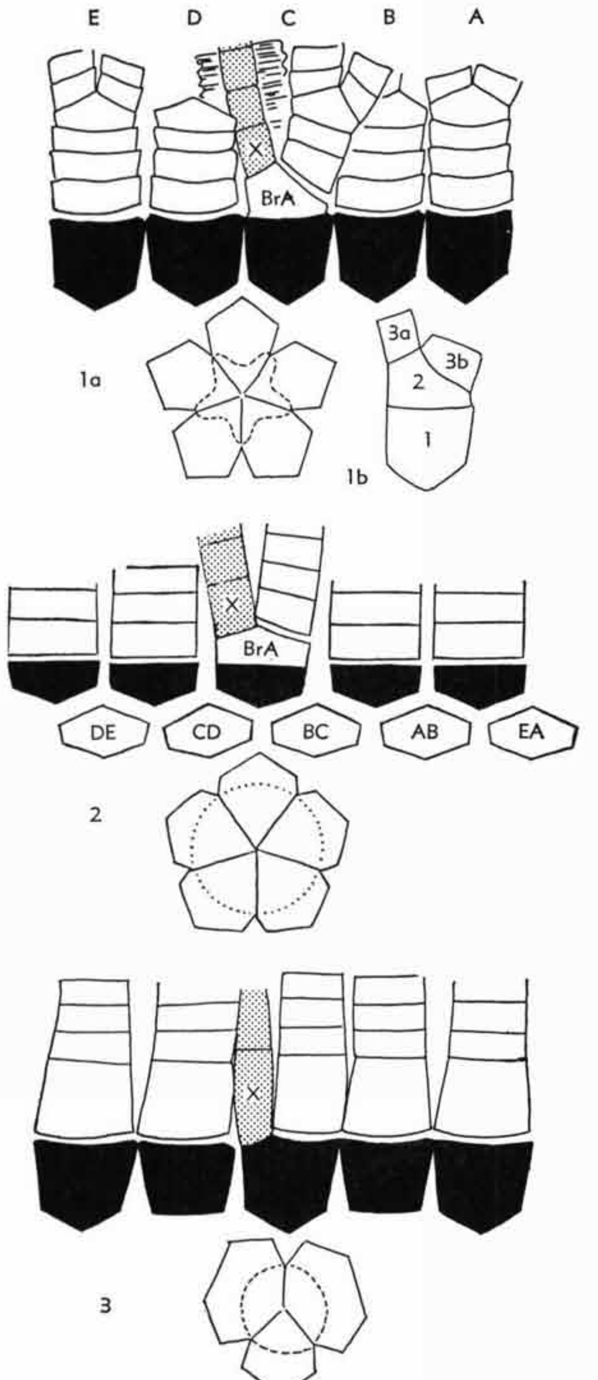


Fig. 11. Structure of inadunate crinoids characterized by absence of multiple radials (not to scale).—*1. Iocrinus* Hall (?L.Ord., Wales, M.Ord.-U.Ord., USA-Canada-England-Wales), Iocrinidae; brachianal articulating with C-radial; *1a,b,* diagram of plate structure and detail of C-ray with lettering of plates referred to in Table 1.—*2. Merocrinus* Walcott (M.Ord.-U.Ord., USA-England), Merocrinidae; with brachianal, resembling *Iocrinus* but dicyclic.—*3. Synbathocrinus* Phillips (M.Dev.-Perm., North American-Europe-East Indies), Synbathocrinidae; anal tube borne by C-radial which functions, therefore, as aniradial. [Explanation: Letter symbols and patterns as in Figures 1 and 2.]

metry. The calceocrinids are far too specialized in directions that do not match characters of *Catillocrinus* and other allagecrinids. Much more plausible is the concept that multiple-armed disparate crinoids of allagecrinid type were produced by fusion of radials with pararadials, as seen in crinoids such as *Calycanthocrinus* (Fig. 6,*2*), in which each radial element (except the B+C-inferradial) bears a single unbranched arm. Whatever their origin, we may distinguish the allagecrinids as a special group of crinoids that lack multiple radials.

CRINOIDS OF THE CYATHOCRINITES GROUP

Many inadunate crinoids belong to this group, typified by *Cyathocrinites* (Fig. 1,*1*). All are dicyclic forms classified in the order Cladida. They are characterized by the presence of only a single plate (identified as anal-X) in the posterior interray, or no anal plate at all in the cup. Whatever the structure of the posterior interray may be, each radial is an undivided plate that is clearly and readily discriminated as part of the uppermost circlet of the dorsal cup. No questions of morphological nature are encountered with respect to the undivided radials occurring in this group.

RADIANAL

Necessarily, some notice already has been taken of the plate in the dorsal cups of many crinoids which has come to be designated as radianal. The discrimination and naming of this plate is attributable to Bather (1890, p. 329), who identified it as the inferradial element of the C-ray, found in some crinoids to occur directly below the C-ray superradial but in others to be shifted laterally toward the left in the direction of the posterior interray. In this laterally moved position, the radianal comes to have the nature of an axillary plate that supports the C-ray "superradial" (=radial) on its right margin and the proximal anal sac plate (anal-X) on its left side (Fig. 8,*1-3*; 9,*3*,*7*). Unquestionably, the radianal is a ray plate and not an interray skeletal element. It may come to lie in line with the C- and D-radials but (except in small part) not above them, and does not rise out of the dorsal cup. In some crinoid groups evidence indicates that it may diminish and disappear by resorption. A question not settled by studies of comparative morphology is identity of the interray plate found next above the posterior basal of some crinoids such as *Cyathocrinites, Delocrinus,* and other cladid inadunates. Commonly it is interpreted to be the proximal plate of the anal tube or sac, called anal-X, but the possibility exists that it is a laterally displaced radianal, with or without succeeding anal plates.

The proximal plate of the C-ray in crinoids such

TABLE 1. *Nomenclature of Proximal C-ray Plates by Various Authors*

C-ray plate (Fig. 11,*1b*)	1	2	3a	3b
WACHSMUTH & SPRINGER, 1879	R	C	X	(IBr)
CARPENTER, 1882	R	C	X	(IBr)
WACHSMUTH & SPRINGER, 1886	Az	R+X	t	(IBr)
BATHER, 1890 (pl. 14)	R or RA	R or C	X	(IBr)
BATHER, 1900 (p. 120)	RA	R	X	(IBr)
BATHER, 1900 (p. 121, 146)	Ri	Rs	X	(IBr)
MOORE & LAUDON, 1943 (p. 14)	RAi	RAs	X	R
MOORE & LAUDON, 1943 (p. 27)	RAi	RAs	X	(IBr)
MOORE & LAUDON, 1944 (p. 140)	RAi	RAs	X	(IBr)
MOORE, 1948 (p. 31)	RAi	RAs	X	R
MOORE, 1952 (p. 616)	R	AR	X	(IBr)
UBAGHS, 1953 (p. 679)	Ri	Rs	X	(IBr)
UBAGHS, 1953 (p. 745)	R	(IBr)	X	(IIBr)
RAMSBOTTOM, 1961 (p. 4)	RAi	RAs	X	(IBr)
MOORE, 1962 (this paper)	R	BrA	X	IBr

EXPLANATION OF LETTER SYMBOLS

AR—aniradial
Az—azygous plate
BrA—brachianal
IBr—primibrach
IIBr—secundibrach
C—costal or brachial
R—radial
Ri—inferradial
Rs—superradial
RA—radianal
RAi—inferradianal
RAs—superradianal
t—tube plate (anal)
X—anal-X plate

as *Iocrinus* and *Merocrinus* should be classed as a radial—not a radianal, as was done by BATHER (1900, p. 120), and not an inferradianal, as was done by MOORE & LAUDON (1943, p. 27; 1944, p. 140), MOORE (1948, p. 31), and RAMSBOTTOM (1961, p. 4). Nomenclature of this plate is considered further in subsequent discussion of the terms aniradial and brachianal.

Although the morphological derivation of plates called radianals in various crinoids is universally agreed upon, their leftward displacement and accompanying changes in size, shape, and contacts with adjoining plates serve to establish them as special structural elements. Their origin as the proximal plate of the C-ray progressively loses significance in the course of evolution of this ray and adjoining plates that come to be developed in the CD-interray. Radianal is a well-chosen name, because it suggests the origin of this plate from a radial element (inferradial) and indicates its special relationship to anal-plate structures.

For purposes of discussion in this paper, radianals are treated as equivalent to the lower component of a compound radial, which they are. Nevertheless, a radianal is entitled to rank as a distinctively independent plate, removed from classification either with radials or anals. In diagrams, the radianal may be identified by its letter symbol (RA) or by a pattern different from those employed for radials (simple or compound) and for anals, or both by letter symbol and pattern. In this paper, oblique cross ruling is adopted for radianals.

Radianal plates are recognized in the monocyclic inadunate order Hybocrinida, the dicyclic inadunate order Cladida, and in the Flexibilia. They are found in no other crinoids. Among the groups mentioned, only *Ottawacrinus* is known to have compound radials in more than one ray (Pl. 1, figs. 3a,b; text-fig. 2,*4*). If the presence of a radianal in combination with the C-radial is accepted as morphologically constituting a compound radial, *Ottawacrinus* is unique in having five compound radials, and all other radianal-bearing crinoids may be grouped together in having only one compound radial. If it is true that the most primitive structural plan of dorsal cups in both monocyclic and dicyclic inadunates calls for the presence of compound radials in all rays, then the undivided radials which prevail in inadunates, especially the cladids, probably were evolved by fusion of two antecedent ray plates rather than by resorption of one of them.

Invariably, radianals are bordered on one side by the C-radial and in all but the rarest exceptions (Fig. 13,*1j*; 14,*3f*) on another side by the posterior (CD) basal. The C-radial is directly or obliquely above it or joined to it on the right; the posterior basal is directly or obliquely below it. Universally, also, the radianal is bordered by anal-X or the anal vent (*Cornucrinus,* (Fig. 8,*4a,b*). In addition, the radianal may adjoin various other plates (Figs. 8-10, 13-14). Normally, the radianal does not reach low enough in the cup to separate the BC- and CD-basals, and therefore does not come into contact with plates of the infrabasal circlet. Exceptions are the unique compound radianal (infer- and superradianal) of *Carabocrinus* (Fig. 9,*2*), and undivided radianal of *Thenarocrinus* (Fig. 9,*3*), that interrupt the basal circlet. At this point I call attention to the word "unique" in the preceding sentence, because now it seems clear that inferradianal and superradianal were incorrectly applied by MOORE & LAUDON (1943, p. 14, 27; 1944, p. 140) to numerous monocyclic inadunates and to *Merocrinus* among dicyclic genera. Unhappily, their ill-advised usage of these terms has been followed by later authors (MOORE, 1948, p. 31; SHROCK & TWENHOFEL, 1953, p. 678-682; RAMSBOTTOM, 1961, p. 3-7). Only *Carabocrinus* possesses an infer- and superradianal. Commonly the lower margin of the radianal adjoins two basal plates (Fig. 9,*1,4-8*; 10,*1,3,5-7*); less commonly it touches only a single basal (CD) (Fig. 10,*2-4*).

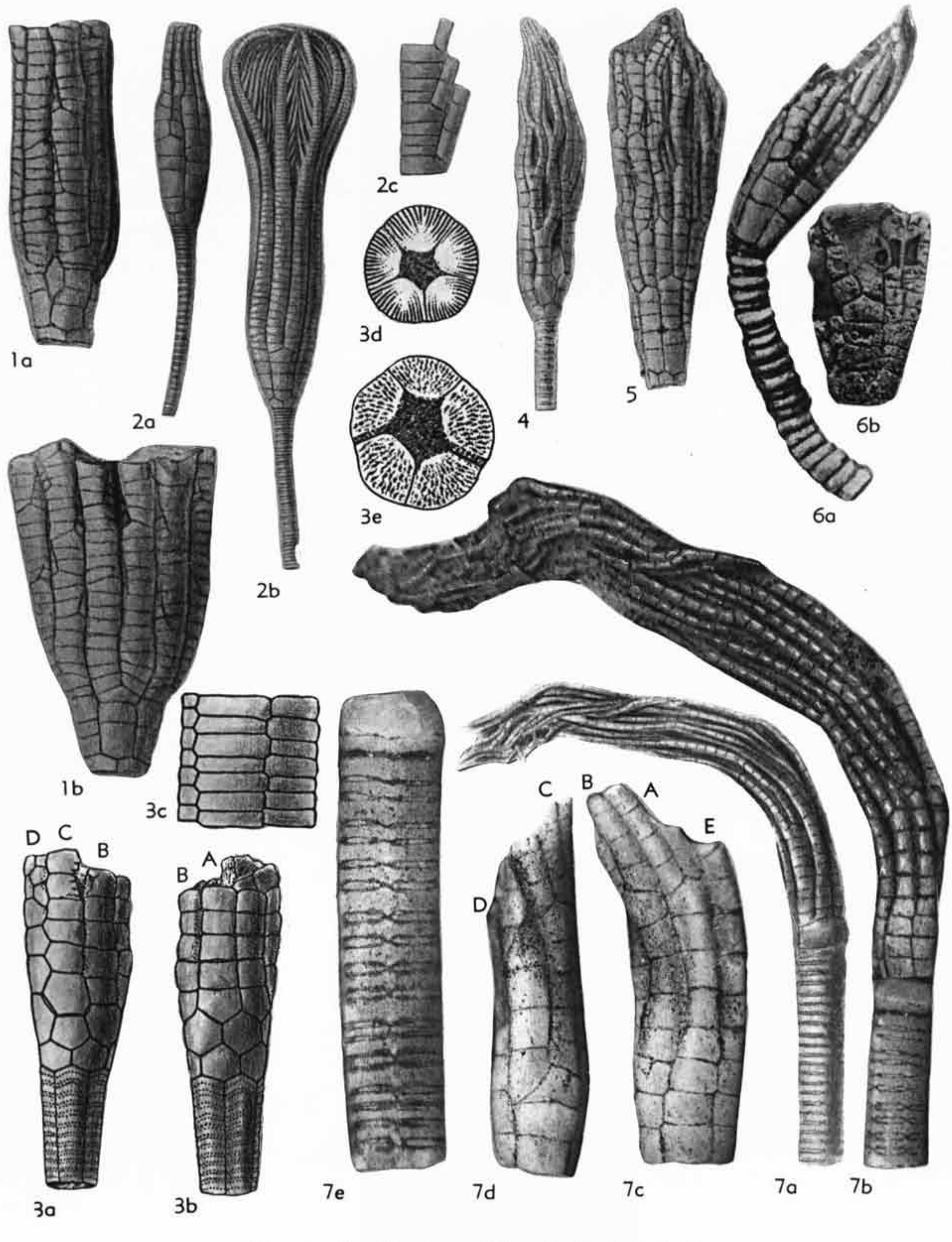
The left and upper margins of the radianal may lie next to anal-X and other plates of the anal series, as well as to an edge of the D-radial (Figs. 7-10, 13, 14, 15). Also, the radianal may be notably larger than adjoining anal plates (Fig. 13,*1a-i*), subequal to them in size (Fig. 13, *1j,2,3,4a-i*), or smaller than at least some of the proximal anals (Fig. 14,*2d*). In some genera and even within some species, the arrangement of the radianal with respect to surrounding plates varies a good deal (Figs. 13, 14).

