

THE UNIVERSITY OF KANSAS  
PALEONTOLOGICAL CONTRIBUTIONS

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# ECHINODERMATA

ARTICLE 8

Serial Number 45

Pages 1-30, Figures 1-5, Plates 1-4

## MORPHOLOGICAL FEATURES OF CRINOID COLUMNS

RAYMOND C. MOORE, RUSSELL M. JEFFORDS, and THEO. H. MILLER

ARTICLE 9

Serial Number 46

Pages 1-86, Figures 1-6, Plates 1-28

## CLASSIFICATION AND NOMENCLATURE OF FOSSIL CRINOIDS BASED ON STUDIES OF DISSOCIATED PARTS OF THEIR COLUMNS

RAYMOND C. MOORE and RUSSELL M. JEFFORDS

ARTICLE 10

Serial Number 47

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## ONTOGENETIC DEVELOPMENT IN LATE PENNSYLVANIAN CRINOID COLUMNALS AND PLURICOLUMNALS

RUSSELL M. JEFFORDS and THEO. H. MILLER

SUPPLEMENT TO ECHINODERMATA ARTICLES 8-10 (Pages 1-18)  
[COLLECTING LOCALITIES, REFERENCES and INDEX]

RAYMOND C. MOORE, RUSSELL M. JEFFORDS, and THEO. H. MILLER



## *The University of Kansas Paleontological Institute*

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[Asterisk (\*) indicates type species of genera]

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## ABSTRACT

Descriptions and illustrations (including also many in accompanying Echinodermata Articles 9 and 10) of both external and internal morphological characteristics of representative crinoid stems are given for the purpose of explaining various terms, including new ones, which are intended for use in the *Treatise on Invertebrate Paleontology*. Also, these features furnish the basis for discrimination of genera and species of many fossil crinoids which are yet unknown from attributes of their dorsal cups and arms. Chiefly important in the study of dissociated parts of crinoid stems are the nature of their 1) sideward-directed exterior surfaces (latera), 2) shape transversely and longitudinally, 3) intercolumnal surfaces of articulation (articula), 4) arrangement in sequence, 5) lateral appendages (cirri), if present, and 6) transverse outlines and longitudinal profiles of the axial canal, with or without associated accessory canals. Holdfast structures, either independently or joined to distal portions of stems, may have value in discrimination of crinoid species. Morphologic terminology is summarized in a glossary.

## INTRODUCTION

## PURPOSE AND SCOPE OF PAPER

The present paper is designed to present some results of studies made by us during the past few years on dissociated fossil remains of crinoids, mostly in collections obtained from Paleozoic formations. The available specimens which number many hundred thousands, chiefly were obtained by bulk collecting at outcrops using stiff wire brushes for sweeping fossils into heaps and shallowly skimming some surfaces with a spade. In this way multitudes of free-weathered skeletal parts of crinoids, especially portions of stems, were brought together and with shaly material for packing, dumped into large sacks for shipment to the laboratory. There, the samples were washed, dried, sieved, and sorted so that crinoid remains from smallest to largest could be segregated. The collections represent more or less richly crinoidal strata ranging in age from Middle Ordovician to Permian and distributed geographically, from Alabama through Tennessee, Kentucky, Ohio, Indiana, Michigan, Illinois, Iowa, Missouri, Arkansas, Kansas, Oklahoma, and Texas to New Mexico.

In addition, very numerous dissociated crinoid stem parts have been loaned to us by the U.S. National Museum, Yale University, and the Universities of Illinois, Iowa, Arkansas, Kansas, and Mississippi State.

Only parts of crinoid columns and holdfasts are considered here and treatment of them is by no means exhaustive. The range of what appears to be significant variations is so great that many aspects of the morphology of crinoid columns must be omitted from present notice. The main purposes of the paper are to describe features which have been found most useful in classifying crinoid columns and to explain morphological terms, including new ones, which are intended for adoption in the crinoid volume of the *Treatise on Invertebrate Paleontology*.

Crinoid stem parts discussed and illustrated in this article are identified in terms of genera and species of fossil whole crinoids to which they are judged to belong, either more or less well known previously described taxa, or new ones. The last type are based at present solely on observed distinctive characteristics of their stem parts, but named genera and species apply to whole crinoids. Such new crinoids are described and figured in the following paper by MOORE & JEFFORDS.

## PREVIOUS WORK

In general, the stalks and holdfasts of crinoids have been far less studied than the dorsal cups or calices and their attached arms. Even so, main morphological features of skeletal parts below the crown are well known in hundreds of genera. Best descriptions and illustrations of modern stalked crinoids are found in the extensive *Challenger* monograph by CARPENTER (1884) and shorter contributions by DÖDERLEIN (1907, 1912) who described and illustrated stalked crinoids obtained by the *Siboga* and *Valdivia* expeditions led by Dutch and German oceanographers. In addition, CLARK (1915 [in 1915-47]) has published somewhat lengthy descriptions and discussions of the stem structures of extant crinoids. As is well known, such echinoderms attached to the sea bottom are very uncommon in comparison to the host of free-swimming stemless crinoids collectively called comatulids.

In contrast with this, a wealth of data on the nature of fossil stem-bearing crinoids is contained in paleontological literature. Mostly this relates to Paleozoic and Mesozoic species, for they far outnumber Cenozoic forms.

Major publications include monographs and other important papers (see references in Supplement following Echinodermata, Article 10) by MILLER (1821), GOLDFUSS (1826-44), D'ORBIGNY (1840, 1849-51), BRONN (1840,

1848), AUSTIN & AUSTIN (1843-49), HALL (1843, 1852, 1859a,b, 1861, 1862, 1866a,b, 1872, 1882), STEININGER (1837, 1853), DE KONINCK & LEHON (1854), EICHWALD (1859-68), C. F. ROEMER (1860), MEEK & WORTHEN (1860, 1865, 1868a,b, 1873), SCHULTZE (1867), TRAUTSCHOLD (1859, 1867, 1879), MEEK (1873), QUENSTEDT (1852, 1874-76, 1882 [1885]), ANGELIN (1878), WACHSMUTH & SPRINGER (1879-85, 1897), DE LORIOI (1882-89), BATHER (1893, 1898, 1899, 1909), WAAGEN & JAHN (1899), WELLER (1900), SPRINGER (1909, 1911, 1917, 1920, 1921, 1922a,b, 1926a,b), WANNER (1916, 1924, 1930a,b, 1931, 1937, 1940, 1949), JAEKEL (1918), GOLDRING (1923, 1942), GISLÉN (1924), EHRENBURG (1929), SCHMIDT (1930, 1931, 1934, 1942), MOORE (1939c, 1962a,b, 1967), MAREZ-OYENS (1940), MOORE & PLUMMER (1940), MOORE & LAUDON (1943), WRIGHT (1950-60), KIER (1952), MOORE & VOKES (1953), YAKOVLEV & IVANOV (1956), RAMSBOTTOM (1961), RASMUSSEN (1961), VAN SANT (1964), ARENDT & GEKKER [HECKER] (1964), and KESLING (1965).

Textbook summaries containing information of value on features of fossil crinoid stems have been given by ZITTEL (1879, 1900, 1913), WACHSMUTH (1896), BATHER (1900), DELAGE & HÉROUARD (1903 [1904]), SPRINGER (1913), CLARK (1913), MOORE & LAUDON (1944), CUÉNOT (1948), MOORE (1952), SHROCK & TWENHOFEL (1953), UBAGHS (1953), and POKORNÝ (1957).

## TECHNIQUES FOR STUDY OF DISARTICULATED CRINOID REMAINS

### COLLECTION AND PREPARATION OF SAMPLES

Indispensable as an approach to utilizing fragmental crinoid remains as fossils potentially useful in stratigraphic studies is the collection of samples from strata of known age in several localities. Collections from units having differing lithologies but comparable ages are useful in evaluating the environmental significance of the fossils. Wide geographic spread of collections, however, facilitates recognition of commonly occurring forms having notable time significance. Wherever obtained, the samples should serve to indicate the nature and abundance of the fossils in assemblages of similar and different ages.

Crinoid fragments freed by weathering from shale or crumbly limestone are most desirable for study because the morphological features are not obscured by matrix and numerous specimens are readily obtained. First effort, therefore, should be to obtain such crinoidal materials in order that numerous specimens can be studied in detail. Fossils weathered from shaly deposits have been gathered in our field work commonly by sweeping outcrop surfaces with a stiff wire brush or by shallow skimming of such surfaces with a shovel; this serves quickly to accumulate piles of weathered-out fossils down

Reference to indices for Paleozoic crinoids by BASSLER (1938) and BASSLER & MOODEY (1943) and for Mesozoic and Cenozoic crinoids by BIESE (1934, 1935-37) and BIESE & SIEVERTS-DORECK (1937, 1939a,b), supplemented by examination of more recent publications shows that species known only from parts of crinoid columns are 253 in Paleozoic formations, 359 in Mesozoic, and 22 in Cenozoic—a total of 634 species. Moreover, at least 59 new crinoid genera with type species based solely on stem parts have been described. These data are summarized in the following paper by MOORE & JEFFORDS, who note that systematic studies of dissociated parts of crinoid columns have been published by more than 400 paleontologists in nearly 700 monographs, memoirs, and shorter papers. This work spans years from the time of LINNÉ to the present.

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to minute size, along with waste rock which can be tossed aside (Pl. 1, fig. 1). When the concentrates, with accompanying dirt and added shale for packing are placed in sacks, they can be shipped to the laboratory without damage from abrasion of specimens on one another. These techniques have the distinct advantage of decreasing collecting time in comparison with more conventional hand picking and wrapping of fossils. Moreover, surprisingly large quantities of excellent crinoidal and other fossil material are obtained with a minimum of effort. The initial differentiation and description of crinoid fragments are aided substantially by the availability of many especially well-preserved specimens, but subsequent routine identifications require only relatively small assemblages.

### METHODS APPLICABLE TO FRAGMENTS FREE FROM MATRIX

Fragmentary crinoidal remains consisting mainly of parts of stems, are best for taxonomic studies when they are obtainable as free specimens without any adhering matrix. Such specimens are available most commonly where fossils have weathered from enclosing shale but they may also be collected from shaly or crumbly limestones. Crinoid remains exposed in relief by weathering



of hard limestone may be broken free with more or less success by use of a cold chisel.

Collections of discrete crinoid fragments need first to be washed thoroughly but carefully in order to obtain specimens as free as possible from any adherent sediment. Dried field samples are soaked in water, washed by decanting until sufficient clay is removed to eliminate clumping, and sieved on about a  $\frac{1}{8}$ -inch screen. The coarse fraction then is washed thoroughly to remove sediment and dried. Supplemental cleaning required to reveal articular and lateral surfaces is done as required using a petroleum product such as varsol, a strong detergent such as "Quaternary O," or placing in a bath for treatment by ultrasonic vibrations. These techniques commonly are useful for treating selected specimens, but, particularly the ultrasonic method, are not convenient for mass treatment of large volumes of material.

The washed and dried samples generally containing a variety of fossils mixed with differing amounts of rock fragments are sieved roughly (as in wire baskets constructed of  $\frac{3}{4}$ -,  $\frac{1}{2}$ -, and  $\frac{1}{4}$ -inch screen) and much of the noncrinoidal material is removed (Pl. 1, fig. 2). The rapid separation of crinoid specimens into lots suitable for taxonomic study is facilitated by dividing the samples into very coarse (ca.  $\frac{1}{2}$ -inch), intermediate (ca.  $\frac{1}{4}$ -inch), and "fine" ( $1/16$ -inch) grades. Washed residues are retained for the finer material.

Sorting of specimens in each size group naturally calls for segregation of stem parts, thecal elements, and arm plates or segments. Comparatively unskilled assistants can accomplish this preliminary sorting effectively. Individual columnals along with groups of columnals joined together are separated from other remains and initially are best divided into assemblages based on their transverse shape. Subdivision of the assemblages is reserved for later discussion in which attention is given to such features as nature of articular surfaces and shape of the lumen.