Variations in size, shape, and position of the radianal, including at least some of those just mentioned with cited illustrations, reflect evolutionary change rather than mere instability. Generally, no question concerning the identity of the radianal is encountered, but crinoids like some individuals of *Cadocrinus variabilis* (Fig. 13,*1c-j*) and *Zeacrinites konincki* (Fig. 14,*3c-f*), if found alone and not associated with specimens having clearly identifiable radianals, would offer problems. In these forms the plate next to the C-radial on its left would probably be labeled as anal-X. Comparisons indicate that it actually is the radianal. *Lebetocrinus grandis* (Fig. 15), from Lower Mississippian rocks of Indiana, has a large plate

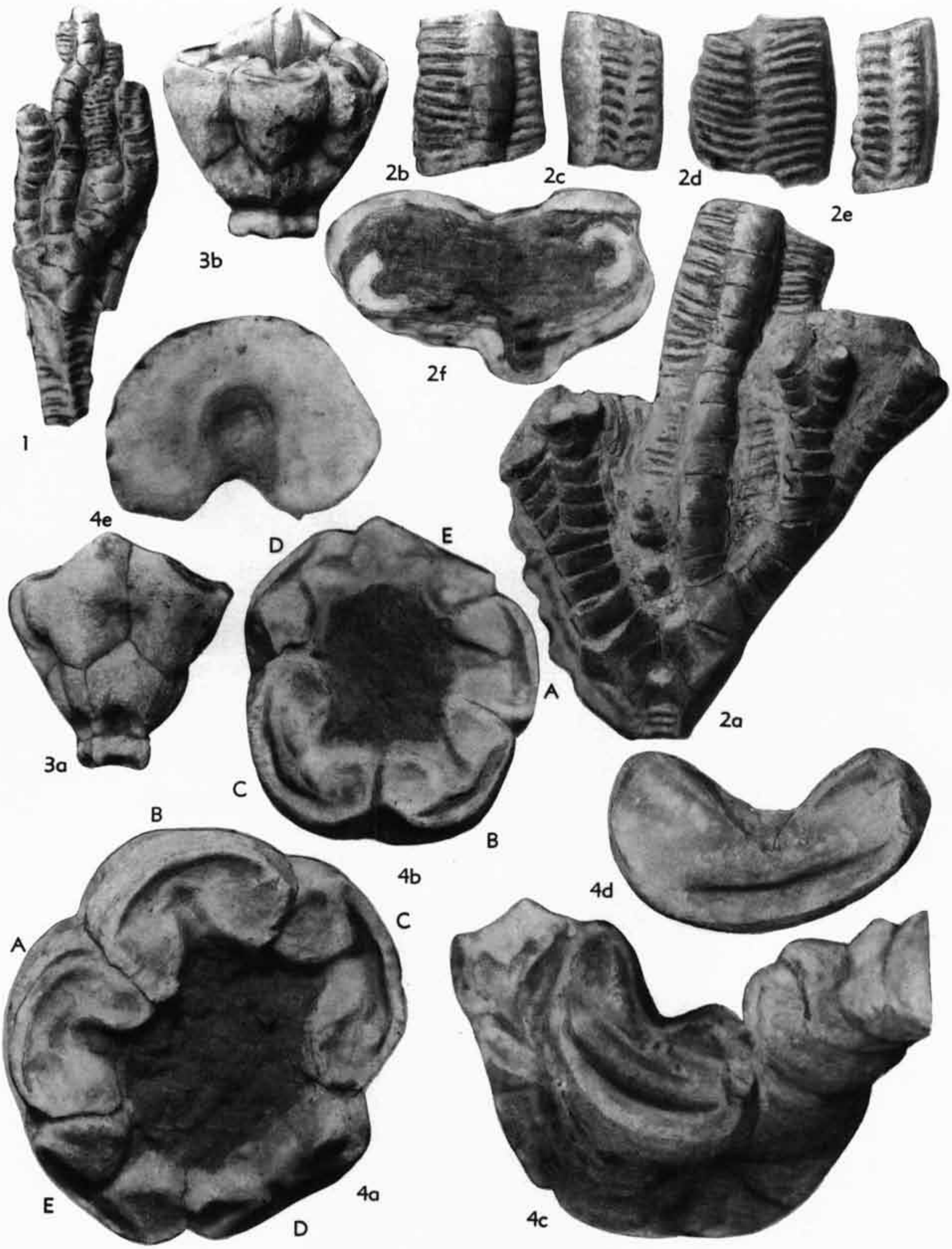
EXPLANATION OF PLATE 1

FIGURE PAGE

1. *Dystactocrinus constrictus* (HALL), (Heterocrinidae), Upper Ordovician (Maysville), Ohio; *1a,b,* incomplete crown (holotype), CD-interray and B-ray views, ×2 (after Meek, 1873) 14
2. *Ectenocrinus* S. A. MILLER, (Homocrinidae); *2a, E. simplex* (HALL), Upper Ordovician, Cincinnati, Ohio; juvenile specimen with regenerated distal parts of arms, BC-interray view, ×1.3; *2b,c, E. grandis* (MEEK), Upper Ordovician, Cincinnati, Ohio; B-ray view of crown with stem and lateral view of part of arm showing nonaxil-brachs and subaxils with proximal ends of ramules on one side of arm, ×2.5, ×3.5 (after Meek, 1873) 12
3. *Ottawacrinus typus* W. R. BILLINGS (Ottawacrinidae), Middle Ordovician (Trenton.), Hull, Ontario; *3a,b,* incomplete crown with proximal part of stem (holotype), some rays indicated by Carpenter letter symbols, C- and A-ray views, former showing small radianal directly below C-radial, which is followed by five primibrachs, ×4; *3c,* side view of columnals from middle part of stem, showing pentameres, ×7.5; *3d,e,* articular surface of columnals from middle and distal parts of stem, showing pentameres with crenellae or short, discontinuous depressions and large, pentagonal lumen, ×6.5 (after Bather, 1913) 36
4. *Heterocrinus propinquus* MEEK, (Heterocrinidae), Upper Ordovician (Eden.), Cincinnati, Ohio; D-ray view of crown with proximal part of stem, ×2.5 (after Meek, 1873) 14
5. *Ohiocrinus laxus* (HALL), (Heterocrinidae), Upper Ordovician (Maysville), Cincinnati, Ohio; AB-interray view of crown, ×2.5 (after Meek, 1873) 14
6. *Ristnacrinus marinus* ÖPIK, (Eustenocrinidae), Middle Ordovician (Jewe), Estonia; *6a,* incomplete crown and part of stem, E-ray view, ×2.5; *6b,* part of crown (holotype), C-ray view showing anal tube plates near left edge, ×2.5 (after Öpik, 1934) 35
7. *Peniculocrinus milleri* (WETHERBY), Middle Ordovician (Trenton.), Tyrone Limestone, Highbridge, Kentucky; *7a,b,* crown and proximal part of stem (holotype, Univ. Chicago no. 6091), WETHERBY's published figure (1880) and photograph showing A-ray slightly at left of mid-line, ×4, ×6; *7c,d,* proximal part of crown (holotype), rays indicated by Carpenter letter symbols, A- and C-ray views, latter showing anal tube near left edge resting on sloping facet of brachianal, ×10; *7e,* proximal part of stem with rounded, seemingly fused basal circlet at summit, ×10 34



Moore — Ray Structures of Some Inadunate Crinoids



Moore — Ray Structures of Some Inadunate Crinoids

interrupting the radial circlet in the posterior interray. This plate was designated as anal-X by KIRK (1940, p. 74), in spite of the unevenness and obliquity of the sutures next to the basal plates, which were noted by KIRK without mention of the possibility that the large plate actually is a radianal. In my judgment radianal, rather than anal-X, is correct.

The only monocyclic crinoids in which a radianal plate is properly distinguished belong to the Hybocrinida (Figs. 7, 8). The C-ray of these crinoids shows the presence of a relatively large inferradial element directly below or slightly at left and below a superradial element which bears a narrow arm (Fig. 7,*1*, 8,*1-3*) or ambulacral structure on the radial plate surface (Fig. 8,*3-4*).

An anal-X plate which abuts on the upper left edge of the radianal occurs within the radial circlet of *Hybocrinus* (Fig. 7,*1*) and *Hybocystites* (Fig. 8,*3*), its lateral margins touching the C- and D-radials; in these genera anal-X is below the upper limit of the dorsal cup. In *Hoplocrinus* (Fig. 8,*1*) the radianal is appreciably larger than the C-radial, which rests on its upper right edge, and it is approximately equal in size to the A-, B-, D-, and E-radials, reaching as high as their summits. *Baerocrinus* (Fig. 8,*2*) also is characterized by an unusually large radianal. In the strongly specialized *Cornucrinus* (Fig. 8,*4*), the radianal is located directly beneath the anal aperture, found on the side of the cup between the C- and D-radials.

Monocyclic crinoids belonging to the order Disparida lack a radianal plate, even though the proximal plate (inferradial) of the C-ray has been so designated by authors in the families Homocrinidae, Calceocrinidae, Haplocrinitidae, and Anamesocrinidae—all with compound radials in three rays—and the Heterocrinidae, and Anomalocrinidae, with compound radials in two rays. Interpretation in this way has been published by BATHER (1890, p. 329, pl. 14; 1893, p. 61; 1900, p. 145-151), MOORE & LAUDON (1943, p. 27; 1944, pl. 52), UBAGHS (1953, p. 679) and others. MOORE & LAUDON (1943, p. 14, 27; 1944, pl. 52) and MOORE (1948, p. 31) have also called this proximal C-ray plate an inferradianal, the next higher one that supports the anal-X plate on its left shoulder being designated as a superradianal. In addition, MOORE & LAUDON (1943, p. 27) in referring to the Allagecrinidae and Synbathocrinidae classified the undivided C-radial itself as a radianal plate. Finally, the large inferradial located beneath the B- and C-superradials of *Pisocrinus* and other pisocrinid genera has been called a radianal by BATHER (1890, pl. 14; 1900, p. 149), MOORE & LAUDON (1944, pl. 54), and UBAGHS (1953, p. 673), or an inferradianal by MOORE & LAUDON (1943, p. 27), who classed the C-superradial as a superradianal. These diverse applications of radianal, inferradianal, and superradianal suggest long-existing confusion rather than significant disagreements.

Two main reasons can be advanced to support the conclusion that neither a radianal nor an inferradianal associated with a superradianal (that is, a compound radianal plate) is correctly distinguished as a part of dorsal-cup structure in the Disparida.

The first reason for rejecting interpretation of the lowermost plate of the C-ray as a radianal or inferradianal is that this most proximal plate of the C-ray

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EXPLANATION OF PLATE 2

FIGURE PAGE

1, 2. Iocrinus subcrassus (MEEK & WORTHEN), (Iocrinidae), Upper Ordovician (Richmond.), Ohio; *1,* specimen (Yale Univ. no. 17110) from Cincinnati, showing lower part of crown, C-ray view, large brachianal prominent, no basals visible above strongly pentastellate stem, ×2.5; *2a-f,* specimen (Univ. Chicago, no. 19178) from Lebanon, Ohio; *2a,* lower part of crown with three attached columnals, brachianal and proximal part of anal tube seen from CD-interray view, D-arm at left, ×3; *2b-e,* distal part of preserved section of anal tube belonging to this specimen from outer, right, inner, and left sides, showing corrugated plates that border armlike axial ridge, ×3; *2f,* proximal view of fragment of tube shown in *2b-e,* outer side of tube directed downward, ×5 40

3, 4. Iocrinus crassus (MEEK & WORTHEN), (Iocrinidae), Upper Ordovician (Maquoketa), Kendall County, Illinois; *3a,b,* dorsal cup (Univ. Illinois, no. X-136, specimen A) with proximal columnal of stem, CD-interray and A-ray views, showing especially the greater height of the posterior side of the cup, which rises to a peak near the right distal corner of the D-radial, ×2.5; *4a-e,* parts of another specimen (B) in same lot, *4a,* ventral view showing radial facets (rays indicated by Carpenter letter symbols), ×5; *4b,* another ventral view of same specimen, ×4; *4c,* photo looking straight downward on facet of C-radial, proximal extremity of B-arm at right, ×5; *4d,* proximal facet of brachianal belonging to same specimen, ×8; *4e,* distal facet of first anal tube plate above anal-X, same specimen, ×10 40

exactly corresponds to that of other rays in all disparid families having compound radials in more than one ray. Since this is so, no good ground is indicated for recognizing a special radial-and-anal relationship such as appears in crinoids having a true radianal. The inferradial of the C-ray in eustenocrinids, homocrinids, calceocrinids, haplocrinitids, anamesocrinids, heterocrinids, and anomalocrinids is just that and nothing more (Figs. 2-5). In pisocrinids the inferradial or inferradials of the B- and C-rays likewise are inferradials and nothing more (Figs. 6, 7,*2*).

The second reason for not accepting radianals or their divided equivalents in the architectural scheme of the Disparida is relationship of concerned C-ray plates with anal-X and other anal plates. When an undoubted radianal is examined, either primitive (as in *Ottawacrinus,* Fig. 2,*4; Cupulocrinus,* Fig. 9,*1*; *Dendrocrinus,* Fig. 9,*5*) or modified in evolution by lateral displacement and altered shape (as in *Hybocrinus,* Fig. 7,*1*; *Hoplocrinus, Baerocrinus, Hybocystites,* Fig. 8,*1-3*; *Carabocrinus, Thenarocrinus, Euspirocrinus, Blothrocrinus, Palaeocrinus, Decado*crinus, Fig. 9,*2-4,6-8*; *Phanocrinus, Cestocrinus, Ampheristocrinus, Corynecrinus, Lasiocrinus, Cromyocrinus, Poteriocrinus,* Fig. 10,*1-7*, and numerous others), the radianal is found invariably to adjoin the C-radial (originally superradial) on one side and anal-X on another side; the radianal may touch other anal plates in addition to the X-plate. An arrangement like this does not exist in the Disparida. Consequently, no plate of the dorsal cup in genera belonging to this order is properly classed as a radianal (or inferradianal associated with superradianal).

ANIRADIAL

The proximal (undivided radial) or next-to-proximal (superradial) plate of the C-ray in various disparid crinoid genera has been designated as an aniradial (MOORE, 1952, p. 607). It is the C-ray plate (radial or superradial but not higher) that supports on an oblique facet at its upper left margin the anal-X plate (as in *Synbathocrinus,* Fig. 11,*3*, with anal-X resting on an undivided radial), or on a superradial (as in homocrinids, Fig. 3,*1,2,4,6,7*; anamesocrinids, Fig. 3,*5;* heterocrinids, Fig. 5,*1-6;* anomalocrinids, Fig. 5,*7*; and some eustenocrinids, Fig. 2,*1*). As first published, the designation of plates called aniradials in some crinoids (e.g., *Heterocrinus, Dystactocrinus, Iocrinus, Merocrinus,* in MOORE, 1952, p. 616) was ill advised in that plates designated as aniradials consist morphologically of superradials *(Heterocrinus, Dystactocrinus)* or axillary brachials *(Iocrinus, Merocrinus),* which fundamentally are quite dissimilar skeletal elements and which should not be denominated at expense of obliterating their respective morphological identities.

The judgment now is expressed that aniradial is a term suitable only for differentiation in supplemental manner of the C-ray plate of the radial circlet which on its left shoulder supports the proximal plate of the anal tube (anal-X). This means that, in my opinion, it should not have independent status like that of the radianal, and emphatically the name is unsuited for designation of the axillary plate above the circlet of radials, which in *Iocrinus* and *Merocrinus* gives rise to a series of brachs[1] on its right side and the anal

[1] The use of adjectives as nouns (adjectival nouns) is especially common in the morphological terminology of crinoids (e.g., radial, for radial plate, brachial, for brachial plate, etc.). This is so thoroughly established by usage that any considerable change is unthinkable. Beginning with BATHER (1892, 1893), it has become common practice to employ such nouns as primibrach, secundibrach, axil, primaxil, etc., using these interchangeably with their adjectival form (primibrachial, axillary, etc.). In the same way I propose to recognize brach (brachial), fixed-brach (fixed-brachial), etc. Later on, reasons for adopting terms such as subaxil and nonaxil-brach are given.

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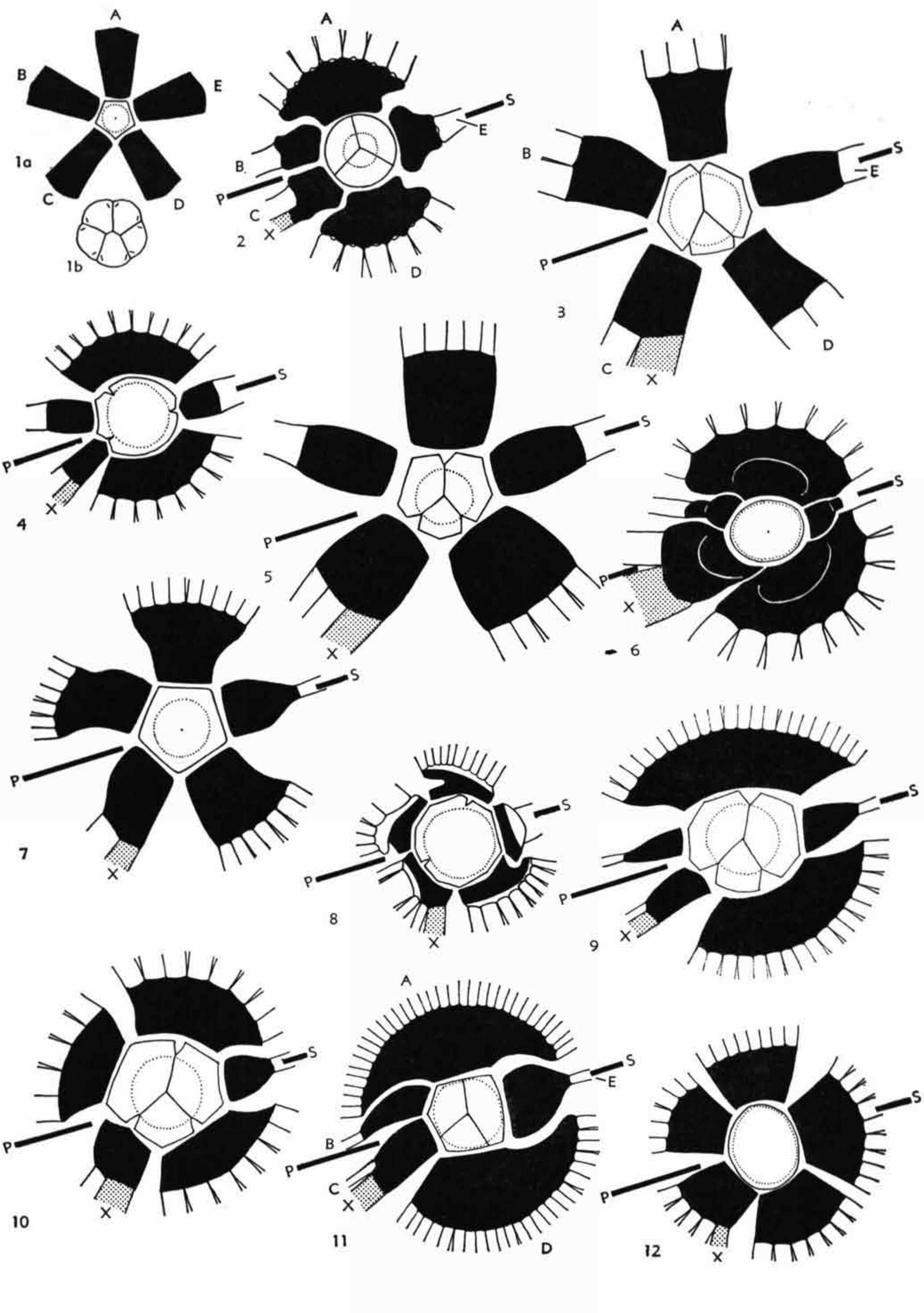
FIG. 12. Structure of inadunate crinoids characterized by absence of multiple radials (not to scale). All genera illustrated belong to the family Allagecrinidae of the monocyclic order Disparida. All except Figure 1 display homocrinoidal bilateral symmetry (P-S).

1. Kallimorphocrinus J. M. WELLER (L.Miss.-Perm., USA-Europe-East Indies); bilateral symmetry in crinoidal plane determined by orals *(1b)* but no evidence of homocrinoidal plane.—*2. Mycocrinus* SCHULTZE (M.Dev., Germany); B-, C-, and E-radials single-armed, C-radial functioning as aniradial.—*3. Allagecrinus* CARPENTER & ETHERIDGE (L.Carb.-Perm., USA-Scotland-East Indies); C- and E-radials single-armed.—*4. Paracatillocrinus* WANNER (Perm., Timor); structurally most like *Mycocrinus.* —*5. Wrightocrinus* MOORE (L.Carb., Scotland, Perm., Timor); B- and E-radials single-armed.—*6. Metacatillocrinus* MOORE & STRIMPLE (L.Penn., Oklahoma); B-, C-, and E-radials single-armed.—*7. Neocatillocrinus* WANNER (Perm., Timor); C- and E-radials single-armed.—*8. Xenocatillocrinus* WANNER (Perm., Timor); only E-radial single-armed.—*9. Eucatillocrinus* SPRINGER (L. Miss., Indiana); B-, C-, and E-radials single-armed.—*10. Allocatillocrinus* WANNER (U.Miss.-L.Penn., USA-Scotland); C- and E-radials single-armed.—*11. Catillocrinus* SHUMARD (L.Miss., Iowa-Indiana-Kentucky-Tennessee); B-, C-, and E-radials single-armed, A- and D-radials bearing very many arms.—*12. Isocatillocrinus* WANNER (Perm., Timor); no radials single-armed. [Explanation: Letter symbols and patterns as in Figure 1; P-S signifies plane of bilateral symmetry.]



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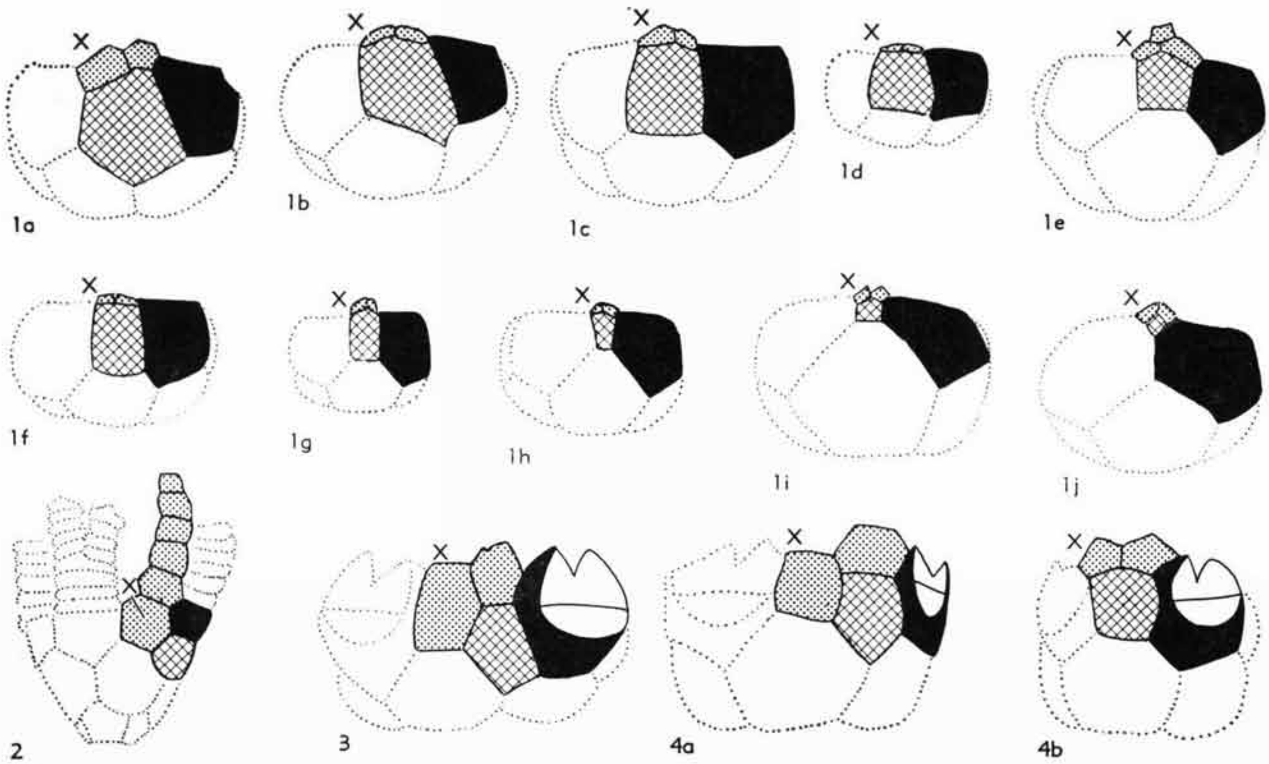


Fig. 13. Variations in the C-radial, radianal, and associated anal plates in selected inadunates.

1. Cadocrinus variabilis (Wanner), Perm., Timor; *1a-j,* CD-interray views of different specimens, ×1.3 (*1a-i,* after Wanner, 1916; *1j,* after Wanner, 1940).—*2. Cupulocrinus kentuckiensis* Springer, M.Ord., Kentucky; CD-interray view, ×1.3 (after Springer, 1920).—*3. Malaiocrinus sundaicus* (Wanner), Perm., Timor; CD-interray view, ×2.5 (after Wanner, 1916).—*4. Malaiocrinus crassitesta* Wanner, Perm., Timor; *4a,b,* CD-interray views of two specimens, ×1.3 (*4a,* after Wanner, 1924; *4b,* after Wanner, 1937). [Explanation: C-radial, solid black; radianal, oblique cross ruled; anal plates, stippled.]

tube on its left side; for this axillary plate the term brachianal, previously mentioned, seems to be most appropriate.

BRACHIANAL

The name "brachianal" was introduced by Bather (1890, p. 330) as a designation for the plate that later almost universally has come to be known as anal-X (or simply X). In this sense, however, brachianal never gained acceptance, especially since Bather (1892, p. 64) himself rejected it. Now, after nearly three quarters of a century, I propose to exhume this long-dead term for application in a slightly different sense, namely, to designate the plate that supports anal-X in crinoids such as *Iocrinus* and *Merocrinus.* Morphologically this plate is an axillary brachial occurring just above the upper rim of the dorsal cup in the C-ray. The nature of its proximal articulation with the C-radial and other characters furnish satisfactory evidence that this axil, which supports the anal tube on its left side and a normal arm on its right side, is not a displaced superradial or a modified ray element produced by evolution of a superradial. It is a special brachial plate. The designation brachianal is ideally suitable (1) because of similarity of the name to radianal, (2) because it indicates the actual nature of this plate as a brachial and its relation to anal-plate structures also, and (3) because brachianal is not to be confused with radianal.

When Hall (1866, p. 5) first described *Iocrinus,* he interpreted both branches borne by the first plate above the C-radial as true arms, adding "no anal plates have yet been observed in any of the individuals examined." Meek & Worthen (1865, p. 147, 148) similarly misconstrued the anal series of *Heterocrinus* [=*Iocrinus*] *crassus* and *H. subcrassus* as an arm, but later (Meek & Worthen, 1873, p. 15) referred to this branch as "an armlike series of anal pieces." Wachsmuth & Springer (1880, p. 65) clearly recognized that the axillary plate of *Iocrinus,* here termed brach-

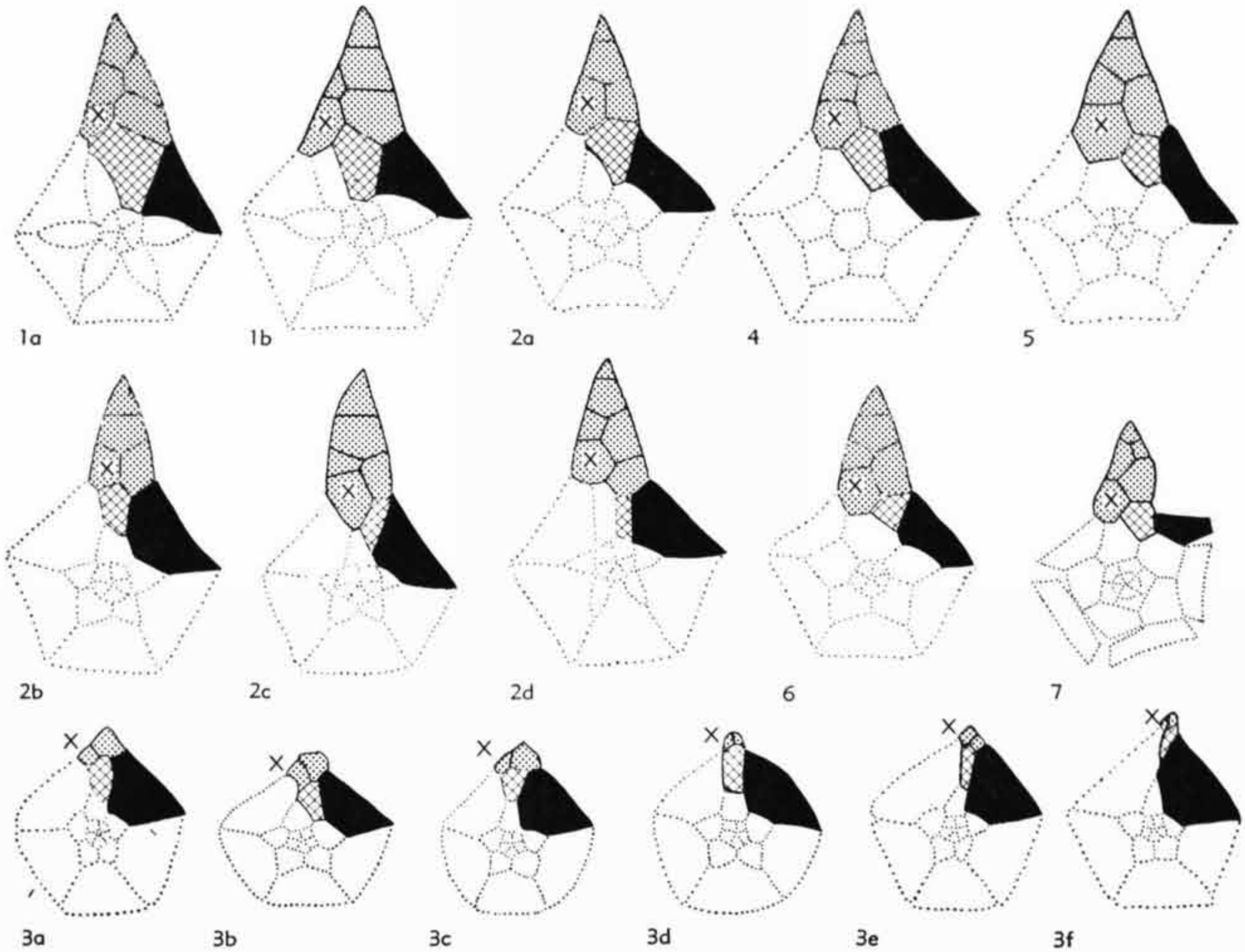


FIG. 14. Variations in the C-radial, radianal, and associated anal plates in some zeacrinitid genera.

1. Zeacrinites magnoliaeformis TROOST in HALL, U.Miss., Alabama; *1a,b,* two specimens, ×1.3.—*2. Z. wortheni* (HALL), U.Miss., Kentucky; *2a-d,* four specimens, ×1.3. —*3. Z. konincki* (BATHER), L.Carb., Scotland; *3a-f,* six specimens, ×1.3.—*4. Alcimocrinus girtyi* (SPRINGER), L. Penn., Oklahoma; specimen, ×1.3.—*5. Eratocrinus elegans* (HALL), L.Miss., Iowa; specimen, ×1.3.—*6. E. commaticus* (S. A. MILLER), L.Miss., Missouri; specimen, ×1.3.—*7. Hydreionocrinus amplus* WRIGHT, L.Carb., Scotland; specimen, ×0.7. [Explanation: Patterns as in Figure 13. Figures 1, 2, 4-6, after Springer, 1926; 3, 7, after Wright, 1952, 1951.]

ianal, is a movable brachial that corresponds to arm plates of other rays but is distinguished by giving rise on one side to a normal arm and on the other to a "rather strong ventral sac" with "its full length forming a highly elevated ridge." They considered the questions, "Shall it be called a brachial?" and "Is the plate, on the contrary, an anal plate?", concluding that "it is a brachial with interradial functions."

The distal facet on the right side of the brachianal, horizontal in *Peniculocrinus* but sloping distinctly in other genera, bears a succession of quadrangular brachs that leads to an axillary arm plate. Because these brachs correspond precisely to primibrach series in each of the other rays (Fig. 11,*1a*), it is appropriate and decidedly preferable, in my opinion, to classify these C-ray brachs as primibrachs, also. Thus, the brachianal is removed from treatment as an arm element, since it is not counted as an axillary primibrach followed by secundibrachs. The left distal facet of the brachianal supports anal-X, which is succeeded by the decidedly armlike plates that form the median outward-facing ridge of the anal tube.