Photography is an indispensable adjunct of crinoid-stem studies after visual sorting of specimens has been well started, if not completed, generally with aid of a good low-power binocular microscope, preferably with long focal range to facilitate handling of specimens. A small number of the best fossils in each differentiated group should be selected and placed in small trays or plastic boxes with index letters or other means of compactly recording the source collection as to horizon and locality and individual numbers to provide for record of separate specimens. Routine making of photographic negatives of standard views (such as one or possibly two side views and at least one articular-facet view of stem parts) is most economically and expeditiously done with a 35-mm. camera equipped for reflex observation of the photographic field. Extension rings or a bellows, or both, are needed for obtaining natural-size or moderately enlarged images of small specimens on the film. Then,

after development of the film, enlargements at desired scales are readily made. In our procedure Leica, Nikon, and Beseler Topcon cameras are mounted so as to be in continuous readiness and illumination with a strobe flash and trial-and-error located backlights has been found most satisfactory. Nearly all prints have been made with Fotorite equipment, duplicate copies being used for mounting one set on 5 x 8 cards and the other on letter-size sheets of bond paper. The cards facilitate classifying specimens zoologically, for those from any source can be laid out on a table for intercomparison. The sheets bring together photographs of specimens belonging to given collections and they help to show differences between assemblages. Either of the photographs may be withdrawn for use in reports, but if desired, they can readily be replaced.

The use of photographs of fossils as a technique in studies of them has utmost value, because it is impossible to make the kinds and numbers of required comparisons of specimens directly. The characters of fossils examined successively, especially when use of a microscope is necessary, cannot be retained in mind sufficiently, whereas comparisons of photographs are easy and frequently this calls attention to need for additional examination of specimens under the microscope. Given care in making photographic prints at recorded magnifications, measurements are more readily made on the photographic prints than directly.

Such techniques as the sawing of sections, for example, longitudinal sections of stems which commonly are needed to show features not visible externally, hardly call for mention. Many such sections are illustrated in this article. Acetate peels and thin sections are useful, but many internal features can be recorded satisfactorily by direct photography (preferably with specimens immersed in a liquid such as varsol or xylol, or wet with a light oil if lights are placed to avoid objectionable reflections, or with use of polaroid filter).

A novel method that provides a photographic record of all sides of a crinoid stem in single panoramic view is useful for work on specimens having dissimilar features in parts of their circumference (e.g., localized projections, attachment scars of cirri). This was devised by R. M. JEFFORDS & T. H. MILLER, who thought of the simple expedient of carefully rolling a stem across a smooth surface of putty or similar plastic substance. In this way a mold of the surface can be formed, every projection of the stem being represented on the putty by a depression and vice versa. When the mold is photographed with low oblique lighting either from upper left (10 o'clock position) or lower right (4 o'clock), a print shows the grooves to have the appearance of ridges if the negative with 10 o'clock lighting is turned 180 degrees, or alternatively, the same effect is obtained by printing the negative with 4 o'clock lighting without turning it upside down (Pl. 2, fig. 5-7). This is because

we are all accustomed to illustrations of fossils with conventional lighting from the upper left. Similarly, most geologists know that valleys shown on vertical air photographs have the appearance of ridges, and oppositely, ridges seem to be valleys if the photograph is oriented in one way or another.

## METHODS APPLICABLE TO FRAGMENTS FIRMLY IMBEDDED IN MATRIX

Crinoid remains enclosed by hard-rock matrix are most difficult to deal with in paleontological study. Mostly, this is because surface features of the articular and lateral surfaces which are readily seen in specimens weathered or washed from soft matrix and which are the main features used in classification generally are incompletely determinable, or in specimens entirely surrounded by matrix it is virtually impossible to discover the sought-for characters either by slow and arduous removal of the matrix with a vibratool or similar equipment or by sectioning the rock.

Specimens of stem parts exposed on the surfaces of limestones may be determinable in fairly satisfactory manner, either breaking them from the rock with a cold chisel or leaving them partly imbedded on slabs. Weathered specimens attached to rock have been collected and studied but on most of them, deterioration or even obliteration of surface features has been effected by solution. Such fossils are not very good, yet many of them can be classified more or less reliably. The extent to which crinoid remains entirely surrounded by matrix, as in parts of well cores, will be indentifiable cannot now be affirmed. In our opinion, the effort to identify many is far from hopeless, but experience will be necessary in order

to determine best methods of preparation and criteria that may be used most successfully for classification.

Some hard sandstones, siltstones, and impure limestones which contain or once contained fragmentary remains of crinoids afford good materials for paleontological investigation because natural or artificial external molds of the fossils permit preparation of latex casts. Such casts commonly are perfect replicas of the original calcareous crinoid fragments and show various morphological characters as well as discrete fragments washed or weathered from shaly deposits. The same methods of study may be applied to both. For purposes of ecological interpretation, molds of crinoid remains in rock matrix may be superior to loose fragments collected from shaly deposits, because the molds in hard rock show the exact placement of the fossils as originally deposited. Good examples of this are furnished by rock samples from late Oligocene crinoid-bearing beds in northwestern Oregon (Nehalem River region) which furnished excellent natural and artificial molds used in studies of the stem parts and other dissociated fragments (MOORE & VOKES, 1953). Mode of occurrence of these fossils and their association with leaves of land plants indicate burial of the crinoids in deep quiet waters in basins not very far from shore. Similarly, crinoid remains in hard sandstone of Middle Pennsylvanian age in southern Oklahoma beds interpreted by some as turbidite deposits indicate deposition of the fossils, essentially *in situ* in a shallow nearshore environment rather than sediment deposited by a deep-water turbidity current.

It is obvious that first efforts in study of crinoid remains should be directed to comprehensive examination of the free specimens because knowledge thus gained is needed to guide investigations of fragments imbedded in rock matrix.

## GENERAL FEATURES OF CRINOID STEM PARTS

### COLUMNALS, PLURICOLUMNALS, CIRRLS, AND PLURICIRRLS

Dissociated parts of crinoid stems include components of the stalk itself and in many species, parts of the side branches called cirri given off by it. The individual skeletal elements of the stem are **columnals** (Fig. 1, 2) and those of the cirri are termed **cirrls**. A few or many of these may remain fastened together and such parts of stalks commonly have been referred to as stem fragments, stem segments, or stem sections, and cirrus fragments, cirrus segments, etc. These designations are somewhat cumbersome as well as imprecise. A stem fragment is any piece, including individual columnals, produced either by natural separation before fossilization or by mechanical breakage of some sort. Stem segment is a vague term applicable both to separate columnals and

to groups of adherent columnals. A crinoid section might refer to a large or small part of the whole but is best reserved for a slice, cut, or fractured part of a stem. The sections may be produced by sawing and grinding for the purpose of studying internal structures and then generally are made in transverse or longitudinal directions. Broken or cut surfaces of crinoidal rock almost invariably show many stem sections oriented at random.

A preferred substitute term for parts of stems consisting of two or more attached columnals is **pluricolumnal** (Fig. 1, 1, 2b; 2, 1). Thus, almost any collection of dissociated crinoid stem parts is certain to contain many columnals and pluricolumnals.

Similarly, a **pluricirral** comprises any two or more cirrls joined together. Dissociated cirrls and pluricirrls, particularly those belonging near the proximal end of a

cirrus, may be difficult to distinguish from small columnals and pluricolumnals. Many fossilized parts of Paleozoic crinoid cirri are distinguished by the presence of small spinelets near the distal end of each cirral, confined to a single side. The axial canal penetrating cirrals commonly is a minute cylindrical tube but in some the canal is transversely dumbbell-shaped or separation of the dumbbell ends may give rise to a pair of cylindrical canals.

### LATERA

All columnals, pluricolumnals, cirrals, and pluricirrals have outer surfaces consisting of the sides which surround them, with straight, curved, or angulated longitudinal profiles. These outward facing sides are named **latera** (sing., **latus**) (Fig. 1,3; 2,1,2). They are bounded on each columnal or cirral by junctions with transversely disposed surfaces which form the two ends of the skeletal element and serve for articulating attachment to contiguous elements. The transverse surfaces, called articula or articular facets, are considered subsequently.

Both individually and collectively in sequence along sides of a pluricolumnal or pluricirral, the latera display several sorts of characters that are useful in differentiating one kind from others and ultimately in distinguishing various groups defined by stem-part types. For purposes of descriptions and measurements the **height** of latera is indicated to be the distance between opposite edges in any plane containing the longitudinal axis of the element (Fig. 2,2). Also, height of latus is identical to that of columnal or cirral. The **length** of latera is construed to be the distance between opposite edges in any plane containing the longitudinal axis of the element measured along the profile of the latus. In straight-sided columnals and cirrals it is evident that length equals height, whereas in all others length exceeds height at least slightly and in many columnals (but not cirrals) greatly. The **width** of latera may be defined as the transverse distance between their abaxial limits and a line connecting their adaxial limits measured perpendicularly to the axis of the element (Fig. 2,2). This is the same as width of the columnal or cirral surface outside of the area of the articulum (articular facet), such surface being called the **epifacet** (Fig. 2,2). The epifacetal width of straight-sided columnals and cirrals is zero, but in some columnals it may be several times greater than height of the latera. Invariably the width of latera (epifacets) is smaller than length (longitudinal profile).

The outlines of columnal and cirral latera viewed perpendicularly to the axes of these stem parts are mostly quadrangular, with height much less than width of the quadrilaterals in columnals but tending to be subequal in cirrals. In side view some latera are lozenge-shaped, lanceolate, oval, or truncate-circular. Many columnals are wafer-thin, with latera reduced to linear.

The dimensions of latera just discussed are partly identical and partly quite different from corresponding ones

of entire columnals and cirrals. The height of latera is the same as that of the stem part to which they belong, but the width of columnals and cirrals may be greater or smaller than height or exactly equal to it. Ratios are discussed later in explaining columnal indices.

Features of the latera of some columnals are marks of attachment (articula) of cirri, known as **cirrus scars** or **cirrus sockets**. Those confined to sides of nodals are termed **nodocirral articula (facets)** (Fig. 1,1,3). Some relatively large cirrus scars are impressed on contiguous columnals (2 to 10 or more) (Pl. 2, fig. 3, 7; Pl. 3, fig. 3a). Chiefly these occur near the distal extremity of crinoid columns and serve for attachment of the rootlike holdfasts termed **radicular cirri**. Commonly cirrus articula on intermediate and proximal columnals of the stalk occur in whorls of 5, but on individual columnals their number may be reduced to 4, 3, 2, or only 1 (Pl. 2, fig. 5-7). Placement of the cirrus scars mostly is at mid-height of the latera (Pl. 3, fig. 5), but in some it is much nearer to one columnar articulum than the other (Pl. 2, fig. 3), and the cirrus facet may be directed straight outward, upward, or downward. Outlines of a large majority of cirrus scars are circular; less common ones are elliptical.

Some crinoid pluricolumnals are distinguished by the presence of longitudinally aligned pores (**cirripores**) which occur at mid-height of the latera of successive columnals (9<sup>1</sup>: Pl. 18, fig. 6-11; 9, Pl. 19, fig. 13). That they represent an abortive sort of cirri, without actual sideward outgrowths, is indicated by transverse sections through the columnals which show canaliculate connections of each pore with the axial canal of the column; also, rarely, a few of the pores are enlarged into typical cirrus articula of diminutive size on the latus surface. Other columnals possess aberrant projections of cirrus nature in having an axial canal connected with that of the crinoid stalk but differing from ordinary cirri in showing no division into component cirrals. Striking examples of such structures which might reasonably be termed **pseudocirri** are found in pluricolumnals of *Pandocrinus stoloniferus* (HALL) and *Hyperexochus immodicus* MOORE & JEFFORDS, n. gen., n. sp. (9: Pl. 1, fig. 4-\*7).

### HOMEOMORPHIC AND HETEROMORPHIC PLURICOLUMNALS

In a study of dissociated parts of crinoid stalks, similarity or dissimilarity of columnals in features of the latera is an important characteristic. This can be ascertained for pluricolumnals consisting of columnal sequences joined together, but not for assemblages of loose individual columnals, except for some kinds of them as noted later. Also, it is obvious that a pluricolumnal composed of only two or three columnals may not be

<sup>1</sup>Cross references to accompanying papers Echinodermata, Articles 9 and 10 are indicated simply and compactly by numbers in boldface type as given here.