The articular facets of a typical brachianal can be seen in some specimens of *Iocrinus* but they have not been studied in other genera. The proximal facet closely resembles the articular facet of the C-radial on which it rests, both facets being marked by a narrow, moderately deep ligament groove located near the outer edge of the facet and showing gentle curvature like that of the exterior surface of the plate (Pl. 2, fig. 4d). The median inner margin of the facet is broadly V-shaped, with the point of the indentation close to a narrow ridge that runs parallel to the ligament groove on its inner side. Shallow, broad concavities occupy subtriangular areas on opposite sides of the V-shaped indentation inside the ridge that borders the ligament groove; these are muscle fields. The distal articular facets of the brachianal show closely similar features but are smaller. In short, the brachianal possesses all morphological characters of a normal axillary brachial as observed in very many inadunate genera.

What about the occurrence of brachianals among inadunate crinoid genera? In view of the somewhat lengthy discussion of this plate just given, it may seem odd to state that only six genera definitely are known to possess such a plate, although three others can be added as almost certainly characterized by them. Eight of the nine genera, taking them all together, are monocyclic forms and the remaining one is a dicyclic crinoid. A question mark associated with a generic name in the following list serves to identify unproved occurrence of brachianals. The monocyclic group includes *Iocrinus* HALL (?L.Ord., M.Ord.-U.Ord.), *Caleidocrinus* WAAGEN & JAHN (M.Ord.), *Peniculocrinus* MOORE, n.gen. (M.Ord.), *Myelodactylus* HALL (M.Sil.-M.Dev.), *Herpetocrinus* SALTER (M.Sil.), *?Eomyelodactylus* FOERSTE (L.Sil.), *?Crinobrachiatus* MOORE, n.gen. (M.Sil.), *?Brachiocrinus* HALL (L. Dev.). The dicyclic brachianal-bearing inadunate is *Merocrinus* WALCOTT (M.Ord.-U.Ord.). All except *Caleidocrinus* occur in North America. Known from Europe are *Iocrinus* (England, ?Wales), *Caleidocrinus* (Czechoslovakia), *Myelodactylus* (Sweden), and *Merocrinus* (England).

Some paleontologists may be inclined to judge that a morphological feature confined to a half-dozen or possibly nine genera is automatically classifiable as unimportant, relatively if not absolutely. This does not follow, because number of occurrences is by no means a proper criterion for evaluation, else *Archaeopteryx*, represented by a single known specimen, would be rated as an unimportant fossil. In my opinion, recognition of the distinction between brachianal and radianal (or incorrectly designated superradianal), as well as between brachianal and C-radial or C-superradial (with aniradial attributes) is indispensable as a guide in the search for truly homologous morphological features among the diverse skeletal structures exhibited by numerous genera. The need is greatest in comparative studies of the earliest inadunates, because these point to ancestral characters and may demonstrate modes of evolutionary development leading to observed groups. Four of the known brachianal-bearing genera come from Middle Ordovician rocks, some as old as Chazyan (Llanvirnian, Llandeilian). RAMSBOTTOM (1961, p. 6) recently has described and figured the fossil that "is almost certainly the oldest known crinoid," originally named *Dendrocrinus cambriensis* HICKS (1873) and reported to come from Tremadocian rocks of Wales. The species is doubtfully referred to *Iocrinus* by RAMSBOTTOM, though he noted its superficial resemblance to *Eustenocrinus* (and I may add *Peniculocrinus*). *I.? cambriensis* was collected from strata now identified as lower Arenigian (Lower Ordovician). Thus, it is possible that crinoids with brachianals are the oldest (*I.? cambriensis* is not known to possess such a plate) or at least among the next-to-oldest (Llanvirnian, Llandeilian) of all inadunates, and other crinoids, also.

Genera of the Myelodactylidae, included in the brachianal-bearing group of inadunates, are obviously specialized in a striking manner, as pointed out in a later part of the present paper. This is consonant with their Middle-Silurian-to-Middle-Devonian stratigraphic range. Whether the myelodactylids are descendants of Ordovician genera such as *Iocrinus* and *Caleidocrinus* is conjectural—possible, but dubitable.

FIXED-BRACHIALS

Inadunate crinoids are supposed to be distinguished by having arms that are freely movable above the circlet of the radials. Many flexible crinoids lack any distinction between parts of the crown definable as dorsal cup and free arms. Camerate crinoids are differentiated from others by having proximal parts of the rays firmly incorporated in the dorsal cup, as well as in possessing a stout-plated, roofed-over tegmen. Distinctions of this sort are not rigorous, even though generally they are well-enough made.

A small number of inadunate crinoids, which surely are not classifiable elsewhere, have dorsal cups composed of close-sutured plates that include a circlet or circlets of plates above the summit of the radials. All are monocyclic and all are interpreted to be primitive. Mostly only a single circlet of brachials is added above the radials (of which two or more are invariably compound) as components of the dorsal cup (e.g., *Eustenocrinus*, Fig. 2,2; primitive *Ecteno-*

crinus, Fig. 3,2*b*; *Dystactocrinus,* Fig. 5,1*a,b*; *Atyphocrinus,* Fig. 5,6*a-c*) but in some of these crinoids two brachial circlets may be incorporated in the dorsal cup (e.g., *Peniculocrinus,* Fig. 2,3; *Ohiocrinus,* Fig. 5,4*a-c*). An interesting observation by Ulrich (1925, p. 94) relates to difference of the dorsal cups belonging to Middle Ordovician species of *Ectenocrinus* as compared with the cups of Upper Ordovician species species assigned to the same genus. In *E. canadensis* (Fig. 3,2*b,c*), from Trentonian rocks of Ontario, the lowermost circlet of primibrachs, all quadrangular in form, is firmly incorporated into the dorsal cup, and the free arms begin with the second primibrachs, which are axillaries. In the relatively abundant *E. simplex* (Fig. 3,2*a*; Pl. 1, fig. 2a-c), from Cincinnatian strata, on the other hand, the arms are free above the radials.

Study of ray structures found in early inadunates, especially disparids, indicates that proximal plates classed as inferradials, superradials, undivided radials, and fixed-brachials are morphologically very much alike, distinctions being dependent mainly, if not solely, on position. The number of dorsal-cup plates in corresponding rays of different crinoids, as well as in different rays of the same crinoid, ranges from one to as many as five (Fig. 5,4*c*). These ray plates are united by close suture, both to one another and to the interradially disposed basal plates at the proximal extremities of the rays. In dorsal cups with multiple-plate rays, evolutionary change in opposite directions can be discerned: on one hand, a tendency of the lowermost pair of plates (compound radial) to fuse together so as to form an undivided "simple" radial, and contrariwise, a loosening of bonds between radials and fixed-brachials and between successive fixed-brachials so that mobility of plates above the summit of the cup is gained.

The foregoing discussion of fixed-brachial plates found in inadunate crinoids will have to be modified radically in order to take account of a new genus of dicyclic crinoids discovered in Pennsylvanian strata of Nevada. A description of this form, with accompanying photograph, has been kindly furnished to me in advance of publication by Dr. N. Gary Lane, of the University of California in Los Angeles. It would be inappropriate to report here the nature of evidence concerning immobility of rather numerous proximal brachials in each ray, but I am allowed to say that fixed-brachials are not confined to Ordovician inadunates and, in addition, to observe that what amounts to very appreciable enlargement of the

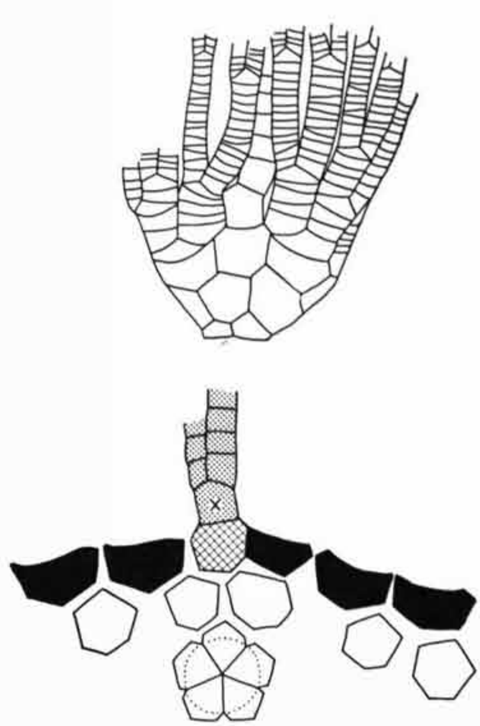


Fig. 15. *Lebetocrinus grandis* Kirk, L.Miss., Indiana; CD-interray view of lower part of crown and diagram showing structure of dorsal cup in relation to anal tube or sac, ×1 (after Kirk, 1940). The large plate separating the C- and D-radials is interpreted as a radianal, though designated as anal-X by Kirk. [Explanation: Patterns as in Figure 13.]

dorsal cup in the Pennsylvanian new genus by incorporation of fixed-brachs surely represents evolutionary specialization. It is not a primitive feature.

FREE-BRACHIALS

Morphological terminology applied to free-brachials of inadunates is reasonably straightforward, offering few problems, except in some groups having strongly specialized arm structure and in various genera, mostly disparids but including several cladids, with branches in free parts of the rays that are doubtfully classifiable as arms (including armlets), ramules, or pinnules. Questions then are encountered on how to define individual free-ray elements and series of these elements (e.g., primibrachs, secundibrachs, axils, ramule-brachs, or pinnulars, etc.). Authors generally are vague in dealing with such matters or use their own nomenclature without explanation, or they ignore classification and nomenclature of free-arm divisions and their component elements, except parts close to the dorsal cup. Attention to this subject is nonetheless needed. At risk of making some elementary and self-evident statements, morphological features of free-brachials—using this term with the broadest possible application to include all nonrigidly connected elements of rays above the dorsal cup—will be considered, citing some selected examples.

TYPES OF FREE-BRACHIAL GROUPS

The simplest sort of free-brachial group consists of the uniserially arranged brachs of an unbranched arm, illustrated by one of the arms of *Allagecrinus* (Fig. 12,*3*) and numerous other inadunates, both monocyclic and dicyclic. The brachs of such an arm are all primibrachs.

At this point it seems appropriate to introduce the query: What is a crinoid arm? Clearly, the arm is not equivalent to the free part of the ray, for in allagecrinids and anamesocrinids more or less numerous independent arms are found to belong to the same ray. It is common practice to describe crinoids such as *Delocrinus* as ten-armed, because the single primibrach of each ray, which is an axillary plate, gives rise to two unbranched series of brachs bearing pinnules on opposite sides in alternation. *Eupachycrinus,* which has more than a single bifurcation of brach series near the cup in two or more rays, is said to possess 12 to 14 arms. Other inadunate genera, interpreted similarly, have 40 or more arms. Accepted usage, therefore, classifies any major brachial-plate series as an arm. Consequent on this, the brachs of each series are successively defined as primibrachs, secundibrachs, tertibrachs, and so on.

What difference, if any, distinguishes minor branches of arms termed armlets and ramules, and how do either of these differ from the branchlets called pinnules? Answers to these questions evidently depend on definitions of ray appendages classed as one or another of these branchlets. In my opinion, it seems most reasonable to define an armlet as a minor arm appendage that is branched, a ramule as an unbranched appendage given off on one side or the other of an arm at intervals of two or more brachs, and pinnules as minor side branches borne on alternate sides by successive brachs. Consistently, used in this way, these terms would have value for diagnoses and descriptions of crinoids. Applying them to various inadunates illustrated in this paper, all free-brachs shown in Figure 2 belong to arms, and those of crinoids included in Figure 3 belong either to arms only (Fig. 3,*4,5*) or to arms and ramules (Fig. 3,*1,2a,b,6, 7a,b*); a pinnulate form is illustrated in Figure 9,*8* *(Decadocrinus)*. The branchlets of arms in *Cicerocrinus* (Fig. 6,*3*) are here considered to be ramules—not pinnules, as indicated by Sollas.

Should a brach be classified as an axil if it gives rise on its distal edge to an armlet, ramule, or pinnule on one facet and to a continuation of the arms, of which it is a part, on the other? For example, *Daedalocrinus* (Fig. 3,*1*), *Drymocrinus* (Fig. 3,*6*), and *Sygcaulocrinus* (Fig. 3,*7*) all possess such brachs separated at intervals by two to four quadrangular nonaxil-brachs. The ramule-bearing brachs unquestionably are axillary, but they are also integral components of a main arm in company with the nonaxil-brachs between them, and structurally they are not at all comparable to the axillary primibrach (primaxil) near the proximal extremity of the free arm. I suggest that they may be distinguished as a subordinate type of arm constituent termed **subaxils.** A diagnosis of *Daedalocrinus* might then include characterization of the arm structure as "two arms to each ray, branching dichotomously on third or fourth primibrach, each pair of arms giving rise to long ramules on their facing, inner sides, borne by subaxils separated by three (rarely two or four) quadrangular nonaxil-brachs." The important consideration bearing on recognizing the specified free-brachial elements as subaxils is elimination of them from the category of arm-division markers that controls classification of brachial-plate series as primibrachs, secundibrachs, tertibrachs, and brachs of higher orders.

BRACHIAL PLATES OF CALCEOCRINIDS

The arms of genera belonging to the Calceocrinidae, especially those of the two lateral rays (A, D) and their accompanying ramules, are unusual. Their structure is described in some detail in another paper (Moore, 1962). Consequently, it is sufficient here merely to note the peculiar grouping together of axillary plates which form the structures called main-axils and the axil-arms borne by the successive axils. The compactness of brachs composing the main-axils suggests classifying them as fixed-brachs, but they are not reckoned to form a part of the dorsal cup and hence, in spite of their close union, are considered to be free-arm plates. The axillary plates that occur at distal extremities of the alphabrach, betabrach, and higher series, and which bear ramules on their right or left sides, are subaxils. This means that all brachs (exclusive of those composing ramules) borne by the primaxil of the main-axil are secundibrachs (subaxils and nonaxils), and all brachs (excluding those of ramules) borne by the secundaxil of the main-axil are tertibrachs (subaxils and nonaxils), etc.

ARMLET-BRACHS, RAMULE-BRACHS, AND PINNULARS

The individual brachial plates belonging to an armlet may be termed armlet-brachs and those of ramules as ramule-brachs. The segments of a pinnule have come to be known as pinnulars. All are channeled on the inner (ventral) side and in exceptionally well-preserved fossils are found to have minute, biserially arranged cover-plates that enclose the groove.

DESCRIPTION AND DISCUSSION OF SELECTED GENERA

BASIS FOR SELECTIONS

The purpose of this section of the paper is to consider some features of morphology, taxonomy, nomenclature, and evolutionary change observed in a few inadunate crinoid groups, both monocyclic and dicyclic, with opportunity for more extended discussion than is possible in pages of the *Treatise* volume on crinoids. Also, some new genera can be introduced, which is not allowable in the *Treatise*. The genera are selected mainly to supplement the references previously given to examples of inadunates characterized by the presence of different numbers of compound radials (5, 3, 2, 1, 0) in the dorsal cup, by various anal-plate arrangements associated with the C-ray, and by structural changes that may be expressed by differently oriented planes of bilateral symmetry. Genera with five compound radials will be considered first.

FAMILIES CHARACTERIZED BY FIVE MULTIPLE RADIALS

Only two families of inadunate crinoids are distinguished by dorsal cups having five compound radials, one in each ray. The monocyclic Eustenocrinidae lack a radianal plate, whereas the dicyclic Ottawacrinidae have a well-developed radianal.

Family EUSTENOCRINIDAE Ulrich, 1925 (p. 99)

Disparids with slender crown, distinguished especially by presence of compound radials in all five rays, some genera with fixed-brachs also; arms commonly branching isotomously, composed of quadrangular nonaxil brachs, bilaterally symmetrical in plane of C-ray. *M.Ord.*

Genus EUSTENOCRINUS Ulrich, 1925 (p. 99)

Text-figure 2,2

[Type-species, **E. springeri* ULRICH, 1925 (p. 100); orig. desig.]

Crown with diameter barely exceeding that of stem; C-superradial supporting anal-X directly above it, followed by long anal tube but no arm; other rays with single fixed-brach above compound radial and bearing free arms that branch on sixth to tenth primibrach. *M.Ord.(Trenton.)*, Ontario.

The most unique character of this genus is its elongate anal tube, with terminal vent surrounded by a small pyramid, unaccompanied by an arm. Other crinoids have less than five arms, but none exhibit the combination of features seen in *Eustenocrinus*. The compound radials in all rays, circlet of fixed-brachs, and pre-emption of the C-ray as an anal tube are characters that denote primitiveness, but these characters do not serve to distinguish *Eustenocrinus* as the ancestor of other groups such as the homocrinids or heterocrinids with fewer compound radials.

Genus PENICULOCRINUS Moore, n.gen.

[Type-species, *Heterocrinus? milleri* WETHERBY, 1880 (p. 153), herein designated; type-specimen, Univ. Chicago, no. 6061]

Crown moderately tall, very slender, width only slightly exceeding diameter of stem (1.5 mm.). Dorsal cup monocyclic, basal circlet low, consisting of five plates with subvertical external surfaces aligned with sides of subpentagonal stem, distal facets extremely wide-angled (150 degrees or more); radials of all rays compound, with inferradials approximately equal in height to superradials and to next-following five or six quadrangular primibrachs; two fixed-brachs in each ray except C-ray, which has only one, located above brachianal. Anal series consisting of plates approximately equal in size to primibrachs, given off from left side of brachianal. Arms uniserial, branching dichotomously at least three times at intervals of five to eight brachs. Stem subpentagonal, with alternating thick and thin columnals, noncirriferous, lumen pentagonal, with angles radial in position. *M.Ord.*, Kentucky.

This diminutive crinoid is an exceptionally interesting form because of the occurrence of compound radials in every ray, as in *Eustenocrinus*, and in addition, because of the presence of an anal series that arises from the left facet of the *Iocrinus*-like brachianal of the C-ray. The genus differs from *Eustenocrinus* in this feature and in the repeated isotomous branching of the arms in each ray. It is interpreted as more primitive than genera of the Homocrinidae, Calceocrinidae, Haplocrinitidae, and Anamesocrinidae, which have three compound radials (B-, C-, E-rays) associated with undivided radials in the other two rays (A, D), and likewise much less advanced than the Iocrinidae, which are characterized by a similar armlike anal series developed from the brachianal but which differ in having five undivided radials.

The generic name (derived from *peniculus,* Latin for small brush used by artists) alludes to the graceful wisplike appearance of the crown, which resembles a slender camel's-hair brush.

PENICULOCRINUS MILLERI (Wetherby) 1880, (p. 153) Moore (n. comb.)

Plate 1, figures 7a-e; Text-figure 2,*3*

[Holotype. University of Chicago, no. 6061, specimen from Tyrone Limestone (Trenton.), Mercer County, Kentucky.]

The specimen here designated as holotype is the only known representative of the species and genus. It is exceptionally well preserved and as seen on the naturally weathered surface of a small slab of fossiliferous limestone reveals the A-C side of the crown from its base to the distal tips of numerous threadlike arm branches. The closely grouped arms are bent in a gentle curve toward the left. The height of the crown, measured along the curve is 25 mm. and that of the dorsal cup, including fixed-brachs, is 3.2 mm. The type specimen includes the proximal part of the stem, attached to the basal circlet; it is 10 mm. long and 1.5 mm. in diameter, without observable diminution in diameter or change in character to the distal extremity of the fragment. When the specimen was first examined, a very slight separation of the basal circlet from the radial plates above was noted. Later, when matrix was being carefully removed from the sides of the dorsal cup and lower parts of the arms, with the object of learning the characters of the concealed posterior side, the partly undercut specimen broke loose in such a way that the entire stem portion with attached basal circlet formed one free piece and the dorsal cup with proximal few millimeters of the arms comprised the other piece. The fracture was fortunate in that no real damage was done to the fossil, and because the two fragments were now entirely visible, they could be studied with ease. Most of the sutures proved to be very readily and surely identifiable, but treatment of the specimen with a temporary stain so accentuated the sutures that no doubts remained as to any of their positions.

The basal circlet consists of five plates which extend subhorizontally over the proximal stem segment and then turn upward abruptly so that their outer extremities are aligned with the sides of the stem. The sutures between the basals run from angles of the pentagonal lumen to angles of the stem, located in radial positions.

The dorsal cup consists of infer- and superradials in each ray, followed by two fixed-brachs in each ray, counting the brachianal as equivalent of a fixed-brach. Inclusion of the fixed-brachs as part of the cup is indicated by the angled offsets of their corners in a manner corresponding to the lateral junctions of the infer- and superradials and denoting immovable union of the adjoined plates. Above the fourth plate (second fixed-brach) in each ray the brachs are laterally separated in a way that indicates a lack of fixed connection between them. These arm segments adjoin one another but are independent. The brachianal is the third plate of the C-ray in upward succession from the basal circlet. Its sloping left margin abuts against the proximal plate of the anal series (anal-X) and its distal edge is in contact with the fixed-brach of this ray which forms part of the upper limit of the dorsal cup. This fixed-brach is succeeded by three nonaxillary free-brachs and then by the first axillary brach of the C-ray.

The anal series consists of five visible brachlike plates which are interposed between the C- and D-rays, with anal-X at its proximal extremity occurring obliquely at left above the brachianal of the C-ray. Higher parts of the anal-plate series are unknown.

The arms of the holotype specimen branch isotomously on the fourth or fifth brach above the fixed-brachs which are classed as belonging to the dorsal cup. Similar bifurcations observed in the A- and B-rays occur on $IIBr_7$ or $IIBr_8$ and on $IIIBr_7$ or $IIIBr_8$ and probably the same is true in other rays. If this division affects all rays, a total of 40 terminal branches (8 to each ray) is indicated.

The surface of the dorsal-cup and arm plates is finely granulose.

The subpentagonal stem is formed of alternating relatively thick and very thin columnals, the edges of the latter being seen only as lenticular intercalations that appear along the angles of the pentagonal stem between the thick columnals. Edges of the thin columnals vanish toward interspaces between angles of the stem.

Occurrence. Tyrone Limestone, Middle Ordovician (Trenton.), High Bridge, Mercer County, Kentucky.

The described characters of *Peniculocrinus milleri* are puzzling but of far-reaching interest. The arrangement of proximal ray plates in a uniform unbroken succession leading to the uniserially composed arms is the same as in *Eustenocrinus* and somewhat similar to that seen in *Paractocrinus,* both of Ordovician age, but neither of these crinoids has a brachianal, as observed in *Peniculocrinus.* These genera and *Peniculocrinus* seem to be among the most primitive known crinoids in having plates defined as infer- and superradials in all rays. Also, comparison with *Iocrinus, Caleidocrinus,* and *Merocrinus* is invited in considering the arrangement of anal plates seen in *Peniculocrinus,* because in each of these genera the anal series is an armlike succession of plates supported by the left side of the brachianal. The brachianal belongs above the summit of the dorsal cup in *Iocrinus, Caleidocrinus,* and *Merocrinus,* which have no divided radials, but it is included among the fixed-brachs in the dorsal cup of *Peniculocrinus.*

Genus RISTNACRINUS Öpik, 1935 (p. 3)

Plate 1, figures 6a,b; text-figure 2,*1*

[Type-species, *R. marinus* ÖPIK, 1934 (p. 4); orig. desig. and monotypy.]

Each ray with two plates in dorsal cup, C-superradial with broad facet on right for articulation with nonaxil primibrach and narrow sloping facet on left for contact with anal-X, which is followed in series by higher anal plates; arms branching isotomously on IBr_1 or IBr_2 and again on $IIBr_3$ or somewhat higher. Stem circular, proximal columnals with even articular surfaces, alternate ones smaller and thinner, others fairly uniform and characterized by bifascial articular surfaces with shallow concave areas on either side of prominent fulcral ridge, which widens around small circular lumen. *M.Ord.,* Estonia.

The elongate plates of the lowermost visible circlet of the dorsal cup were interpreted by ÖPIK as basals or possibly infrabasals, the next higher plates being classed as radials and the succeeding one or two plates, including the proximal axils in each ray, as superradials. Such a classification is quite inadmissible. The elongate plates are exactly in line with the next higher, so-called radials and marked off from them by well-aligned transverse sutures, producing an arrangement that is only matched in other crinoids by the two elements of compound radials. It is inconceivable that the elongate plates are radially disposed basals and more inconceivable that they are infrabasals, even though such plates belong in radial position. No student of crinoids could be expected to entertain seriously the postulate that five basals, supposedly present in ancestors of *Ristnacrinus,* somehow have vanished from their interradial positions between the supposed infrabasals and radials, leaving no trace. BATHER (in ÖPIK, 1934, p. 6) suggested that the elongate plates are inferradials, and this conclusion seems to me inescapable.

The plates distinguished by ÖPIK as radials are actually superradials and those termed superradials by him are primibrachs.

The characters of *Ristnacrinus,* as now understood, seem to agree best with those recognized in *Peniculocrinus* and *Eustenocrinus,* which also are Middle Ordovician crinoids. Accordingly, *Ristnacrinus* is classified here as belonging in the Eustenocrinidae.

Family OTTAWACRINIDAE Moore & Laudon, 1943 (p. 55)

Dicyclic; conical dorsal cup distinguished by presence of compound radials in all rays, inferradial of C-ray (directly below superradial) constituting primitive radianal that on its left adjoins anal-X plate, which rests on posterior basal occupying space between radianal plus overlying radial and compound radial of D-ray. *M.Ord.*

The diagnosis and content of this family indicated by MOORE & LAUDON when they selected *Ottawacrinus* as type-genus are very unlike those given in this paper, mainly because concepts of the nature of *Ottawacrinus* that guided grouping of genera with it in 1943 were derived from SPRINGER (1911), rather than BATHER (1913). MOORE & LAUDON (1943, p. 55; 1944, p. 158) considered the nature of the radial facets, the steep-sided form of the dorsal cup, the relatively large anal sac, and the pattern of arm branching to be most significant morphological characters. Thus, they grouped together *Ottawacrinus* (M.Ord.), *Cradeocrinus* (U.Dev.), *Iteacrinus* (U.Dev.), *Lasiocrinus* (L. Dev.-L.Miss.), *Goniocrinus* (L.Miss.), *?Alsopocrinus* (L.Dev.), and *?Pagecrinus* (M.Dev.), recording the range of the family as Ordovician to Mississippian. The lack of any assigned genera occurring in Upper Ordovician or Silurian rocks may be noted. It is now evident that none of these genera belong with *Ottawacrinus.* Also, since *Ottawacrinus* cannot be assigned to a family other than the Ottawacrinidae, for the present it stands alone and the known stratigraphic distribution of the family is confined to Trentonian rocks.

Genus OTTAWACRINUS W. R. Billings, 1887

Plate 1, figures 3a-e; text-figures 2,*4*

[Type-species, **O. typus* W. R. BILLINGS, 1887 (p. 49); orig. desig., monotypy, and adoption of specific name *typus*] [=*Salagastiana* RUSCONI, 1952, type-species, **S. simetrica* RUSCONI, 1952]

Characters of the family. *M.Ord.,* Canada (Ontario).

As now defined, *Ottawacrinus* is represented by only the single species, *O. typus,* and this is known solely from the holotype specimen and some associated arm fragments. This statement requires explanation, inasmuch as SPRINGER (1911) has described and figured fossils from Kirkfield, Ontario, identified as *O. typus* and at the same time published a new species named *O. billingsi*. BATHER (1913, p. 13) has pointed out very important differences between the holotype of *O. typus* and the forms reported on by SPRINGER, though he went no farther than to suggest that these forms seemed not to be congeneric with *Ottawacrinus*. The new name *Grenprisia* is introduced for them in a later part of the present paper.

The dorsal cup of *Ottawacrinus typus,* which in the holotype is complete and well preserved, is diminutive and slender, its diameter at the base (3 mm.) and summit (4.2 mm.) being smaller than that of the proximal part of the stem (4.5 mm.) at a distance of approximately 250 mm. from the crown. The sides of the cup are very steep—nearly vertical—and although the base of the arms is clearly marked, their outer surfaces are confluent with the sides of the cup. BATHER (1913), who studied BILLINGS' type-specimen closely, has reported that the plates of the dorsal cup are united by close sutures but plainly visible, and no doubt exists as to the compound nature of the radials observed in all rays. The inferradial of the C-ray must be given separate designation, because unquestionably it is a radianal (Fig. 2,*4*), which is larger than the A-, B-, D-, and E-inferradials and different from them in shape. The radianal is not shifted leftward even in the slightest degree, and therefore is interpreted to be very primitive. Its lower left margin rests against the large posterior basal and its upper left margin touches the large anal-X. The suture between anal-X and the basal is not obliquely inclined, but is perpendicular to the axis of the cup. A pair of anal plates, followed by others, occurs above anal-X, indicating the presence of an anal sac rather than an anal tube.

The proximal parts of the arms of *Ottawacrinus* are parallel to one another and closely apposed, except on the posterior side of the crown where the lower part of the anal sac intervenes between the C- and D-rays. Judging from the size and bifurcations shown by some arm fragments associated with the holotype specimen, BATHER (1913, p. 4) concluded that the arms branch at least twice. Ramules or pinnules are lacking.

The stem of *Ottawacrinus* is circular in transverse section and distinguished by prominent longitudinal divisions which define five series of superposed columnal pentameres. Laterally adjoined pentameres may differ slightly in thickness and the suture between them tends to have a zigzag vertical course (Pl. 1, figs. 3c-e). BATHER (1913, p. 6) has called attention to the distinctly uparched outer edges of the pentamere columns (Pl. 1, figs. 3a,b), a feature that was not mentioned or illustrated by BILLINGS. At the top of the stem, each arched pentamere fits into an indentation between visible parts of contiguous pairs of infrabasal plates. Finally, the very large pentagonal lumen with radially disposed angles and the pattern of distinct crenellae (median and proximal regions of stem) or irregular, discontinuous, radiating impressions on the articular faces of columnals (distal region of stem) remain to be noted (Pl. 1, figs. 3d,e). These are significant features that may have generic importance, and as pointed out by SIEVERTS-DORECK (1957), justify assignment to *Ottawacrinus* of stem fragments described by RUSCONI (1952) from supposed Upper Cambrian (doubtless not older than Ordovician) strata of Argentina as the types of a new genus, *Salagastiana*.

Several diagnostic features of *Ottawacrinus,* especially the occurrence of compound radials in all rays, nearly vertical sides of the dorsal cup, diameter of crown approximately equal to that of the stem, and repeated dichotomous branching of the arms, suggest genera of the Eustenocrinidae. *Ottawacrinus* possesses a circlet of infrabasals, however, and it has a large anal-X that interrupts the circlet of radials, not to mention other characters which are not found in eustenocrinid genera. *Ottawacrinus* is distinguished by the presence of an undoubted radianal and seems to have a strong anal sac.

FAMILIES CHARACTERIZED BY THREE MULTIPLE RADIALS ONLY

The Homocrinidae (Pl. 1, fig. 2), Calceocrinidae, Haplocrinitidae, and Anamesocrinidae are families of disparid inadunates characterized by the presence of three compound radials in the dorsal cup. They occur in the B-, C-, and E-rays (Figs. 1,*8*; 3,4). No radianal (or infer- and superradianal) occurs but in several genera the C-superradial has the characters of a radianal, supporting anal-X, followed by an anal tube or sac, on its left shoulder. Genera placed in these families are clearly distinguished from others and none offers problems that call for consideration here.

FAMILIES CHARACTERIZED BY TWO MULTIPLE RADIALS ONLY

The Heterocrinidae (Pl. 1, figs. 1,4,5), Anomalocrinidae, and (with special qualifications) Pisocrinidae are families of monocyclic inadunates distinguished by having compound radials in only two rays. In the first two families mentioned, undivided radials occur in the A-, B-, and D-rays, compound radials being found in the other two (C, E) rays (Figs. 1,6; 5,7). In the Pisocrinidae (Fig. 6) an inferradial or inferradials occur in the B- and C-rays but only a superradial in the E-ray (except *Quiniocrinus,* Fig. 6,5). This arrangement of dorsal-cup plates defines a bilateral symmetry that corresponds to the perfectly developed bilateral symmetry of calceocrinids coinciding with the E-ray in position. *Quiniocrinus* (Fig. 6,5) is an especially interesting member of the Pisocrinidae in having separate compound radials in the B- and C-rays, and on this account it may be interpreted as more primitive than *Pisocrinus* and other genera having a fused B+C-inferradial.

No genus belonging to the families here mentioned has a radianal (or infer- and superradianal), but in all genera the C-superradial has aniradial characters.