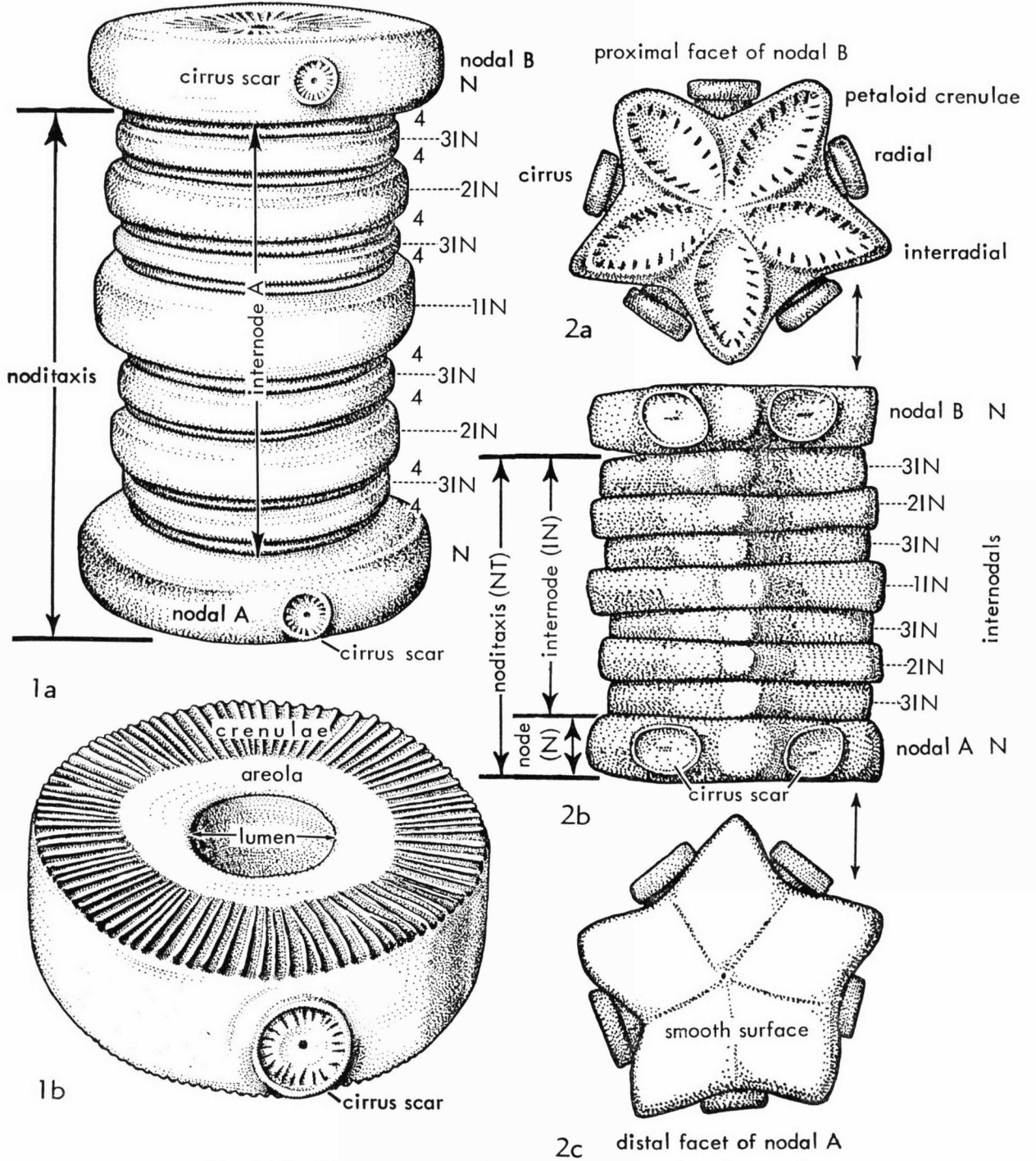


FIG. 1. Morphological features of crinoid columnals and pluricolumnals.

1. Oblique views of heteromorphic pluricolumnal and single columnal with some morphological terms applied to them. *1a*. Complete noditaxis and additional nodal, nodals characterized by size and presence of cirrus scars, 15 internodals divisible into four orders on basis of their sequence in origin by intercalation between nodals, large priminternodal

(1IN) midway between nodals, two secundinternodals (2IN), four tertinternodals (3IN) and eight quartinternodals (4IN) distributed regularly in upper and lower parts of noditaxis, each characterized by progressively diminishing size. *1b*. Single columnal showing nearly straight sides and features of articulum. (Continued on facing page.)

very helpful unless they are associated with longer parts of stems with characteristics matching those of the short pluricolumnals.

Bearing these reservations in mind, crinoid pluricolumnals can be classed in one or the other of two groups: 1) those in which all columnals appear to be

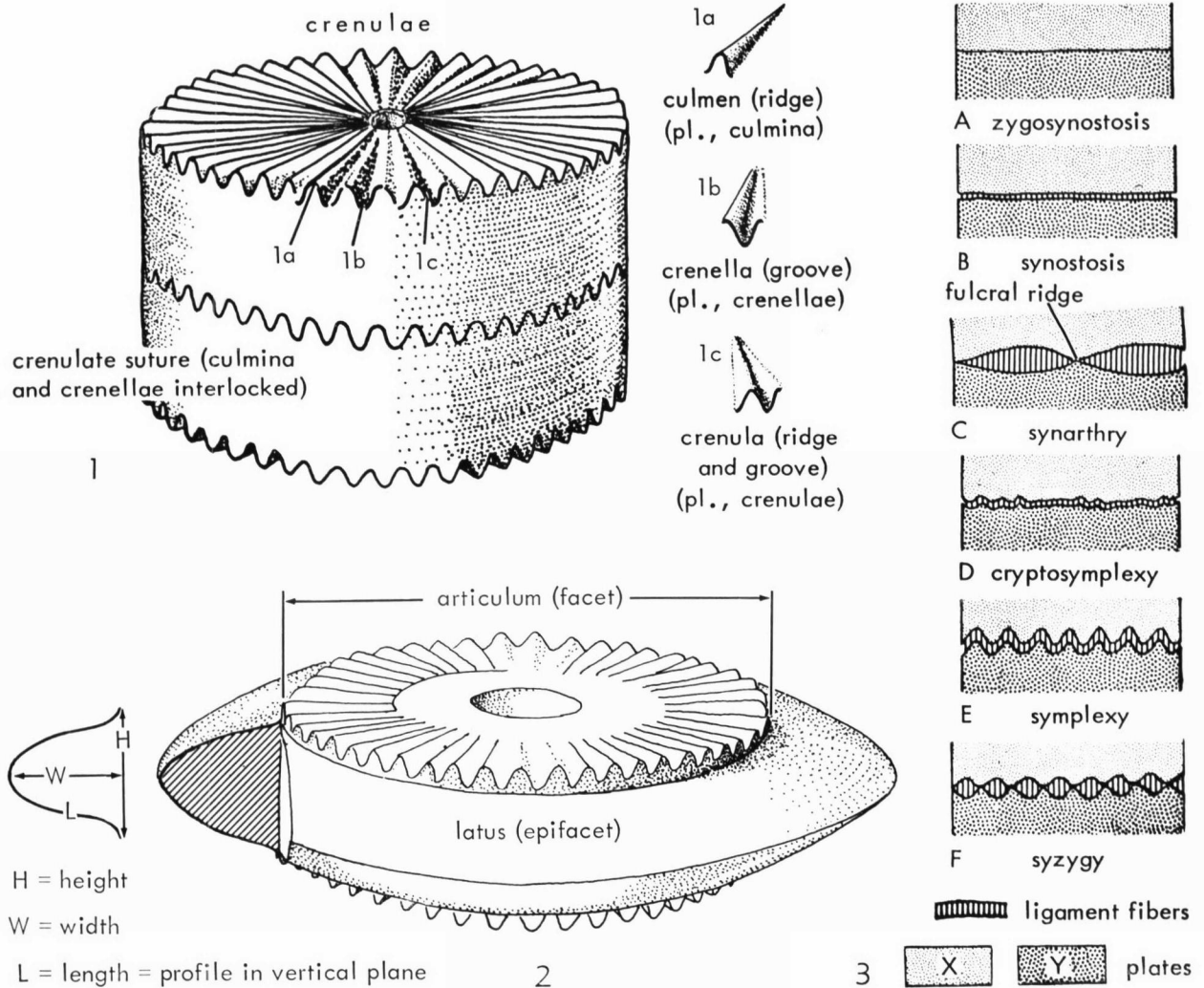


FIG. 2. Morphological features of crinoid columnals.

1. Straight-sided columnals joined by interlocked ridges and grooves of articular surfaces marked externally by crenulate suture, single ridge (1a, culmen) and groove (1b, crenella) together forming a crenula (1c).
2. Columnal with relatively wide extrafacetal area (epifacet) showing adopted methods of defining height (H), width (W) and length (L) of epifacet (latus).
3. Diagrammatic transverse profiles of juxtaposed crinoid articular facets showing types of articulation.

(Fig. 1.)

2. *Isocrinus* pluricolumnal consisting of complete noditaxis and additional nodal (B). 2a. Downward view of nodal B showing proximal parts of five cirri located radially, with zygocirri attached to cirrus scars on nodal, petaloid divisions of articulum separated abaxially by narrowly triangular epifacetal areas,

very short crenulae nearly surrounding lanceolate areolar floors, and miniscule lumen. 2b. Side view of pluricolumnal showing nodals with oval cirrus scars containing short fulcral ridge, and internodals of three orders, entire noditaxis composed of eight columnals. 2c. Upward view of nodal A.

identical, termed **homeomorphic** (Fig. 2,1) (9: Pl. 6, fig. \*5; Pl. 12, fig. \*2), and 2) those in which successive columnals have more or less widely different characteristics, termed **heteromorphic** (Fig. 1) (Pl. 3, fig. 5; 9: Pl. 10, fig. \*3-4). Both of these terms relate to relatively short stem portions and thus they differ from so-called xenomorphic stems distinguished later, which may be composed of either homeomorphic or heteromorphic columnals, or both. The articularia of all columnals in homeomorphic pluricolumnals generally are substantially identical in their characters, like the readily observed latera; with few exceptions, the articularia of all heteromorphic pluricolumnals also are similar to one another, though width and height of the columnals and features of their latera are unlike. Accordingly, it is the nature and arrangement of successive columnal latera, that chiefly distinguish different sorts of heteromorphic pluricolumnals.

Homeomorphic pluricolumnals may be of many different sorts. They call for no special discussion here, because each is distinguished by identity or near-identity of its component columnals.

Heteromorphic pluricolumnals are composed of two or more kinds of dissimilar columnals, some of which are distinctly greater in diameter (Pl. 3, fig. 3b) or height (Pl. 2, fig. 4) than others, or in both, and in configuration of their latera, including ornamentation. Also, any combination of these may distinguish some pluricolumnals from others.

Some apparently homeomorphic pluricolumnals, viewed externally, actually are heteromorphic (e.g., *Dianthicoeloma \*insuetum* MOORE & JEFFORDS, n. gen., n. sp., 9, Pl. 7, fig. \*1-3) as readily proved by longitudinal sections, which reveal thin internodals that are not exposed at their outer margins. Such stems are not uncommon. They may be termed **pseudohomeomorphic**.

## NODALS, INTERNODALS, AND NODITAXES

In heteromorphic stems, the largest, most prominent columnals are differentiated as **nodals** and varying numbers of smaller columnals between pairs of successive nodals are designated as **internodals** (Pl. 2, fig. 3; Pl. 3, fig. 3a,b).

In many crinoids each nodal is distinguished by bearing cirri, commonly arranged in whorls of five but in many crinoid columns with a smaller number down to a single cirrus. In fossils, the cirri readily become detached from the stalk and then are represented on the nodals only by their scars of attachment (Pl. 3, fig. 5). Nodals bearing cirri are termed **cirrinodals** (Pl. 2, fig. 3). Nodals lacking any articularia for attachment of cirri are termed **nudinodals** (*nudi-*, naked or bare). (Pl. 2, fig. 4).

Some internodals may resemble homeomorphic pluricolumnals in being essentially identical to one another, or they may differ systematically in diameter and height

(Pl. 3, fig. 3a,b) as result of the order in which they were introduced by intercalation between the limiting nodals. In this way, slight to very obvious differences may mark a first-order internodal (**priminternodal**) as distinct from a pair of second-order internodals (**secundinternodals**), one located above and the other below the priminternodal. In the same way, third-order internodals (**tertinternodals**) may be introduced above and below each secundinternodal (Fig. 1). Fourth-, fifth-, and even higher-order internodals appear in some crinoid stems, each generally distinguished by smaller size than other columnals of the internodal sequence (collectively termed an **internode**). Additional discussion of the introduction of internodals is given by JEFFORDS & MILLER (10).