FAMILIES CHARACTERIZED BY A SINGLE MULTIPLE RADIAL

In this group belong the Hybocrinida, among monocyclic inadunates, and a host of dicyclic cladids. Different genera show a wide variety of posterior interray arrangement of plates (Figs. 9, 10) and dissimilar orientations of planes of bilateral symmetry (Fig. 1). It is necessary to remember that "one compound radial only" invariably refers to the C-ray and signifies radianal (inferradial in origin) and radial (superradial in origin). Whether the radianal occurs more or less directly beneath the C-radial, obliquely below it at the left, or even with it at the left makes no difference. The presence of a radianal qualifies an inadunate for classification in the category here considered, with the single exception of *Ottawacrinus.* This is because no three-compound-radial or two-compound-radial crinoid has a radianal.

Family DENDROCRINIDAE Bather, 1890 (May) (p. 383)

[First publication of this family name has been erroneously attributed to S. A. MILLER, 1889 (as by MOORE & LAUDON, 1943, p. 52) inasmuch as MILLER's paper containing what appears to be the oldest use of the name forms part of the 16th Annual Report of the Indiana Department of Geology & Natural History (for 1888), bearing the imprint date 1889. Statement appears in this volume (p. 327) that it contains chapters by MILLER and MILLER & GURLEY that had been published previously in 1890, thus indicating untrustworthiness of the recorded printing date as 1889. Actually, MILLER's original publication of numerous crinoid family names, several of them new but not so recorded, was in December 1890 (Am. Geologist, v. 6, p. 340-357) and his paper was printed without change in the Indiana report cited, suggesting a date for at least part of the volume as late as 1891. Paleontologists concerned with questions of priority in publication dates—since they must seek to comply with present international Rules—encounter special difficulties in dealing with the ill-recorded, two-or-three-times repeated publication of papers (sometimes with significant changes, sometimes without alteration) by HALL, MEEK & WORTHEN, MILLER, MILLER & GURLEY, and others.]

Dicyclic; cup steeply conical, with five infrabasals, radianal directly below C-radial or obliquely at left below it; anal-X in line with radials, resting on posterior basal and followed by other anal plates arranged irregularly or in series; radial facets curved, somewhat narrower than greatest width of radials; arms rounded, slender, repeatedly branching with strong tendency toward heterotomy, with armlets or ramules but no pinnules. *M.Ord.-M.Dev.*

A prominent feature of the anal sac in the type-genus is its unusual height, pointed distal extremity, and thin, plicate plates, so arranged that vertical folds on them are aligned. In some genera this definite pattern is not seen. Ordovician representatives of the family commonly show the presence of small interradial plates between neighboring proximal primibrachs, which is interpreted as an archaic feature suggestive of the Flexibilia.

In addition to the genera referred to the Dendrocrinidae by MOORE & LAUDON (1943, p. 52)—*Dendrocrinus* (M.Ord.-M.Sil.), *Esthonocrinus* (M.Ord.), *Antihomocrinus* (M.Sil.-L.Dev.), *Follicrinus* (L. Dev.), *Parisangulocrinus* (L.Dev.), *Bactrocrinites* (L. Dev.-U.Dev.), *?Vosekocrinus* (L.Ord.)—the new genus *Grenprisia* is here assigned to the family. Also, the genera mentioned in discussion of the Ottawacrinidae as included by MOORE & LAUDON in that family *(Ottawacrinus, Cradeocrinus, Iteacrinus, Lasiocrinus, Goniocrinus, ?Alsopocrinus, ?Pagecrinus)* seem to be better classified with the Dendrocrinidae than elsewhere—excepting the five-multiple-radial *Ottawacrinus,* of course. Among the genera mentioned, the type of arm branching, absence of pinnules, and the form and structure of the dorsal cup, suggest dendrocrinid affinities, though the radial articular facets are relatively wider than in *Dendrocrinus*.

Genus GRENPRISIA Moore, n.gen.

[Type-species, *Ottawacrinus billingsi* SPRINGER, 1911 (p. 40); orig. desig., herein] [=*Ottawacrinus* SPRINGER, 1911, p. 37 (*non* W. R. BILLINGS, 1887)]

This new generic name, formed by rearranging the letters of the surname SPRINGER and adding terminal letters *-ia,* gender feminine, is introduced for application to crinoids designated *Ottawacrinus typus* W. R. BILLINGS and *O. billingsi* SPRINGER, n.sp., in SPRINGER's (1911) paper on Middle Ordovician fossils from Kirkfield, Ontario. Likewise, *Grenprisia* may include additional species that are judged to have generic features like those of *G. billingsi*. *M.Ord.,* Canada (Ontario).

The original descriptions of *Ottawacrinus* and of its type-species (BILLINGS, 1887, p. 49) were reasonably accurate, except for the author's failure to recognize the presence of compound radials in all five rays, even though he recorded such a plate in the "right posterior" (C) ray. He did not use the term radianal, of course, since this was not introduced until later (BATHER, 1890, p. 329), but he correctly described this element of the C-ray and its relation to the large anal plate (X) resting on the truncate distal extremity of the posterior basal.

BATHER (1913) redescribed and figured BILLINGS' holotype of *Ottawacrinus typus* in a paper prepared early in 1910 and submitted to the Geological Survey of Canada in July of that year (BATHER, 1913, p. 12), without knowing of SPRINGER's paper on Kirkfield echinoderms, also transmitted to the Geological Survey of Canada in June 1910. SPRINGER's contribution was published some time early in 1911, for BATHER (1913, p. 12) reported that he received a copy of it in June of that year. With SPRINGER's descriptions and excellent illustrations before him, BATHER was able to point out features of the holotype of *O. typus* that evidently were not known to SPRINGER and certainly not considered by him. For whatever reason or reasons, SPRINGER never returned to his supposed *Ottawacrinus* specimens, so far as publications reveal. His reference to the genus in the second edition of ZITTEL's *Text-book of Palaeontology* (SPRINGER in ZITTEL, 1913, p. 215) gives a diagnosis corresponding to that accepted in his Kirkfield paper, which is readily explained by the probable earlier-than-1913 date of SPRINGER's writing for this textbook and by the October 1913 date of publication of BATHER's notes. Nothing indicates that BATHER communicated to SPRINGER his findings in study of *Ottawacrinus* before they were published.

GRENPRISIA BILLINGSI (Springer), 1911 (p. 40) (Moore, n.comb.)

[Holotype, specimen illustrated by SPRINGER in pl. 4, fig. 1a; paratypes, other specimens referred to *Ottawacrinus billingsi* by him on this plate]

The characters of this species are adequately described and illustrated by SPRINGER in the reference cited. It is unnecessary to republish them here. *M.Ord.(Trenton.),* Ontario.

GRENPRISIA SPRINGERI Moore, n.sp.

[Holotype, specimen illustrated by SPRINGER in his 1911 paper, pl. 4, fig. 6; paratypes consisting of specimens illustrated by him in pl. 4, figs. 5, 7] [=*Ottawacrinus typus* SPRINGER, 1911, p. 37 (*non* W. R. BILLINGS, 1887)]

It is quite unnecessary to repeat in this paper the descriptions given by SPRINGER (1911, p. 37-39) for the crinoids called by him *Ottawacrinus billingsi* and *O. typus* and to copy his illustrations of them. I agree fully with the views of BATHER that the fossils dealt with by SPRINGER are significantly different from *Ottawacrinus* in their obvious lack of compound radials in rays other than the C-ray and in their possession of interradial plates between proximal primibrachs. In addition, the stem of *Grenprisia billingsi,* at least, differs from that of *G. springeri* ("*O. typus*" of SPRINGER) in showing angles of the lumen located in the middle of columnal pentameres, rather than between them, as well as, seemingly, in the greater thinness of the columnals and lack of markings on their articular surfaces. In so far as can be judged, the arrangement of plates near the base of the anal sac on its posterior side differs importantly in *Grenprisia* and *Ottawacrinus,* but whether the great size of the sac in *Grenprisia* and the peculiar heterotomous branching of the arms are diagnostic features is not known.

The specimen illustrated in Plate 4, figure 1a of SPRINGER's (1911) paper is the holotype of *Grenprisia billingsi* and others referred to this species and figured by him are classed as paratypes. All were obtained from Trentonian, Middle Ordovician, strata at Kirkfield, Ontario.

The fossils described and illustrated by SPRINGER (1911) under the name *Ottawacrinus typus,* which here are rejected from classification with that species, differ in several ways from *Grenprisia billingsi,* as pointed out by SPRINGER (1911). It shares with *G. billingsi* morphological characters that remove it from *Ottawacrinus*. Therefore, as matters stand, it requires renaming. I designate this species as *Grenprisia springeri* MOORE, n.sp., and select the specimen illustrated in SPRINGER's Plate 4, figure 6, as holotype, those shown in figures 5 and 7 of this plate being classed as paratypes. *G. springeri* also comes from Trentonian rocks at Kirkfield, Ontario.

FAMILIES CHARACTERIZED BY NO MULTIPLE RADIALS

Here belong the monocyclic inadunate families Iocrinidae, Myelodactylidae, Synbathocrinidae, Zophocrinidae, Belemnocrinidae, and Allagecrinidae. In addition, a large majority of the dicyclic (cladid) families are characterized by undivided radials and thus belong in this group. Only a small selected fraction of these crinoids are given consideration in this paper, choice of them being guided mostly by morphological features which they display and by decisions to recognize some new genera.

Family IOCRINIDAE Moore & Laudon, 1943 (p. 29)

Monocyclic; cup conical, steep-sided; basals five; radials five, undivided and equal, except that C- and D-radials reach slightly higher than others. Brachianal supporting short series of primibrachs on right facet and anal tube on inclined left facet. Arms repeatedly branched isotomously, lacking ramules or pinnules. Anal tube with armlike midrib on outer side, bordered by lateral and inner-side parts by horizontally plicate thin plates, elliptical in cross section, tall, reaching approximately to arm extremities. Stem pentagonal to pentastellate, composed of alternating thick and thin columnals. *?L.Ord., M.Ord.-U.Ord.*

MOORE & LAUDON (1943) included *Myelodactylus* and *Ammonicrinus,* along with *Iocrinus,* in this family. Under provisions of Rules calling for application of priority of publication to family-group taxa, as recommended by the Copenhagen (1953) International Zoological Congress and now adopted in the Code of Zoological Rules, grouping of genera given by MOORE & LAUDON would have to be known as Myelodactylidae S. A. MILLER, 1883. The removal of *Myelodactylus* from the family assemblage, as in the present paper, allows Iocrinidae to be recognized.

Ammonicrinus is removed from the Iocrinidae, because UBAGHS (1952, p. 204) has demonstrated that this genus is not an inadunate, but belongs to the Flexibilia. This leaves *Iocrinus* standing alone seemingly. Another genus, however, may be recognized as belonging with it—*Caleidocrinus* WAAGEN & JAHN, from Middle Ordovician rocks of Czechoslovakia, which SPRINGER (1920, p. 442) considered to be equivalent to *Iocrinus* but which is regarded by RAMSBOTTOM (1961, p. 6) as distinct. I agree to classifying *Iocrinus* and *Caleidocrinus* as the only presently known genera of the Iocrinidae.

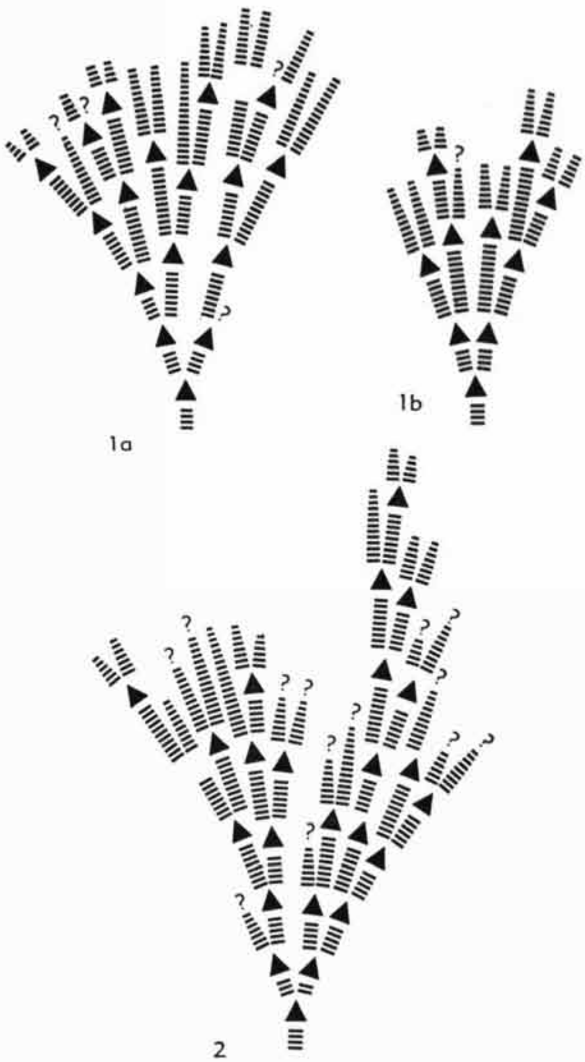


FIG. 16. Pattern of arm branching in *Iocrinus*—*1. I. subcrassus* (MEEK & WORTHEN); *1a,* middle ray (?A) of specimen from Cincinnati, Ohio, illustrated in Plate 3, figure 3a; *1b,* middle ray (?A) of specimen from Cincinnati, Ohio, illustrated in Plate 3, figure 3b.—*2. I. crassus* (MEEK & WORTHEN); D-ray of specimen figured by MEEK & WORTHEN (Ill. Geol. Survey, v. 6, pl. 23, fig. 1, 1875), from Kendall County, Illinois. [Explanation: Axils represented by triangles, nonaxil-brachs by short bars, which in each brach series are plotted according to numbers counted on the specimen.]

Genus IOCRINUS Hall, 1866 (p. 5)

[Type-species, *Heterocrinus (Iocrinus) polyxo* HALL, 1866; by monotypy (=*Heterocrinus subcrassus* MEEK & WORTHEN, 1865, p. 148, subj., here based on designation of specimen illustrated in HALL's (1872) pl. 5, fig. 1, as holotype of *H. (P.) polyxo*, other figured specimens being referable to MEEK & WORTHEN's *H. crassus*)]

Characters of the family but distinguished by lack of interradial plates, reported to occur in *Caleidocrinus,* and by strongly pentagonal stem. *?L.Ord.(L. Arenig.), M.Ord.-U.Ord.,* North America, Europe.

IOCRINUS SUBCRASSUS (Meek & Worthen), 1865 (p. 148)

Plate 2, figures 1, 2a-f; text-figure 16,*1a,b*

Specimens from collections of Yale University and the University of Chicago here figured show characters of the posterior side of the dorsal cup and lower part of the arms and anal tube. The axillary nature of the brachianal is especially well defined in Plate 2, figure 2a, with the armlike median part of the anal sac rising from its left facet. The corrugated sides of the sac are illustrated from all sides. These photographs closely correspond to the exceptionally fine, very long sac of *I. shelvensis* figured by RAMSBOTTOM (1961, pl. 1, fig. 6) showing part of a specimen from Llanvirnian (early Chazyan) rocks of Shropshire, England. The U-shaped plates near the lateral margins of the sac, as seen in a broken section of it (Pl. 2, fig. 2f), are puzzling, since they lie just inside the pairs of apposed corrugations seen on the exterior of the sac in these positions (Pl. 2, figs. 2c,e). *U.Ord.,* Ohio, New York.

IOCRINUS CRASSUS (Meek & Worthen), 1865 (p. 147)

Plate 2, figures 3a,b, 4a-e; text-figure 16,2

Specimens here illustrated are from collections of the University of Illinois. They are of value chiefly in revealing features of the articular facets of the radials (Pl. 2, figs. 4a-c), the proximal facet of the brachianal (Pl. 2, fig. 4d) and proximal facet of the second anal plate (Pl. 2, fig. 4e). A diagrammatic representation of the pattern of branching observed in the D-ray of a specimen of *I. crassus* figured by MEEK & WORTHEN is given in Figure 16,2; up to eight bifurcations are present. *U.Ord.,* Illinois.