A complete internode with one of the contiguous nodals is termed then a **noditaxis** (*-taxis*, series or row; pl., **noditaxes**) (Fig. 1).

## ARTICULA

The successive columnals of crinoid stems and successive cirrals of their sideward directed appendages are joined to one another by transversely disposed surfaces called **articularia** (sing., **articulum**), otherwise known as articular facets (Fig. 1). Features displayed by them are indispensable for differentiation of crinoid genera and species based on characters of their columns. Nearly all dissociated fossil crinoid columnals and pluricolumnals display features of the articularia clearly, but because these morphological characters of columns attached to dorsal cups and calices of most crinoids which have been used to distinguish described genera and species are unknown, the dissociated columnals and pluricolumnals commonly cannot be correlated with previously recognized fossil crinoid taxa. Extensive surveys of crinoids with attached columns in several museum and university collections, including the large Springer collection in the U.S. National Museum, support this conclusion. Integration of systematic paleontological classification based on studies of "whole" fossil crinoids and disarticulated remains of fossil crinoids is accordingly seriously impeded.

Morphologically, all columnal articularia are divisible into two parts; **lumen** (pl., **lumina**), which is the opening in the plane of the articularium of the axial canal that traverses each columnal longitudinally, and **zygum** (pl., **zyga**), which is the entire area of the articularium outside of the lumen (Fig. 1). The zygum (Gr., bond or yoke) bears the ligament fibers that unite contiguous columnals.

The lumen may be extremely minute, or oppositely, so large that the surrounding zygum is reduced to a narrow band. The transverse shape of the lumen commonly is circular but it may be elliptical, pentagonal, quinquelobate, or pentastellate (see Fig. 5). Rarely, it is accompanied by accessory perforations which are isolated passageways for nerves, nutrient-bearing canals, and extensions of the so-called chambered organ within the theca.

In pentamer and circular stems, the zygum almost invariably includes a tract characterized by grooves **crenellae** (sing., **crenella**) and ridges **culmina** (sing., **culmen**). The whole tract is termed **crenularium**. **Crenulae** (sing., **crenula**) is a convenient designation for collective reference to combined crenellae and culmina. Some columnals are characterized by a narrow peripheral ridge termed **articular rim**.

Parts of columnal articula commonly lack crenulae and these, located between the inner border of the crenularium and edge of the lumen, in circular and pentagonal columnals consist either of an undivided flat to nearly flat space (**areola**) or a narrow to moderately broad elevated tract (**perilumen**) next to the lumen in addition to an areola (Fig. 1, *1b*). Rarely, the crenularium extends to the perilumen, an areola being absent. If both perilumen and areola are lacking, the crenularium extends to borders of the lumen.

Many columnals, especially nodals, have small or large extrafacetal areas surrounding the articula. These are named epifacetal tracts, or **epifacets** (Fig. 2, 2).

In some transversely circular crinoid stalks moderately large cirri with wide, low proximal cirrals are given off by a pair of columnals which may be distinguished as binodals and then the apposed articula of the **binodal** bear radially disposed furrows leading from the axial canal of the column to that of the cirrus. These furrows, called **fossulae**, differ from adjacent crenellae in their greater width and depth, in leading to the cirrus axial canal, and in reaching the columnal lumen, unlike the generally shorter crenellae. The cirrus scars on the latera of binodals may impinge on adjacent internodal latera.

### SUTURES AND TYPES OF COLUMNAL ARTICULATION

The articula of columnals and cirrals are held together by ligament fibers with allowance of considerable mobility in stalks and most cirri but very little flexion of many stalks. The externally visible edges of articula are called **sutures** (Fig. 2, 1). They are smooth or coarsely to finely crenulate.

Actually, it is appropriate to distinguish **internal sutures**, defined as the junction of contiguous columnals throughout the areas of apposed articula inside of their peripheries, as well as **external sutures**. In longitudinal sections internal sutures appear to be linear and depending on articular features intersected, they may be even or uneven, some partly crenulate and some with localized angulations or other irregularities.

Some columnals have articula entirely devoid of markings. Their smooth plane surface fits tightly against the similarly featureless articulum of a contiguous columnal. Such juncture is termed **synostosis** and the type of articulation **synostosomal** (Fig. 2, 3, *B*). Differential movement of synostosially united columnals is minimal and separation of them after death of the crinoid is relatively easy.

The most common type of articulation in cylindrical and pentagonal crinoid stems provides an interlocked arrangement of the crenulae of adjoining columnals, with culmina of one facet into crenellae of the other. The

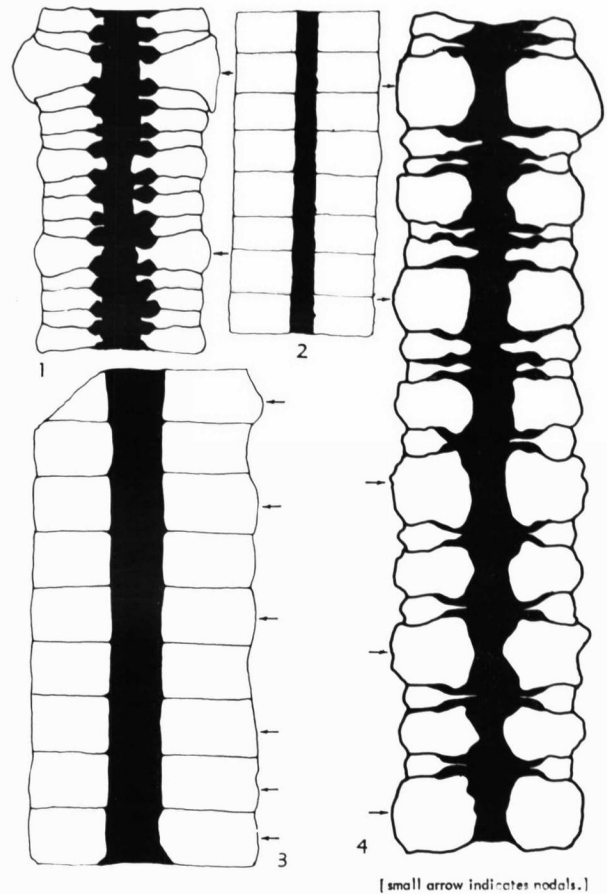


FIG. 3. Median longitudinal sections of pluricolumnals showing (1, 4) nature of complex axial canal (black), with internal sutures, claustra, jugula, and spatia and contrasting straight-walled simple axial canal (2-3),  $\times 3$ . [Nodals marked by small arrows; type species of genera indicated by asterisk (\*)].—1. *Heterostelechus keithi* MILLER, n. sp., from Gunsight Limestone, Upper Pennsylvanian, in McCulloch County, Texas (specimen E 706-1).—2. *Mooreanteris waylandensis* MILLER, n. gen., n. sp., from Wayland Shale, Upper Pennsylvanian, in Eastland County, Texas (specimen E 733-31), each columnal bearing cirripores and on this basis interpreted as nodal.—3. *Floricyclus granulatus* MOORE & JEFFORDS, n. gen., n. sp., from Wayland Shale, Upper Pennsylvanian, in Stephens County, Texas (specimen E 682-1), straight-sided axial canal having apparently wide axial canal because section intersects stellate lobe.—4. *Heterostelechus texanus* MOORE & JEFFORDS, n. gen., n. sp., from Waldrip Limestone, Lower Permian, in Coleman County, Texas (specimen E 62B-11), showing well-defined noditaxes and complex axial canal.

type of union is defined as **symplexy** (**symplectial**) (Fig. 2,3,E), though generally it has been referred to as **syzygy** (**syzygial**) by authors. True syzygy (Fig. 2,3,F), is characterized by meeting of the culmina of apposed facets, with depression of the crenellae occupied by ligament, so that sutures have a finely beaded appearance. Syzygial articulations are common in the arms of many crinoid, especially Articulata, but not in stems. Ill-defined symplectial articulations of columnals are distinguished as **cryptosymplectial** and such articulation is termed **cryptosymplexy**.

Columnals of elliptical outline and some with transversely circular section have a rather flexible articulation, in which, however, differential movements of adjoined columnals is confined to a plane disposed at right angles to a median **fulcral ridge** extending across the articulum (see Fig. 5; 9, Pl. 3, fig. 8-10; 9, Pl. 4, fig. 4\*7). The stem may bend back and forth in this direction at each intercolumnal articulation and progressive or abrupt shifting in orientation of the fulcral ridges on successive articula may provide for movement in different directions (9, Pl. 6, fig. 6-11). In columnals with elliptical articula the fulcral ridge invariably is located on the major axis of the ellipse. Descriptions of columnals of this type should record the angular **divergence of fulcral ridges** on the two opposite articula, for this may have value in discrimination of genera and species. Union of columnals with one another in this way is termed **synarthry** and the type of articulation **synarthrial** (also designated as **bifascial articulation**). It is confined to some camerates (Paleozoic) and articulates (Mesozoic-Cenozoic). Weak, ill-defined articulations of synarthrial type are differentiated as **cryptosynarthrial** representing connection classed as **cryptosynarthry**.

Elliptical columnals differ from other types in having only a rudimentary crenularium or none at all. The outer margin of the facet may be featureless or marked by a somewhat elevated narrow rim. The long axis of the facet coincides with the location of a generally prominent fulcral ridge, which is adjoined on opposite sides by broad, essentially smooth ligament areas known as **bifascial fields** (9, Pl. 4, fig. 4\*7). The lumen almost invariably is a small circular to slightly elliptical opening medially placed on the fulcral ridge. The ratio of the short to long axis of the facet provides a

shape index which is useful; as for other facets, measurements preferably are stated in terms of radii. The shape indices may range from less than 28 (MOORE, 1939, p. 229) to at least 96 (circular stems have value of 100).

Special terminology is employed for the articular facets of some columnals of the pentamer group, chiefly Mesozoic and Cenozoic in age. These commonly have a strongly petaloid arrangement of the very short crenulae, distributed around five ovoid smooth areas, termed **petals**, which are designated as **floors** (Fig. 1,2a). The floors may be flat and nearly even with the crenulae, gently concave or slightly convex. Smooth areas between the petaloid crenulae are known as **radial spaces**, because their position is radial, the petals being interradiial. The whole pattern sometimes is designated as a **petalodium**.

The facets of crescentic, trapezoidal, and other special shapes of columnals display varied sorts of morphological features which correspond only in part to those of circular, elliptical, and pentagonal stems.

### AXIAL CANALS AND INTERNAL STRUCTURES OF COLUMNALS

Morphological features of the axial canal and internal structure of crinoid columnals have considerable importance for taxonomic studies based on dissociated stem parts.

The **axial canal** generally penetrates the exact center of crinoid columns longitudinally (Fig. 3), but it may be located slightly to very appreciably off center (9, Pl. 20, fig. 3, \*9-10). In transverse shape, as seen in cross sections normal to its axis and as shown by outline of the lumen on articular surfaces, the axial canal varies from perfectly circular (9, Pl. 12, fig. \*9; 9, Pl. 23, fig. \*2) to weakly quinquelobate (9, Pl. 3, fig. \*12; 9, 11, \*5), sub-pentagonal to sharply angled pentagonal, and short- to long-rayed pentastellate with truncate, rounded, or narrowly pointed extremities (9, Pl. 3, fig. 7; 9, Pl. 25, fig. \*10, \*15; 9, Pl. 26, fig. 9-13). Other shapes are elliptical to almost linear. In size, the canal ranges from so diminutive as to be barely discernible to a diameter only a little smaller than that of the columnals, which then are reduced to narrow annuli.

Studied in median longitudinal sections, columnal axial canals are classifiable as **simple** or **complex** (Fig. 3,

### EXPLANATION OF PLATE 1

#### Bulk Collecting of Fossil Crinoid Remains

#### FIGURES

1. Weathered slope at outcrop of Belknap Limestone Member, Thrifty Formation, Upper Pennsylvanian, in Texas (loc. Pdq), with many dissociated crinoid fragments suitable for wire-brush sweeping as effective means of bulk collecting and loading in sample sack (lower right) (bands on hammer handle 0.1 ft. wide).
2. Washed and screened concentrate of crinoid columnals and pluricolumnals from New Providence Formation, Lower Mississippian, at Button Mould Knob, south of Louisville, Kentucky (loc. Maa), *ca.*  $\times 1$ .



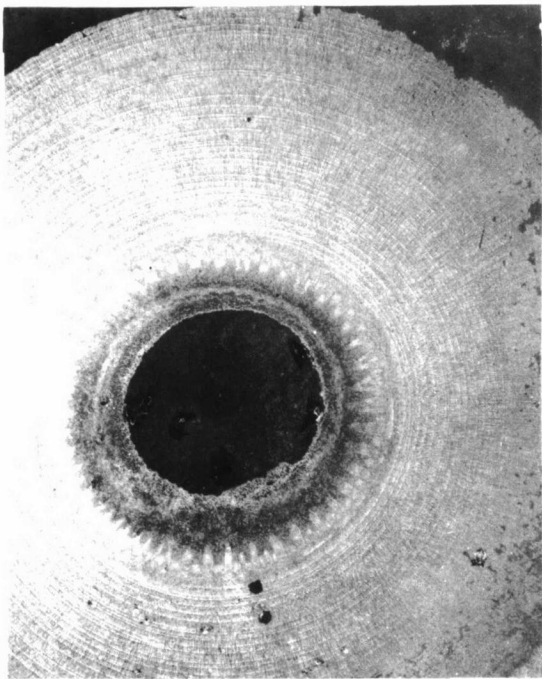


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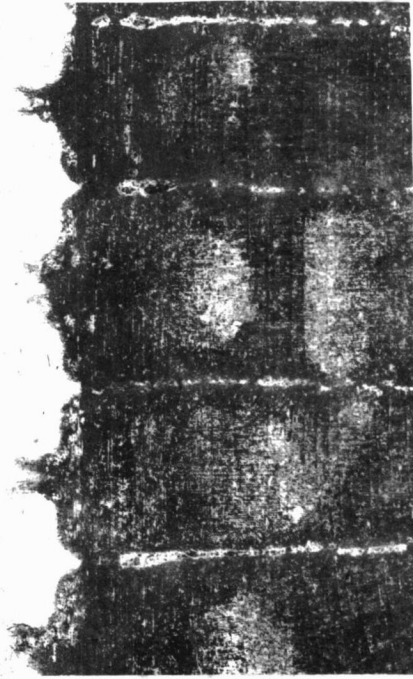


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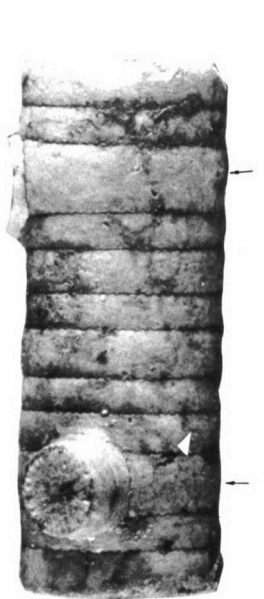
Moore, Jeffords, & Miller--Morphological Features of Crinoid Columns



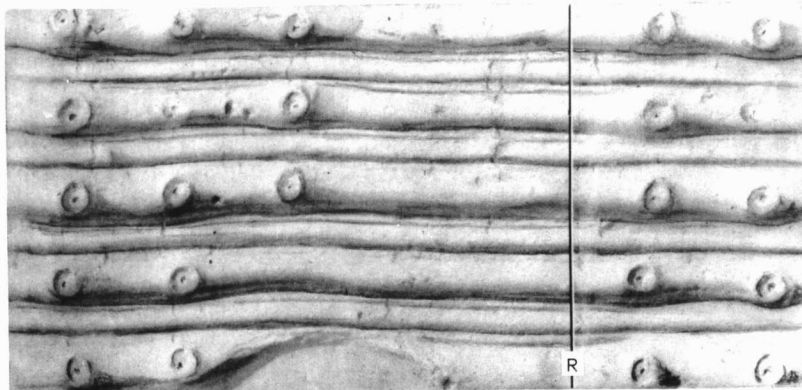
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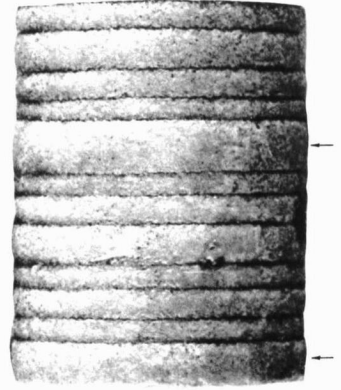


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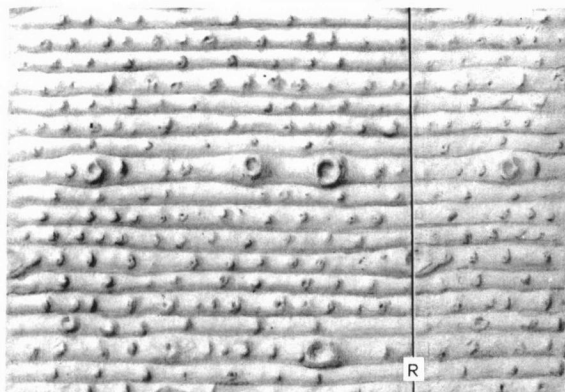


\*5

*Blothronagma* \*cinctutum

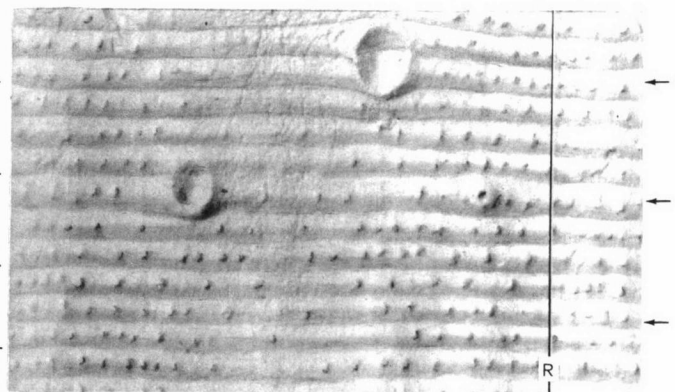


*Cyclocaudex* plenus (1-4)



\*6

*Baryschyr* \*anosus (\*6-7)



7

4; Pl. 3, \*1b, 4, 6-9; Pl. 4, fig. 7) and extensive observations indicate that this distinction may express both ontogenetic and taxonomic differences. Simple axial canals are typically straight-sided, through-going passageways that lack noteworthy localized expansions or constrictions. Complex ones possess varied sorts of intercolumnally located expansions, termed **spatia** (sing., **spatium**), and mid-columnally placed constrictions, called **claustra** (sing., **claustrum**, obstruction) (Pl. 3, fig. 1b, 4, 9a; Pl. 4, fig. 7). As seen in longitudinal sections of pluricolumnals, the spatia may be low or tall and laterally (peripherally) rounded, truncate, or sharp-pointed. The claustra exhibit longitudinal profiles ranging from clavate, angularly truncate, to bluntly or sharply lanceolate. Adaxial surfaces of the claustra may be smooth or uneven, with small denticle-like projections, and they may be convex, essentially straight, or somewhat concave. The locally constricted part of a complex axial canal, between adax-

ially facing edges of opposed parts of any given claustrum (Pl. 3, fig. 9a), is called **jugulum** (pl., **jugula**), signifying throat. In transverse shape, jugula are commonly stellate, with five narrow rays indenting the claustrum (Pl. 3, fig. 8). Thickened borders of a claustrum next to rays of a jugulum are termed **jugular ramparts** and in facet views of some well-preserved columnals these appear as subtriangular elevations between rays of the jugulum, all below the level of the luminal margin on the articulum (Fig. 4).

Cross sections of columnals, both transverse and longitudinal, are requisite for determination of internal structural features. Properly located transverse sections at or near the mid-height of nodals are likely to reveal one or more canals extending from the columnal axial canal to an attachment articulum of a cirrus or to articula of cirri. These intracolumnal passageways are named **canaliculae** (sing., **canalicula**) (9, Pl. 26, fig. 14). Pas-

## EXPLANATION OF PLATE 2

### Sections, External Side Views, and Replicas of Crinoid Pluricolumnal Rolls (Impressions made on molding clay.)

[Nodal columnals indicated by small arrows; asterisks (\*) denote type species of genera and type specimens of species]

#### FIGURES

- 1,2. Microstructure of crinoid columnals providing evidence of growth increments; parts of transverse and longitudinal sections of *Cyclocaudex plenus* MOORE & JEFFORDS, n. gen., n. sp., from Belknap Limestone (1, UKPI-Pdq175) and Wayland Shale Member, Graham Formation (2, UKPI-Pt1001), both Upper Pennsylvanian, in Texas.—1. Projection of thin section showing radial alignment of honeycomb microcells crossed by concentric growth lines resembling tree rings, *ca.*  $\times 7$ .—2. Projection of acetate peel showing horizontal and vertical alignments of honeycomb microstructure which record expansion of columnals during growth, internal intercolumnal sutures marked by prominent light bands, forked longitudinal sections of claustra directed toward axial canal (light area at left), *ca.*  $\times 6$ .
- 3,4. Side views of pluricolumnals belonging to *Cyclocaudex plenus*, specimens (E732-57, E5-58) collected from Wayland Shale in McCulloch and Coleman Counties, Texas.—3. Specimen with noditaxis of 7 columnals (instead of normal 8, consisting of nodal + 7 internodals), tertinternodal (3IN) expectable next above lower cirrinodal entirely concealed or lacking,  $\times 3.5$ .—4. Specimen with nodals lacking cirrus scars (thus distinguished as nudinodals) and noditaxis also lacking one tertinternodal,  $\times 3.5$ .
- 5-7. Replicas of crinoid pluricolumnal rolls consisting of impressions made in molding clay by specimens rolled

across smoothed surface of clay so as to show sides (latera) of columnals around their entire circumference in manner comparable to a Mercator projection of the earth's surface. Of course, convexities and prominences on sides of columnals produce depressions on the clay and concavities such as grooves along sutures and hollowed cirrus scars are represented on the clay by elevations. Oblique lighting of the impressed clay from 4 o'clock position and inversion of photographs to give apparent lighting from 10 o'clock serve to reverse topography of the clay impression visually. Illustrated examples represent two species from the Dornick Hills Formation, Middle Pennsylvanian, in southern Oklahoma (loc. Pca). In each figure repeat position of left margin is indicated at right by vertical line and letter "R" (for repeat).—\*5. *Blothronagma \*cinctutum* MOORE & JEFFORDS, n. gen., n. sp., impression of type specimen (UKPI-\*Pca18a), showing aligned cirrus scars in three rays and lack of scars in other two rays,  $\times 1.7$  (orientation same as in side views of type specimen, Echinodermata, Art. 9 (Pl. 15, fig. \*2a-c).—\*6,7. *Baryschyr \*anosus* MOORE & JEFFORDS, n. gen., n. sp., impression of type specimen (UKPI-\*Pca21b) and of another example (UKPI-Pca20d), corresponding to side views given in Echinodermata, Art. 9 (Pl. 14, fig. \*6-7, except that the roll impression and side view of the type specimen are inverted with respect to each other),  $\times 1.7$ .