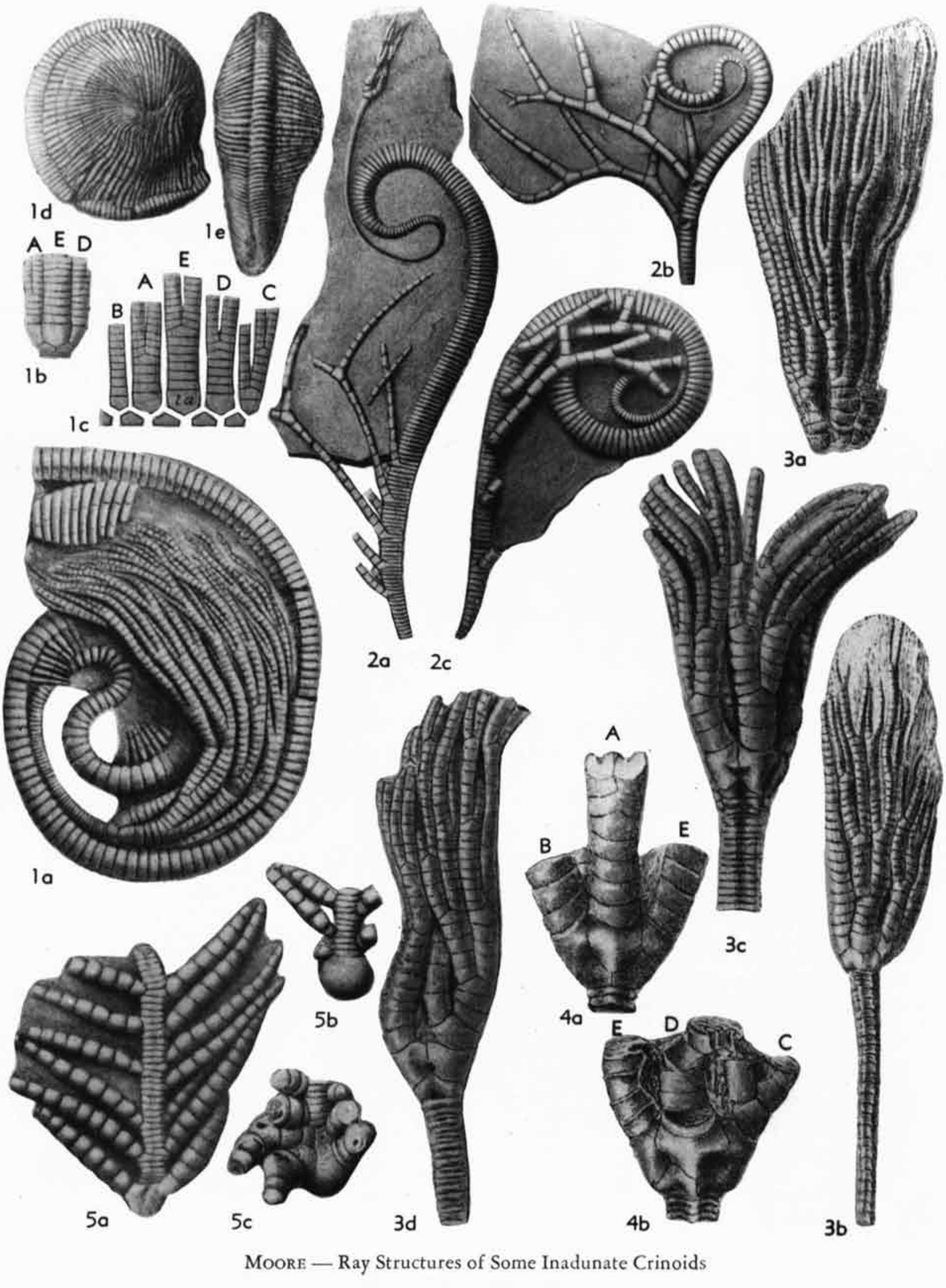
Family MYELODACTYLIDAE S. A. Miller, 1883 (p. 278)

Monocyclic inadunates chiefly characterized by distinctive features of doubly recurved and coiled stem in conjunction with specialized cirri borne by parts

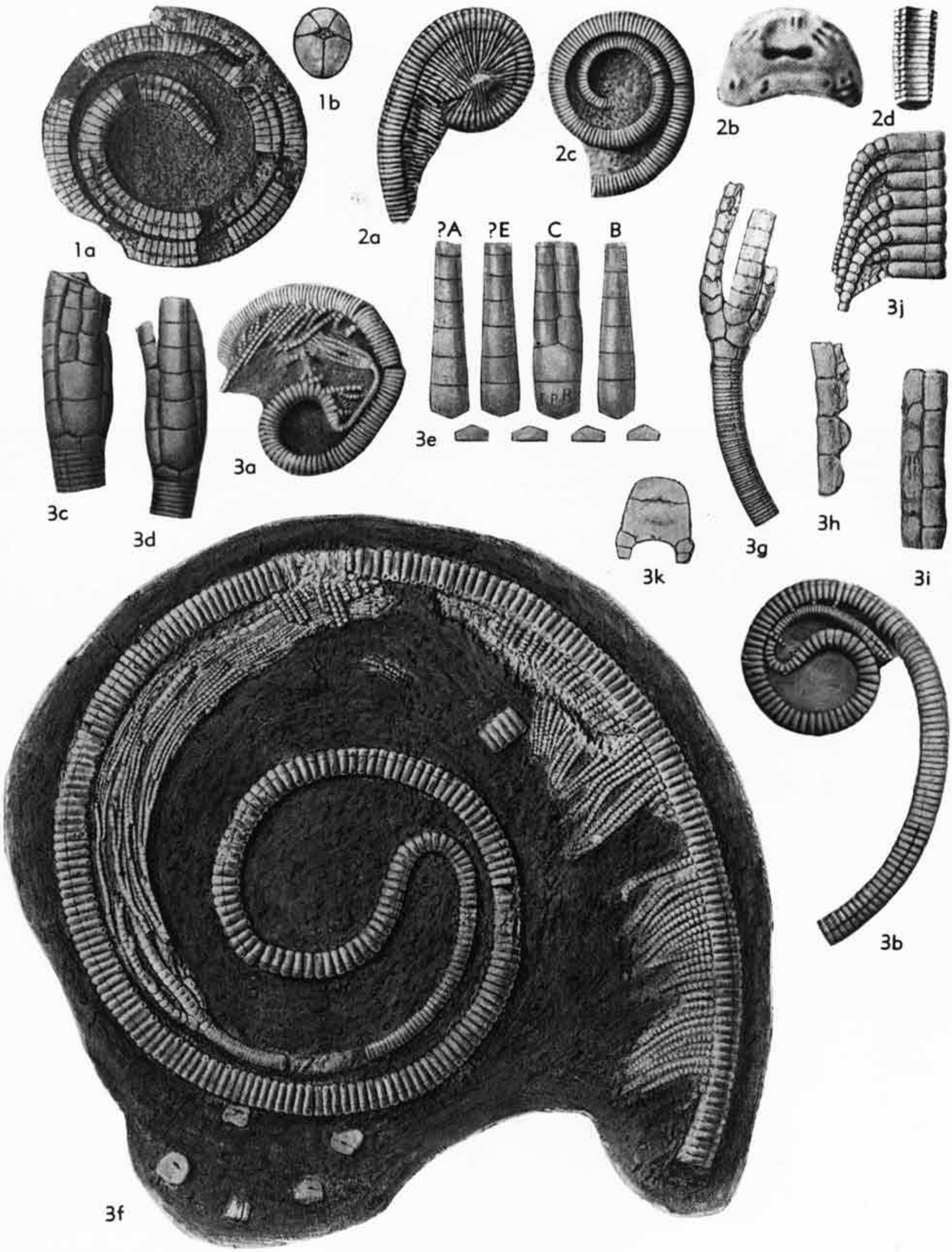
EXPLANATION OF PLATE 3

FIGURE — PAGE

1. *Myelodactylus keyserensis* SPRINGER, (Myelodactylidae), Lower Devonian (Helderberg.), Keyser Formation, near Keyser, West Virginia; *1a-c,* nearly complete crown and most of stem (U.S.N.M., no. S2111a, one of SPRINGER's syntypes, herein designated as lectotype), *1a* showing anterior side with E-ray next to stem, A-ray with many branches nearly central, and unbranched B-ray at top, ×2; *1b,c,* dorsal cup and proximal part of arms, with accompanying plate analysis, rays indicated by Carpenter letter symbols, ×2; *1d,e,* two closely enrolled specimens (U.S.N.M., no. S2111b,c, herein designated as paralectotypes) with cirri entirely concealing crown, views from side and in plane of the coil, ×2 (all after Springer, 1926) 41
2. *Crinobrachiatus brachiatus* (HALL), MOORE, n. comb., (Myelodactylidae), Middle Silurian (Niagaran), Rochester Shale, Lockport, New York (U.S.N.M., no. S2101); *2a,* specimen with crown and most of stem, showing extreme tenuousness of proximal part of stem beyond recurved bend, also great thickness of medial and distal regions of stem, ×2; *2b,* specimen with most of stem but lacking crown, branching cirri very long and stout, ×2.5; *2c,* specimen showing stem with distal extremity tapering to a point, crown missing, ×2 (all after Springer, 1926) 43
3. *Iocrinus subcrassus* (MEEK & WORTHEN), (Iocrinidae), Upper Ordovician (Cincinnatian), Cincinnati, Ohio; *3a,* nearly complete crown (basal circlet lacking), lectotype of *Heterocrinus (Iocrinus) polyxo* HALL, showing many-branched arms composed of brachs with shingle-like slight overlaps characteristic of *I. subcrassus,* ×1.3; *3b,* another crown with attached stem, referred by HALL to *I. polyxo,* ×1.3; *3c,d,* crown from CD-interray and A-ray sides, *3c,* excellently showing brachianal with attached anal tube and C-ray arm, ×2 (*3a,b,* after Hall, 1872; *3c,d,* after Meek, 1873) 40
4. *Iocrinus crassus* (MEEK & WORTHEN), (Iocrinidae), Upper Ordovician, Cincinnati, Ohio; *4a,b,* A- and D-ray views of complete dorsal cup with attached parts of stem and arms, included by HALL in his *Heterocrinus (Iocrinus) polyxo,* ×2 (after Hall, 1872) 40
5. *Brachiocrinus nodosarius* HALL (Myelodactylidae), Lower Devonian (Helderberg.), New Scotland Limestone, Schoharie, New York; *5a,* lectotype (N.Y. State Mus., no. 4080/1), herein designated; *5b,c,* distal parts of two other specimens showing swollen terminal expansion; all ×1.3 (all after Springer, 1926) 43



MOORE — Ray Structures of Some Inadunate Crinoids



Moore — Ray Structures of Some Inadunate Crinoids

of stem; crown elongate, slender; dorsal cup monocyclic, diminutive, composed of four or five basals and four or five radials, C-ray with brachianal that supports normal arm on right and anal tube on left; arms long and slender, branching dichotomously or heterotomously, nonpinnulate. *M.Sil.-M.Dev.*

Genus MYELODACTYLUS Hall, 1852 (p. 191)

Plate 3, figures 1a-e; Plate 4, figures 2a-d

[Type-species, **M. convolutus* HALL, 1852 (p. 191); subseq. desig. SPRINGER, 1926, p. 8]

Distal part of stem spirally coiled, bearing close-spaced row of long, slender cirri on each side of coil, cirri disposed parallel to one another in manner that conceals proximal part of stem and crown, which lies against inner curve of coiled stem in reversed position, that is, with tips of arms pointed backward in direction of distal part of stem. Dorsal cup diminutive, composed of five basals and five undivided radials. Arms slender, branching heterotomously; C-ray with brachianal that bears slender anal tube. *M.Sil.-L.Dev.*, North America, Europe.

That the type-species of *Myelodactylus* was misinterpreted by HALL as a crinoid arm is unimportant taxonomically in view of the distinctive features of the fossil that provide adequate basis for generic differentiation. Later discoveries have added greatly to knowledge of the peculiar morphology of this inadunate group. Like other genera of the family, *Myelodactylus* has a doubly bent S-shaped slender stem next to the crown. This proximal part of the stem is composed of circular, thin columnals that lack cirri. Columnals belonging to distal parts of the stem have a crescentic shape, and bear paired cirri, with a shallow but well-marked concavity between the cirrus sockets faced toward the inside of the stem-coil (Pl. 4, figs. 2c,d). *Myelodactylus* is distinguished from *Herpetocrinus,* which most closely resembles it, by the presence of five rays (instead of four) in the dorsal cup and crown, by weak development or lack of longitudinal divisions of distal columnals, and notably elongate, rather than short, beaded cirrals. SPRINGER (1926) interpreted *Myelodactylus* in such an extremely broad manner that all genera and species of the Myelodactylidae were included in it. In my judgment, this is not warranted, though it must be admitted that generic allocation of some inadequately known forms described as species is doubtful.

The following species are here considered referable to *Myelodactylus*: *M. convolutus* HALL (M.Sil., N.Y., Ind., Tenn., Sweden); *M. brevis* SPRINGER (M.Sil., Tenn.); *M. extensus extensus* SPRINGER (M.Sil., Tenn., Eng.); *M. extensus bijugicirrus* SPRINGER (M.Sil., Tenn.); *M. schucherti* SPRINGER (L.Dev., Tenn.); *M. keyserensis* SPRINGER (L.Dev., W.Va.); *M. gorbyi* S. A. MILLER (M.Sil., Tenn.); *?M. bridgeportensis* S. A. MILLER (M.Sil., Ill.); *?M. dicirrocrinus* (EHRENBERG), (M.Dev., Ger.).

EXPLANATION OF PLATE 4

FIGURE PAGE

1. *Eomyelodactylus rotundatus* (FOERSTE), (Myelodactylidae), Lower Silurian (Medinan), Brassfield Limestone, near Xenia, Ohio; *1a,* incomplete, somewhat weathered coiled stem (holotype) lacking crown, ×2; *1b,* articular surface of columnal showing pentameres and lens-shaped lumen, centrally placed pentamere at top belonging on outer margin of coil, ×5 (after Foerste, 1919) 43
2. *Myelodactylus convolutus* HALL, (Myelodactylidae), Middle Silurian (Niagaran); *2a,b,* specimens (U.S.N.M. no. S2104) from Rochester Shale, Lockport, New York, showing convergent cirri in stem coil, crown hidden beneath them, and articular surface of single crescentic columnal, ×1.3, ×5; *2c,d,* specimens (U.S.N.M., no. S2105) from Laurel Limestone, St. Paul, Indiana, well coiled but cirri not preserved, with view of inner side of stem showing concave surface and cirri sockets along edges, ×1.3, ×2 (all after Springer, 1926) 41
3. *Herpetocrinus fletcheri* SALTER, (Myelodactylidae), Middle Silurian (Wenlockian), Dudley, England *(3a-e),* Gotland, Sweden *(3f-k); 3a,b,* British Mus. and U.S. Natl. Mus. specimens, latter (U.S.N.M., no. S2110) with removable crown showing four rays only, ×1.3, ×2; *3c-e,* proximal parts of crown and stem (U.S.N.M., no. S2110), with plate analysis, *3c* from C-ray side showing large brachianal, *3d,* from opposite, probably E-ray side, ×7.5; *3f,* exceptionally complete and well-preserved specimen showing double-reverse-coiled stem, crown in inverted position along inner curve of stem, and beaded cirri, ×2; *3g,* proximal part of crown and stem, same specimen as *3f,* anal tube comprising median row of broad, low plates, brachianal below and at right of anal-X but radials incorrectly represented, ×6; *3h,i,* anal tube plates from right and left sides, accompanied by cover plates, ×6; *3j,k,* columnals with attached cirri, lateral and articular views, ×4 *(3a-e,* after Springer, 1926; *3f-k,* after Bather, 1893) 42

Examples of secondary homonymy are found in reviewing the literature describing species that have been assigned to *Myelodactylus*. BATHER (1893, p. 50) published the names *Herpetocrinus bijugicirrus* BATHER and *H. alternicirrus* BATHER for fossils from the Middle Silurian of Gotland, at the same time treating them as varieties (=subspecies) of *H. ammonis* BATHER. SPRINGER (1926, p. 12) transferred this species and its two named subspecies to *Myelodactylus*, in the same paper publishing descriptions and illustrations of fossils named *Myelodactylus extensus* var. *bijugicirrus* SPRINGER and *M. extensus* var. *alternicirrus* SPRINGER. Thus we find the identical subspecific names *bijugicirrus* and *alternicirrus* associated with different species within the same genus. The Rules provide that publication (prior to 1961) of a zoological name for a division of a species designated as a variety does not of itself determine status of the name as one of subspecific rank. In paleontology, however, names originally published for so-called varieties are considered to be subspecific names. If this is accepted, the names just cited must be dealt with; if the fossils named varieties by BATHER and SPRINGER are not considered to represent subspecies, the Rules call for treating them as infrasubspecies and their names have no standing. I reject the interpretation that the named divisions of *M. ammonis* and *M. extensus* constitute infrasubspecies, and therefore proceed with consideration of them as subspecies.