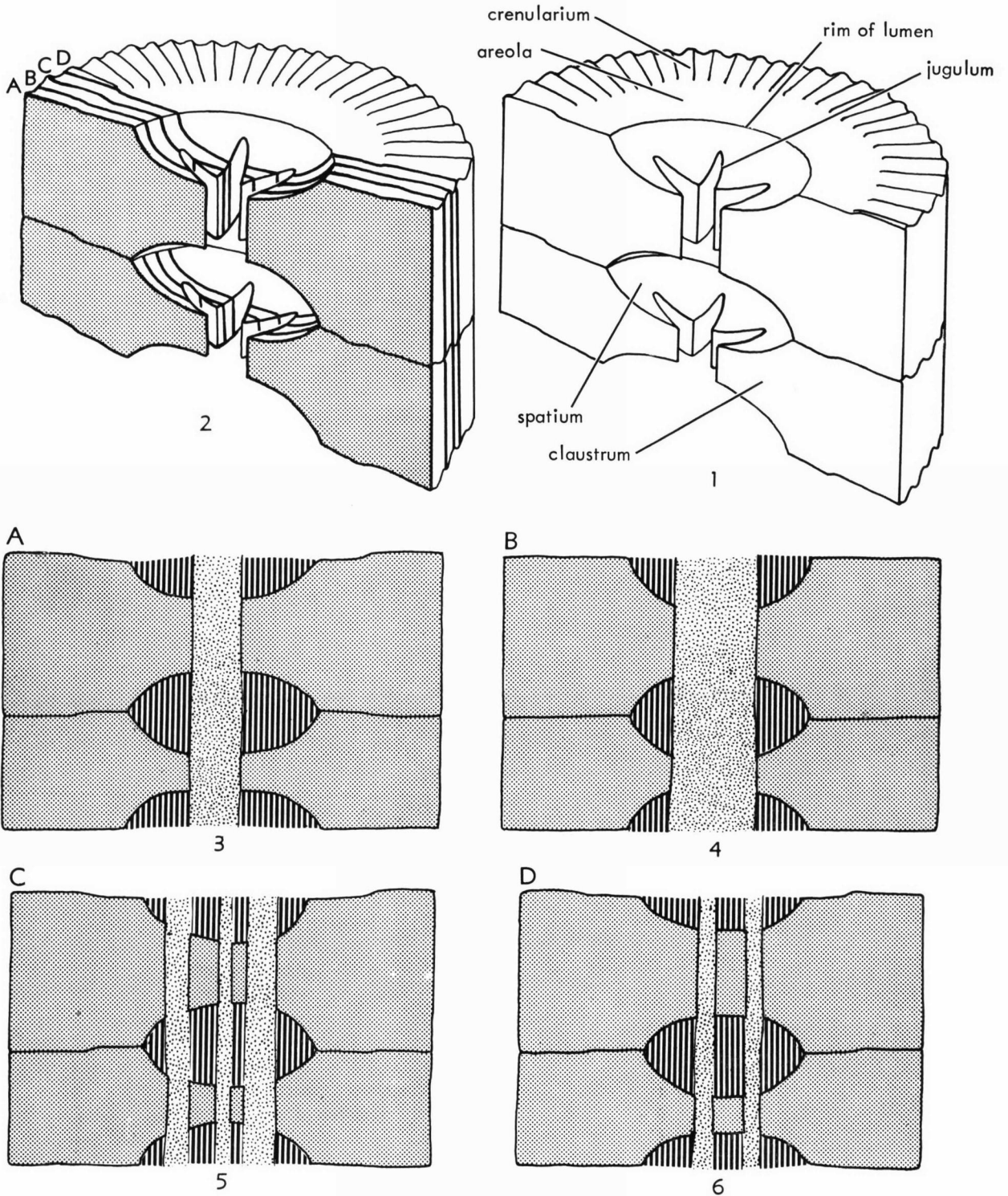


FIG. 4. Features of complex axial canal with accompanying longitudinal sections of pluricolumnal (diagrammatic).

1. Oblique view of medially sectioned specimen showing terminology, large circular lumen (intercept of axial

canal in plane of articulum) marking outer limit of a spatium, sloping curved floor of spatium formed by

sageways from the columnal axial canal to cirri may also be intercolumnal, in grooves (**fossulae**) of the apposed columnal articularia (9, Pl. 12, fig. 7). Transverse sections of both nodals and internodals of heteromorphic columns and of any columnal of a homeomorphic column are likely to show significant microstructural characteristics such as concentric growth lines which resemble tree rings and they may allow identification of obscure or strongly defined differentiation of outer (**cortical**) and inner (**medullary**) portions of the columnal (Pl. 2, fig. 1; 9, Pl. 3, fig. \*2b, \*11b). The boundary between these regions may be gradational or quite sharp.

Longitudinal sections of columnals and especially of pluricolumnals are best suited to reveal microstructural attributes of these skeletal parts, as well as important features of open-space divisions of the axial canal (**spatia**, **jugula**) and bordering medullary portions of columnals (**claustra**, **jugular ramparts**). In some longitudinally sectioned fossil crinoid columns, each of its component articulated elements appears to consist of uniformly dense calcite, with or without discernible honeycomb microstructure (Pl. 3, fig. 9a,b). Possibly this reflects mode of preservation more than anything else. Numerous well-preserved columnals seen in longitudinal section exhibit a dense calcitic cortex and distinctly spongy or microlamellate to microreticulate medulla. This latter region commonly is iron-stained or otherwise differentiated in color so as to show a finely banded structure with the bands arranged parallel to adaxial and intercolumnal borders of the columnal. Also, sections of a few stems display strongly marked differentiation of a narrow adaxial zone of dense calcite (correlated with perilumina of articular surfaces) and a relatively broad next abaxial zone of spongy nature (correlated with areolae of the articularia). The dense zone surrounding the axial canal is distinguished as **inner medulla** and the spongy zone as

**outer medulla** (Pl. 4, fig. 7a-c). In these stems the cortex resembles the inner medulla.

An exceptional internal structure, the function of which we cannot plausibly guess, occurs in best-preserved pluricolumnals of an Upper Pennsylvanian crinoid from Texas (*Preptopremnum rugosum* MOORE & JEFFORDS, n. gen., n. sp.). Lower and upper parts of the medulla of each columnal contain moderately wide, low cavities which surround the axial canal with their major axes, as seen in longitudinal section, gently inclined to the horizontal. The cavities are named **cavannuli** (sing., **cavannulus**, hollow ring) (Pl. 4, fig. 7a-c). The inner (adaxial) extremities of cavannular pairs approach one another, whereas the outer (abaxial) extremities diverge. The cavities are separated from articular surfaces of the columnals and outer parts of the intercolumnar spatia by a thin wall of medullary tissue.

Another curious, very rarely preserved internal structure which has been observed in longitudinal sections of some Upper Pennsylvanian crinoid pluricolumnals (e.g., belonging to *Cyclocaudex plenus* MOORE & JEFFORDS, n. gen., n. sp., and *Preptopremnum rugosum*) is a smoothly straight-sided tube running through the center of the axial canal (10, Pl. 1, fig. 11). Its diameter equals that of the jugula. No skeletal walls surrounding the tube have been detected, existence of the tubular structure (possibly originally consisting only of soft parts) is defined by difference in coloration of materials in the tube (here simply called **axial tube**) and surrounding claustra and fillings of spatia.

Collectively, all of the described axial-canal structures have value in combination with articular and lateral characteristics for intercomparison of columnals and pluricolumnals which ultimately may lead to discrimination of fossil crinoid genera and species.

## XENOMORPHIC CRINOID COLUMNS

Many crinoid specimens, especially ones displayed in museum collections, have complete or nearly complete columns attached to the "head" or crown. Very commonly, these columns are so uniform in appearance from end to end, whether homeomorphic or heteromorphic,

that dissociated columnals and pluricolumnals derived from them cannot be separated into groups representing derivation from upper (proximal), intermediate, or lower (distal) regions of the complete stalk. In other crinoids, the proximal part of the stem (termed **proxis-**

- 
- claustral surface leading to pentastellate jugulum, vertical walls of which are formed by adaxial extremity of girdling claustrum.
2. Same pluricolumnal showing positions of four longitudinal sections, median section (*A*) in front of drawing, others (*B-D*) parallel to it in off-median positions and thus intersecting stellate jugular passageway in manner yielding different appearance of sections (3-6).

3. Median section (*A*), solid stereom gray tone, inferred extension of chambered organ and accompanying soft structures of axial tube in jugula and central part of spatia stippled, and ligament-filled annulus of spatia vertically ruled.
4. Section in plane *B* (patterns as in 3).
5. Section in plane *C* (patterns as in 3).
6. Section in plane *C* (patterns as in 3).

tele) perceptibly differs from intermediate (**mesistele**) and distal (**dististele**) portions of the stalk. Such columns with morphologically differentiated regions are definable as **xenomorph** (*xeno-*, foreign) since columnals and pluricolumnals derived from different portions of the whole stem are perceptibly dissimilar (foreign) to one another (Pl. 4, fig. 1-6).

Since the proxistele portions of all crinoid columns are last-formed and the dististele parts are earliest-formed, differences between them have ontogenetic significance. Dissociated columnals and pluricolumnals derived from crinoid stalks with dissimilar proxistele, mesistele, and dististele parts may or may not be determinable as belonging to a single taxon. Naturally, this complicates discrimination of the kinds of crinoid animals which produced columnals and pluricolumnals of this sort. If seemingly distinct groups are described and named as fossil remains of separate taxa, ultimately some of them are likely to be determined as synonyms. This is not harmful if meanwhile the dissociated crinoid remains, like conodonts, are found to be trustworthy markers in stratigraphic correlation, and possibly significant fossils in paleontological interpretations.

The xenomorph nature of crinoid columns is especially common in genera of the subclass Flexibilia and

such Articulata as *Apiocrinites*, in which proxistele columnals tend to be much lower and wider than those of mesistele and dististele regions. This led TERMIER & TERMIER (1949, p. 55) to propose that crinoid stalks of this type be set apart as Pachyproxa, others found in most crinoids being designated as Tenuiproxa. These distinctions have morphological interest in relation to ontogeny but are negatively useful in classification, for they impede proper correlations of dissociated xenomorph stem parts. A few striking examples of xenomorph columns of flexible crinoids are illustrated (Pl. 4, fig. 1-6). STRIMPLE (1963, p. 15) has pointed to evidence that a small number of most proximal columnals in some fossil crinoids are differentiated from more distal ones by becoming permanently fastened to base of the theca in manner that would prevent introduction of new columnals between the "captured" proximal columnals (called **basilarids**) and the bottom-most plates of the theca. Such a condition has been convincingly described and illustrated by PHILIP (1961, p. 154) in a species of *Eucalyptocrinites* from the Lower Devonian of Tasmania, which shows narrowed basilarids accompanied by a girdling calcite plug within the basal concavity of the calyx. These unusual examples of xenomorphy in crinoid columns hardly illustrate problems encountered in most studies of dissociated stem parts but nevertheless are worthy of notice.

## MEASUREMENTS AND INDICES OF COLUMNALS AND PLURICOLUMNALS

### NATURE AND PURPOSE OF INDICES

Studies of columnals and pluricolumnals directed toward recognizing characteristics useful for differentiating genera and species of fossil crinoids require various measurements of morphological elements, normally recorded in millimeters, and means of expressing interrelationships between them. The latter can be given in mathematical terms as ratios, which for convenience are multiplied by 100 in order to convert them to whole numbers (Fig. 5). Such numbers are designated as **indices**. Letter symbols adopted for columnal and pluricolumnal morphological features and indices applicable to them are listed in the following tabulation.

#### *Symbols Employed for Columnal and Pluricolumnal Measurements and Indices*

areola—A  
 areolar index—Ai  
 articulum (articular facet)—F  
 articular (facetal) index—Fi  
 columnal—K  
 crenularium—C  
 crenularial index—Ci  
 diameter—D  
 divergence of fulcral ridges on opposite columnal articularia—DFR  
 epifacet (latus)—E  
 epifacetal (lateral) index—Ei  
 facet (articular)—F

facetal index—Fi  
 height (of columnal)—KH  
 height index—Hi  
 internode (internodal)—IN  
 internodal index—INi  
 latus (epifacet)—E  
 lateral (epifacetal) index—Ei  
 lumen—L  
 luminal index—Li  
 maximum—y  
 minimum—x  
 nodal—N  
 nodal index—Ni  
 noditaxis—NT  
 perilumen—P  
 periluminal index—Pi  
 radius—R  
 shape indices, areolar—ASi  
 columnal—KSi  
 crenularial—CSi  
 epifacetal (lateral)—ESi  
 facetal (articular)—FSi  
 luminal—LSi  
 periluminal—PSi  
 zygial—ZSi  
 zygum—Z

Determination of columnal indices is simplest in dealing with circular stem parts having articularia with lumen and extraluminal differentiated areas also limited by circles. Then diameter of the lumen can be measured

directly and each extraluminal (zygal) division of the articulum is ascertained by the addition of two opposite radii belonging to it.

Circular columnals and pluricolumnals possessing pentagonal, quinquelobate, or pentastellate lumina and possibly other parts of the articulum similarly shaped require the computation of mean diameters consisting of the sum of opposite maximum and minimum intercepts. The same applies to pentagonal, quinquelobate, and pentastellate columnals of pluricolumnals, with or without similarly shaped divisions of their articularia.

Stem parts with elliptical articularia call for measurements of maximum and minimum radii in order to derive figures for mean diameter.

## DESCRIPTION OF INDICES

### NODITAXIAL INDICES

Here belong nodal and internodal indices, of which one is reciprocal of the other.

*Nodal index (Ni)*.—Ratio of height of nodal (N) to total height of noditaxis (NT) containing it  $\times 100$ .  $Ni = NH/NTH \times 100$ .  $Ni + INi = 100$ .

*Internodal index (INi)*.—Ratio of total height of internode (IN) to that of noditaxis (NT) containing it  $\times 100$ .  $INi = INH/NTH \times 100$ . The sum of internodal and nodal indices invariably is 100.

### COLUMNAL INDICES

Measurements of width and height of columnals and width of the articular facet and epifacet furnish means for mathematical expression of ratios between them as indices. They include columnal height index, articular facet index, and epifacetal index (Fig. 5, Table 1).

*Columnal height index (KHi)* [also simply termed height index].—Ratio of columnal (K) height (H) to its diameter (KD)  $\times 100$ .  $KHi = KH/KD \times 100$  (Fig. 5, A-F). For columnals other than circular in transverse outline (e.g., elliptical, pentagonal, pentastellate), width is considered to be the sum of short radius (KR<sub>x</sub>) and long radius (KR<sub>y</sub>). The height index of such columnals is expressed as  $KHi = KH/(KR_x + KR_y) \times 100$  (Fig. 5, G-I).

*Articular facet index (Fi)* [also simply termed facet index].—Ratio of total width (diameter) of articular facet (articulum) to that of columnal  $\times 100$ . For circular facets this is expressed as  $Fi = FD/KD \times 100$  (Fig. 5, A-F). Computation of the facet index of pentagonal, pentastellate, quadrangular, and elliptical facets requires determination of mean diameter (FR<sub>x</sub> + FR<sub>y</sub>) and this may apply to diameter of the columnal as well. For such columnals the index is expressed as  $Fi = (FR_x + FR_y)/KD \times 100$ , or  $Fi = (FR_x + FR_y)/(KR_x + KR_y) \times 100$  (Fig. 5, G-I). The facet index of a circular articulum borne by a non-

circular columnal is computed as  $Fi = FD/(KR_x + KR_y) \times 100$ .

*Epifacetal index (Ei)*.—Ratio of two radial intercepts of epifacet to total width (diameter) of columnal  $\times 100$  (Fig. 5, C, G-I).  $2ER/KD \times 100$ , or  $(ER_x + ER_y)/KD \times 100$ , or  $(ER_x + ER_y)/(KR_x + KR_y) \times 100$ , or  $2ER/(KR_x + KR_y) \times 100$ .

### FACET-PART INDICES

Morphological divisions of columnal articularia may be measured in manner permitting expression of their relationships as mathematical indices, thus providing convenient means of indicating comparisons among all sorts of facets. These facet-part indices include luminal index and its reciprocal called zygal index, periluminal index, areolar index, and crenularial index (Fig. 5, Table 1).

*Luminal index (Li)*.—Ratio of total width (diameter) of lumen to that of columnal articulum  $\times 100$  (Fig. 5). Depending on shapes of the lumen and articulum mean diameters may need to be determined for either or both. For a circular lumen the luminal index is determined as  $Li = LD/FD \times 100$  (Fig. 5, A-D), or  $LD/(FR_x + FR_y) \times 100$  (Fig. 5, G, I). A pentagonal or pentastellate lumen of a circular facet is indicated as  $Li = (LR_x + LR_y)/FD$  (Fig. 5, E-F), and a noncircular lumen belonging to a noncircular facet is represented by  $Li = (LR_x + LR_y)/(FR_x + FR_y) \times 100$  (Fig. 5, H, J). The sum of luminal and zygal indices must equal 100.

*Zygal index (Zi)*.—Ratio of total width (diameter) of zygum (possibly sum of minimum and maximum radial intercepts) to that of articulum  $\times 100$  (Fig. 5, A-J).  $Zi = ZD/FD \times 100$ , or  $(ZR_x + ZR_y)/FD \times 100$ , or  $(ZR_x + ZR_y)/(FR_x + FR_y) \times 100$ , or  $ZD/(FR_x + FR_y) \times 100$ .

*Periluminal index (Pi)*.—Ratio of two radial intercepts of perilumen (possibly PR<sub>x</sub> + PR<sub>y</sub>) to total width (diameter) of columnal articulum (possibly FR<sub>x</sub> + FR<sub>y</sub>)  $\times 100$  (Fig. 5, C).  $Pi = 2PR/FD \times 100$ , or  $(PR_x + PR_y)/FD \times 100$ , or  $(PR_x + PR_y)/(FR_x + FR_y) \times 100$ , or  $2PR/(FR_x + FR_y) \times 100$ .  $Pi + Ci + Li$  (and possibly + Ai) = 100.

*Areolar index (Ai)*.—Ratio of total width (diameter) to that of columnal articulum (facet)  $\times 100$ . For areolae having elliptical, pentagonal, quinquelobate, or pentastellate outlines, and peripherally circular ones adjoining pentagonal to pentastellate perilumina or lumina, mean diameter of the areola is used (sum of minimum and maximum radial intercepts) (Fig. 5, E-J).  $Ai = 2AR/FD \times 100$  or  $(AR_x + AR_y)/FD \times 100$ . It may be noted that invariably  $Ai + Ci + Li$  (possibly + Pi) = 100.

*Crenularial index (Ci)*.—Ratio of total width (diameter) of crenularium to that of columnal articulum (facet)  $\times 100$ . Again mean diameters may need to be used for either the crenularium or facet or both (Fig. 5).  $Ci = 2CR/FD \times 100$ , or  $(CR_x + CR_y)/FD \times 100$ , or  $(CR_x + CR_y)/(FR_x + FR_y) \times 100$ , or  $2CR/(FR_x + FR_y) \times 100$ . The sum of  $Ci + Li$  (and possibly  $Ai + Pi$ ) = 100.

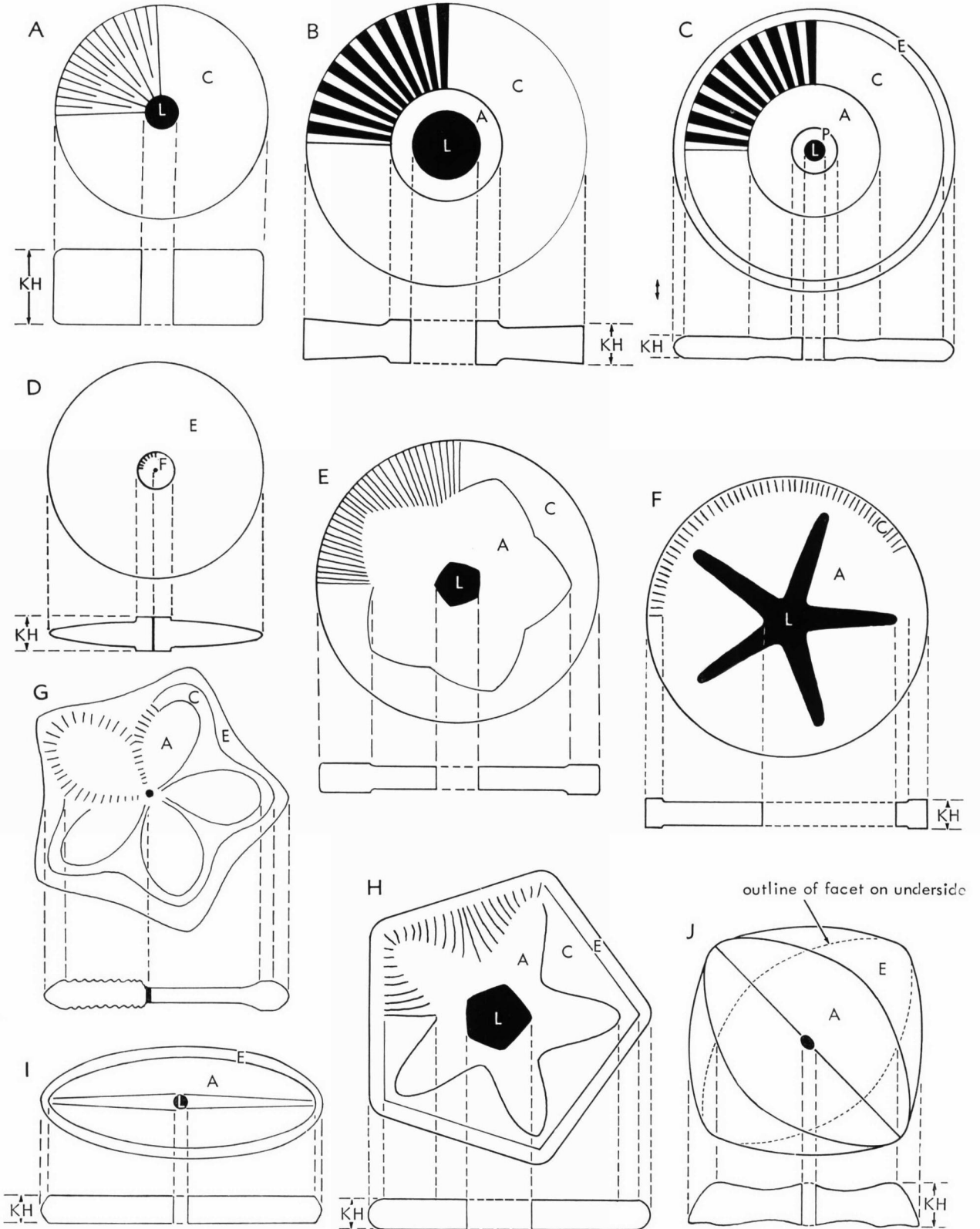


FIG. 5. Diagrammatic facetal views and median longitudinal sections of different sorts of columnals designed to illustrate determination of various columnal indices given in tabulation placed on opposite page.



TABLE 1. Columnal Indices Determined from Measurements of Specimens Illustrated in Figure 5.

LD / FD = Li ◀	(LRx + LRy = LD) / (FRx + FRy = FD) = Li ◀
A 3.6 / 20.0 = 18.0	E (0.65 + 0.85 = 1.50) / (10.0) = 15.0
B 4.8 / 20.0 = 24.0	F (0.85 + 3.75 = 4.60) / (10.0) = 46.0
C 1.4 / 18.5 = 7.6	G 0.3 / (3.5 + 5.4 = 8.9) = 3.4
D 0.4 / 3.6 = 11.5	H (0.90 + 1.15 = 2.05) / (4.0 + 5.0 = 9.0) = 22.8
2PR / FD = Pi ◀	(ARx + ARy = AD) / (FRx + FRy = FD) = Ai ◀
C 2.0 / 18.5 = 10.8	E (2.10 + 3.20 = 5.30) / (10.0) = 53.0
2AR / FD = Ai	F (0.45 + 3.50 = 3.95) / (10.0) = 39.5
B 3.1 / 20.0 = 15.5	G (0.40 + 4.14 = 4.54) / (3.5 + 5.4 = 8.9) = 51.0
C 6.0 / 18.5 = 32.4	H (0.90 + 3.20 = 4.10) / (4.0 + 5.0 = 9.0) = 45.6
D 2.0 / 3.6 = 55.5	(CRx + CRy = CD) / (FRx + FRy = FD) = Ci ◀
2CR / FD = Ci ◀	E (1.05 + 2.10 = 3.15) / (10.0) = 31.5
A 16.4 / 20.0 = 82.0	F 1.3 / (10.0) = 13.0
B 12.1 / 20.0 = 60.0	G (0.80 + 3.25 = 4.05) / (3.50 + 5.40 = 8.9) = 45.5
C 9.0 / 18.5 = 48.7	H (0.60 + 2.10 = 2.70) / (4.00 + 5.00 = 9.0) = 30.0
D 1.2 / 3.6 = 33.3	(FRx + FRy = FD) / (KRx + KRy = KD) = Fi ◀
2ER / KD = Ei ◀	G (3.5 + 5.4 = 8.9) / (4.5 + 5.5 = 10.0) = 89
C 1.5 / 20.0 = 7.5	H (4.0 + 5.0 = 9.0) / (4.5 + 5.5 = 10.0) = 90
D 16.4 / 20.0 = 82.0	KH / (KRx + KRy = KD) = KHi ◀
KH / KD = KHi ◀	E 2.2 / (10.0) = 22.0
A 7.0 / 20.0 = 35.0	F 1.1 / (10.0) = 11.0
B 1.5 / 20.0 = 7.5	G 1.2 / (4.25 + 10.0 = 14.25) = 8.4
C 3.0 / 20.0 = 15.0	H 3.7 / (9.55 + 11.6 = 21.15) = 17.4
D 2.4 / 20.0 = 12.0	
(LRx + LRy = LD) / (FRx + FRy = FD) = Li ◀	Li + Ai + Ci = 100.0
I (0.60) / (3.00 + 9.50 = 12.50) = 4.8	E 15.0 + 53.0 + 31.5 = 99.5
J (0.50 + 0.75 = 1.25) / (6.80 + 11.65 = 18.45) = 6.8	F 46.0 + 39.5 + 13.0 = 98.5
	G 3.4 + 51.0 + 45.5 = 99.9
	H 22.8 + 45.6 + 30.0 = 98.4
[A (areola) here treated as equivalent to bifascial fields]	
(ARx + ARy = ARD) / (FRx + FRy = FD) = Ai ◀	Li + Pi + Ai + Ci + 100.0
I (2.4 + 9.0 = 11.4) / (3.0 + 9.50 = 12.50) = 91.5	A 18.0 + 82.0 = 100.0
J (6.5 + 10.7 = 17.2) / (6.8 + 11.65 = 18.45) = 93.0	B 24.0 + 15.5 + 60.0 = 99.5
(FRx + FRy = FD) / (KRx + KRy = KD) = Fi ◀	C 7.6 + 10.8 + 32.4 + 48.7 = 99.5
I (12.5) / (4.2 + 10.05 = 14.25) = 87.8	D 11.5 + 55.5 + 33.3 = 100.3
J (18.45) / (9.5 + 11.65 = 21.15) = 87.0	
(ERx + ERy = 2ER) / (KRx + KRy = KD) = Ei ◀	FRx / FRy = FSi ◀
I (0.45 + 1.2 = 1.65) / (14.25) = 11.6	I 3.0 / 9.5 = 31.5
J (0.0 + 4.2 = 4.2) / (21.15) = 19.9	J 6.8 / 11.65 = 58.4
KH / (KRx + KRy = KD) = KHi ◀	KRx / KRy = KSi ◀
I 1.8 / (14.25) = 12.6	I 4.25 / 10.00 = 42.5
J 3.7 / (21.15) = 17.5	J 9.50 / 11.65 = 81.5