A first step in seeking to solve the problem of duplicated subspecific names in *Myelodactylus* is to rectify the errors made by BATHER and SPRINGER in failing to designate one of two recognized divisions of their species as nominate. One of the subspecies of *M. ammonis* must bear the name *M. ammonis ammonis* and one of *M. extensus* must be *M. extensus extensus*. We are provided, then, with an easy way to remove difficulties, which otherwise would remain. I suppress BATHER's *Herpetocrinus ammonis bijugicirrus*, substituting for it *H. ammonis ammonis*, but accept his *H. ammonis alternicirrus*. Similarly, I suppress SPRINGER's *Myelodactylus extensus alternicirrus*, substituting for it *M. extensus extensus*, but accept his *M. extensus bijugicirrus*. In this way duplication of names disappears. The secondary homonymy is removed.

Genus HERPETOCRINUS Salter, 1873 (p. 118)

Plate 4, figures 3*a-d*

[Type-species, *H. fletcheri* SALTER, 1873, p. 118; by monotypy]

Like *Myelodactylus*, but crown more slender and elongate; dorsal cup with four basals and four radials, latter succeeded by four small arms that repeatedly branch heterotomously; anal tube larger in diameter than arms, very long. Cirri composed of short, rounded cirrals, having beadlike appearance. *M.Sil.*, Europe, North America.

The serpent-like, coiled and doubly bent stem, from which this genus derives its name, is a striking feature that is exceptionally well shown in the large specimen from Gotland figured by BATHER (reproduced in my paper, Pl. 4, fig. 3c). It reveals very clearly the differences that characterize proximal, middle, and distal parts of the stem. The cirri, which resemble short strings of beads, are seen in the distal region (Pl. 4, fig. 3j). Attention may be called to the position of the crown closely parallel to the curved stem, the ray next to it probably being the E-ray, which, if true, indicates that *Herpetocrinus* was bilaterally symmetrical in the same way as genera of the Calceocrinidae and *Homocrinus* (Figs. 1,*8*, 4,*3b*). The anal tube is seen near the base of the crown (row of thick plates near middle) and at intervals as far as the overlapping cirri near the summit of the crown.

The reversed position of the crown, with its top pointed toward the distal region of the stem, which would be downward if the stem were straightened out and placed in normal attitude, is specially interesting, for it suggests analogy with the calceocrinids. That these crinoids were pelagic, as suggested by SPRINGER, seems probable, and if free-swimming, the coiled stem almost surely was oriented in a vertical plane, presumably with the thick, heavy distal part of the stem directed downward. BATHER (1893, p. 45) has suggested that *Herpetocrinus* may very well have possessed power of locomotion, but he did not offer conjectures as to the means of movement, whether by pulsations of the cirri or partial coiling and uncoiling of the stem itself. He judged that the extra long and numerous cirri near the distal end of the stem in some species (e.g., *H. flabellicirrus*) were suited for temporary clinging to foreign objects, such as corals and perhaps the stems of attached crinoids.

BATHER's (1893) understanding of the structure of *Herpetocrinus* seems to have been far from adequate, as well as lacking in accuracy, for (p. 39) he reported that the cup contains five radials (emended to four radials in description of his plate 1), "all(?) except 1.post.R divided horizontally. . . . *x* rests on left upper slope of r.post.R^4 and partly abuts on 1.post R and r.post R^8." These statements cannot be correlated with illustrations furnished (e.g., those reproduced on Pl. 4, figs. 3f,g of this paper), which seem to show a relatively tall circlet of basals, followed in the C-ray by a single axillary plate (presumably the right posterior inferradial of BATHER, since it supports anal-X on its sloping left distal facet); then the plate on its right distal facet (undoubtedly a brachial, in my opinion) must be BATHER's so-called right posterior superradial. I conclude that SPRINGER's analysis of the dorsal cup and proximal arm plates (Pl. 4, figs. 3c-e) shows the true construction, both because he had specimens from England that were better suited for determination of essential structures, and because his illustrations of *Herpetocrinus* agree with well-established determinations of the structure of *Myelodactylus* (Pl. 3, figs. 1a-c), except for the presence of five radials, instead of four, in *Myelodactylus*. BATHER's work on the cup structure of *Herpetocrinus* may be disregarded, therefore.

Genus EOMYELODACTYLUS Foerste, 1919 (p. 19)

Plate 4, figures 1a,b

[Type-species, *Myelodactylus (Eomyelodactylus) rotundatus* FOERSTE, 1919, p. 19; by orig. desig. and monotypy]

Stem close-coiled, without known reverse curvature in proximal region, composed of moderately stout, even columnals of circular to elliptical shape, not concave on inner side, each columnal divided into pentameres of unequal size, those on inner side of stem being notably largest, relatively large lens-shaped lumen eccentrically placed slightly outward from center. *L.Sil.*, Ohio.

Genus BRACHIOCRINUS Hall, 1858 (p. 278)

Plate 3, figures 5a-c

[Type-species, *B. nodosarius* HALL, 1859, p. 118; by monotypy]

Known only from stem fragments, which are characterized by extremely stout, moderately short cirri given off from opposite sides of stem nearly in plane and in oblique proximal direction, cirri thickening in diameter away from stem and then tapering toward outer end, each pair borne by two successive columnals, which are separated by two to five columnals without cirri; distal extremity of stem consisting of a rounded to spheroidal smooth bulbous enlargement; proximal part of stem and crown unknown. *L.Dev.*, New York.

In spite of the incompleteness of information concerning *Brachiocrinus* and the fact that it is represented only by the type-species, this genus is highly distinctive. Almost the sole reason for synonymizing it with *Myelodactylus*, as was done by SPRINGER, is HALL's mistake in thinking that the fossils on which he erected the two genera consisted of parts of crinoid arms. Specimens assigned to *Brachiocrinus* have extremely little in common with *Myelodactylus convolutus*. The outstanding distinguishing character of *Brachiocrinus* is its remarkable cirri. As noted by SPRINGER (1926, p. 20), in no other crinoid are cirri found that in part may appreciably exceed the stem in diameter and girth. He has recorded measurements of some specimens which show a stem diameter of 3 mm. and cirrus diameter of 4 mm.

Brachiocrinus is here recognized as an independent genus primarily because of the uniqueness of its morphological features. I add the comment that absence of discovered dorsal cups or crowns definable as belonging to this genus is no more compelling reason for denying *Brachiocrinus* its own taxonomic status among crinoids than absence of attached arms and stem furnishes ground for refusing recognition of many genera described on the basis of distinctive dorsal cups only.

Genus CRINOBRACHIATUS Moore, n.gen.

Plate 3, figures 2a-c

[Type-species, *Myelodactylus brachiatus* HALL, 1852, p. 232; orig. desig. herein]

Stem with exceptional variation in diameter, ranging from large in distal region to almost threadlike in proximal region, bent in open S-shaped curve that, unlike *Herpetocrinus* and *Myelodactylus*, does not enclose crown, which is located well beyond the strongly curved part of stem but prevailingly is not preserved with the stem; cirri few, unusually robust and some very long, confined to part of stem on distal side of S-shaped coil and tending to be somewhat widely spaced, cirri composed of elongate cylindrical cirrals and branching in two or three places, directed obliquely upward; at distal extremity stem tapers to a point. *M.Sil.*, New York.

SPRINGER (1926, p. 16) has given an excellent, detailed description of the type-species and only known representative of this genus. He rightly emphasized the very peculiar nature of the cirri and remarkable differences between the distal and proximal parts of the stem. An unusually large collection of specimens was obtained by him, many of them exceptionally well preserved and some nearly complete. SPRINGER discovered one specimen (Pl. 3, fig. 2a, this paper) with the crown attached to the stem. He observed that the cup and arms have a general resemblance to *Iocrinus*, but he was unable to determine details of their structure. Careful preparation of 34 other most promising specimens showed that in every one the crown was missing, which, in Springer's opinion indicated that they were snapped off at the time of death of the crinoid. Accordingly, he judged that *C. brachiatus* "must have been peculiarly sensitive to disturbance or change of conditions, causing it to cast off the crown, as certain existing crinoids cast off their arms on being brought to the surface" (Springer, 1926, p. 18).

Very obviously, *Crinobrachiatus* presents numerous morphological features that are remote from those found in *Myelodactylus, Herpetocrinus,* and other myelodactylid genera. Peculiarities of the strongly recurved, partly coiled stem are sufficient to classify it as a member of the Myelodactylidae, but surely it is not congeneric with any other members of the family.

Family SYNBATHOCRINIDAE S. A. Miller, 1889

Monocyclic; crown tall and slender; cup small, truncate conical, generally steep-sided, composed of five or three basals and five subequal radials, which are undivided, though in one genus *(Theloreus)* distinct traces of transverse sutures in B-, C-, and E-radials denote antecedent infer- and superradials distributed as in Homocrinidae, C-radial distinguished as aniradial that supports anal-X on its distal left margin, all radials characterized by large, subhorizontally disposed articular facets which extend so far inward that central cavity of cup is appreciably constricted; arms unbranched, nonpinnulate. *M.Sil.-M. Perm.*

Of the six genera grouped in this family, two *(Phimocrinus,* L.Dev.-M.Dev.; *Theloreus,* M.Dev.) are marked by the presence of five basal plates, whereas the remaining four genera *(Synbathocrinus,* M. Sil.-U.Penn.; *Storthingocrinus,* M.Dev.; *Stylocrinus,* M. Dev.; *Taidocrinus,* Perm.) have only three basals, except for some specimens assigned to *Taidocrinus,* which show the presence of four basals. Synbathocrinids with three basals possess two large plates and a small one, the latter being located in the AE-interray in *Synbathocrinus* and *Taidocrinus,* but in the DE-interray in *Storthingocrinus* and *Stylocrinus.*

Genus THELOREUS Moore, n.gen.

[Type-species, **Phimocrinus jouberti* Oehlert, 1882, p. 353; orig. desig. Moore, herein]

Dorsal cup truncate conical, very steep-sided, with five subequal basals clearly visible from side, since they form approximately one-third height of cup, and five nearly equal-sized radials, those of A- and D-rays being definitely undivided, whereas those of B-, C-, and E-rays exhibit well-marked traces of transverse sutures that denote antecedent division of these plates into relatively tall inferradial and short superradial portions; radial facets wide and deep, marked by transverse ridge and ligament furrow near outer margin and broad muscle fields occupying large inner area, margins of facets next to small central cavity of cup narrowly but not deeply notched; C-radial with characters of aniradial, indicated by beveled left distal edge for reception of anal-X, which impinges also on right distal margin of D-radial. Nature of arms unknown, but probably uniserial, unbranched. Stem relatively large, circular in transverse section. *M.Dev.,* West Germany.

The name *Theloreus* (gender masculine) given to this new genus is derived by rearrangement of the letters of the proper name Oehlert and addition of the ending *-us.* The importance of the remnant marks of infer- and superradial elements found in the B-, C-, and E-radials amply warrants separation of this crinoid from *Phimocrinus,* and recognition of it as an independent genus serves to emphasize the significance of its homocrinoidal affinities. The nature of the radial articular facets found in *Theloreus* provides an authentic stamp of synbathocrinid relationships, indicating that the genus is properly classified in the Synbathocrinidae and pointing to derivation of other members of the family from homocrinoidal ancestors. The plane of bilateral symmetry, well defined in *Theloreus* (Fig. 17), is located in the E-ray and BC-interray, as in the Homocrinidae, Calceocrinidae, and Anamesocrinidae.

THELOREUS JOUBERTI (Oehlert), Moore (n. comb.)

Text-figure 17

Characters of the genus. Measurements of the dorsal cup that comprises the holotype specimen, as recorded by Oehlert (1882, p. 354), are: height, 10 mm., diameter at summit, 8 mm., diameter at base, 4 mm. Seemingly, these measurements are more trustworthy than those scaled from Oehlert's figure (pl. 8, fig. 1) reported to show natural size, for the height of the cup in this figure is only 7.5 mm. Also, the plate diagram (*op. cit.,* p. 353) intended to show the structure of the dorsal cup as erroneous in representing the D-radial as divided and the C-radial as undivided, for this plainly disagrees with illustrations of the posterior and anterior sides of the cup (pl. 8, fig. 1a,b) given by Oehlert; these correspond respectively to the lower left and right sketches in Figure 17 of the present paper. The surface of the cup appears smooth to the naked eye, but at low magnification fine close-spaced granules are visible.

Occurrence. Lower Devonian sandstone, Department of the Sarthe, western France, southwest of Paris.

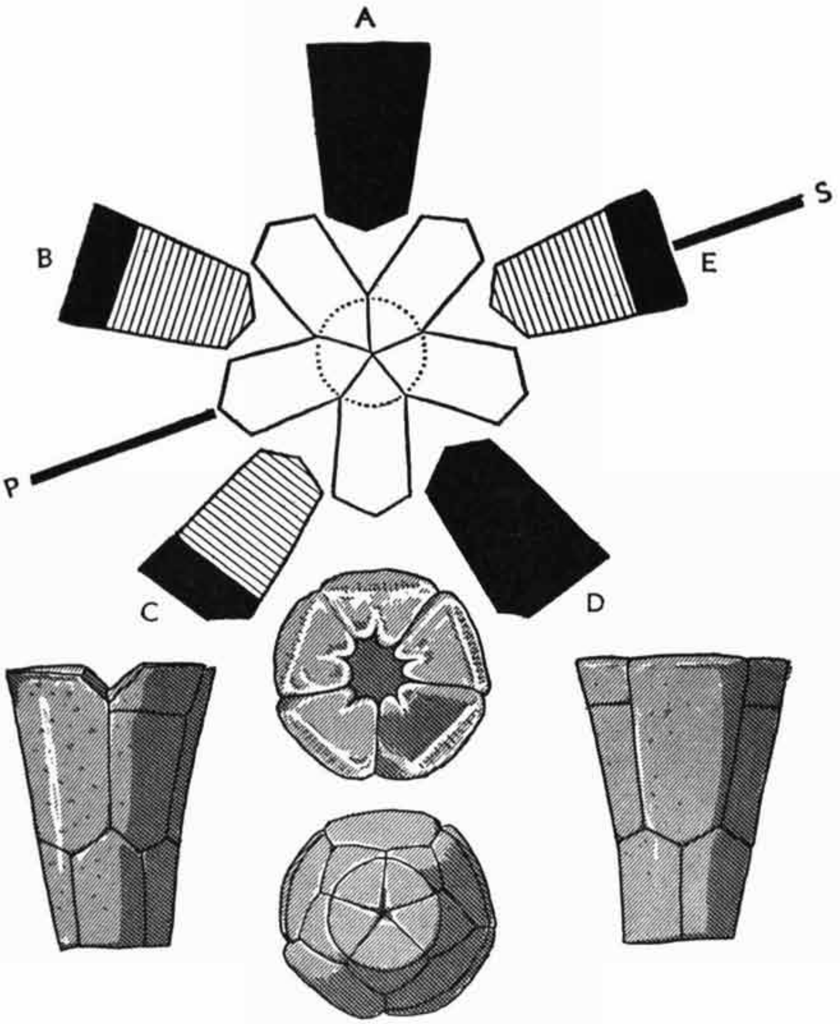


FIG. 17. Structural features and bilateral symmetry of *Theloreus jouberti* (OEHLERT), above, and views of dorsal cup, below (from left to right, posterior, ventral, dorsal, anterior sides) (after Oehlert, 1882). [Explanation of structural diagram: undivided radials and superradial elements of B-, C-, and E-rays, solid black; inferradial elements of B-, C-, and E-rays, ruled; P-S, plane of bilateral symmetry.]

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