- A. Relatively thick circular columnal with articular facet occupied by narrow circular lumen (L) and wide crenularium (C) (KH, columnal height).
- B. Thin circular columnal with large circular lumen surrounded by narrow areola (A).
- C. Thin circular columnal with narrow perilumen (P) and narrow epifacet (E) beyond crenularium.
- D. Circular columnal with small articulum (F) and very wide epifacet.
- E. Circular columnal with pentagonal lumen and broad, slightly pentastellate areola.

- F. Circular columnal with strongly stelliform lumen and narrow peripheral crenularium.
- G. Pentagonal columnal with petaloid articular facet.
- H. Pentagonal columnal with large pentagonal lumen and pentastellate areola.
- I. Elliptical columnal with paired areolar areas (bifascial fields) divided by fulcral ridge occupying long axis of facet.
- J. Quadrangular (nodal) columnal with elliptical articular facets oriented differently on opposite sides.

## SHAPE INDICES

Mathematical expression of the shape of various morphological features of crinoid columnals can be given as ratios of small to large dimensions multiplied by 100 for statement as whole numbers like other indices described here. Because any circular or evenly annular shape is equidimensional ( $1/1 \times 100 = \text{index of } 100$ ), only shapes which depart from circularity are usefully considered. Among these may be columnal (transverse) shape index and shape indices for epifacet, facet, lumen, zygom, perilumen, areola, and crenularium (Fig. 5, Table 1).

*Columnal shape index (KSi)*.—Ratio of minimum columnal radius to maximum radius  $\times 100$  (Fig. 5, G-J, Table 1, I-J).  $KSi = KR_x / KR_y \times 100$ .

*Epifacetal shape index (ESi)*.—Ratio of minimum radius of epifacet (latus) to maximum radius  $\times 100$ .  $ESi = ER_x / ER_y \times 100$ .

*Articular (facetal) shape index (FSi)*.—Ratio of minimum articular radius to maximum radius  $\times 100$  (Fig. 5, G-J, Table 1, I-J).  $FSi = FR_x / FR_y \times 100$ . The shape index of all circular columnal articularia is 100, whereas that of a

broadly oval articularium may be 95 and that of a narrowly elliptical facet 20 or smaller. The shape index of an evenly pentagonal articularium is 81 and that of a strongly pentastellate one possibly less than 50.

*Luminal shape index (LSi)*.—Ratio of minimum radius of lumen to maximum radius  $\times 100$  (Fig. 5, E-F, H-J).  $LSi = LR_x / LR_y \times 100$ .

*Zygal shape index (ZSi)*.—Ratio of minimum radius of zygom to maximum radius  $\times 100$  (Fig. 5, E-J).  $ZSi = ZR_x / ZR_y \times 100$ .

*Periluminal shape index (PSi)*.—Ratio of minimum radius of perilumen to maximum radius  $\times 100$ .  $PSi = PR_x / PR_y \times 100$ .

*Areolar shape index (ASi)*.—Ratio of minimum areolar radius to maximum radius  $\times 100$  (Fig. 5, E-J).  $ASi = AR_x / AR_y \times 100$ .

*Crenularial shape index (CSi)*.—Ratio of minimum radius of crenularium to maximum radius  $\times 100$  (Fig. 5, E, G, H).  $CSi = CR_x / CR_y \times 100$ .

In a similar manner indices for morphological elements of the axial canal, such as jugulum, claustrum,

## EXPLANATION OF PLATE 3

## Longitudinal Sections and Features of Articularia and Latera of Crinoid Pluricolumnals

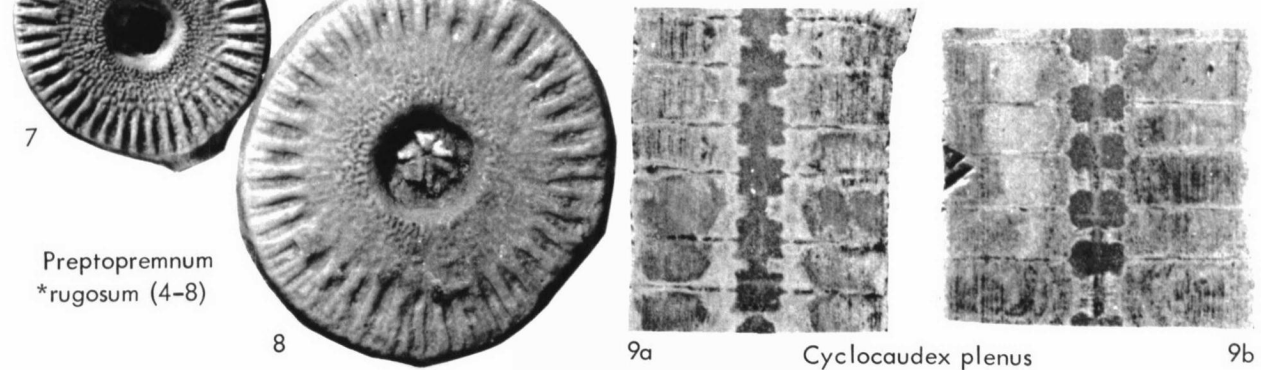
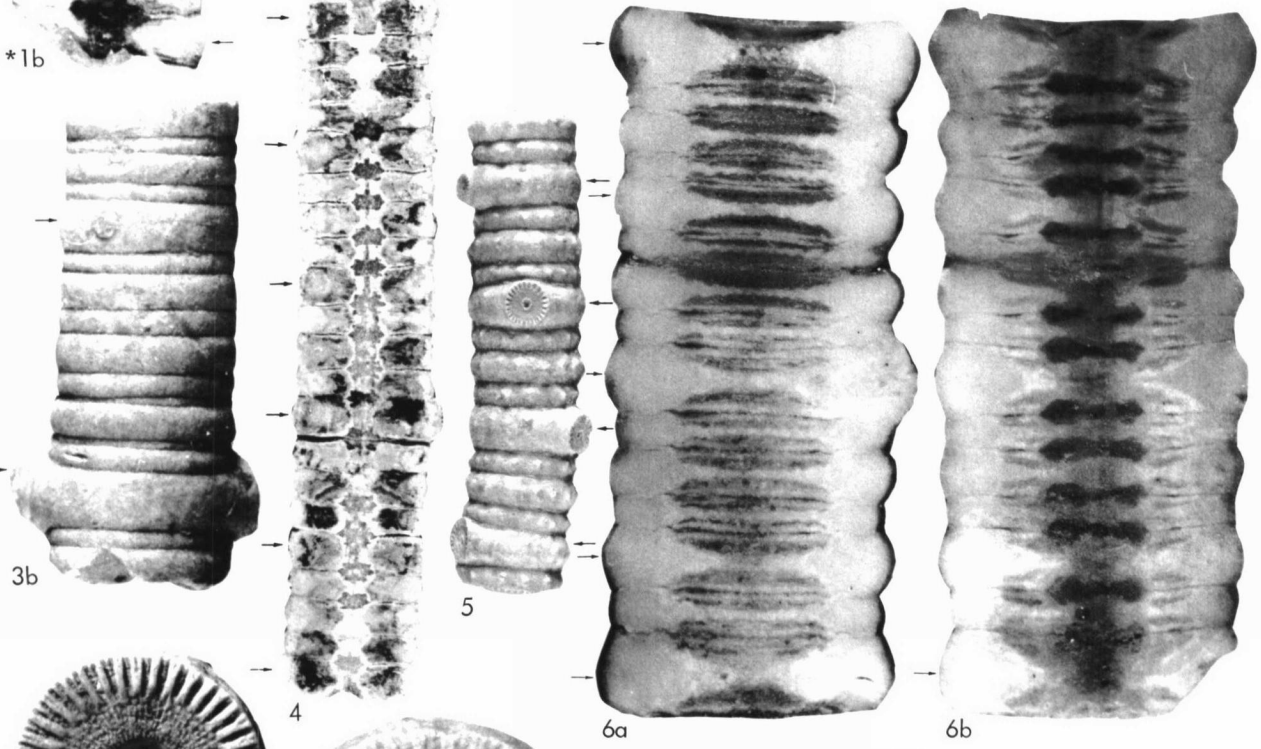
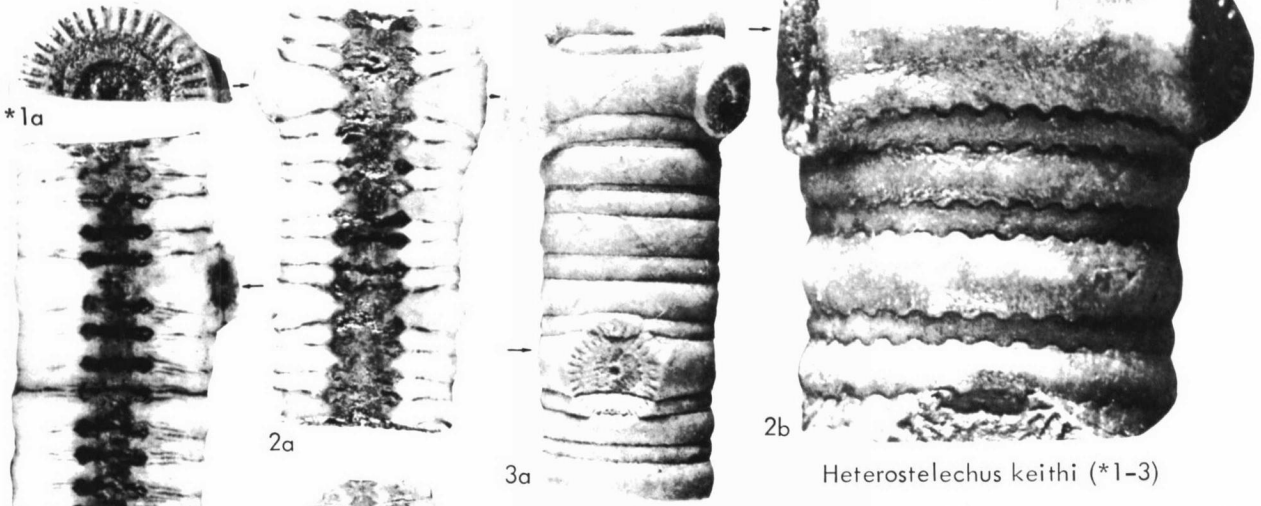
[Heteromorphic pluricolumnals (nodals marked by small arrows); asterisks (\*) denote type species of genera and type specimens of species]

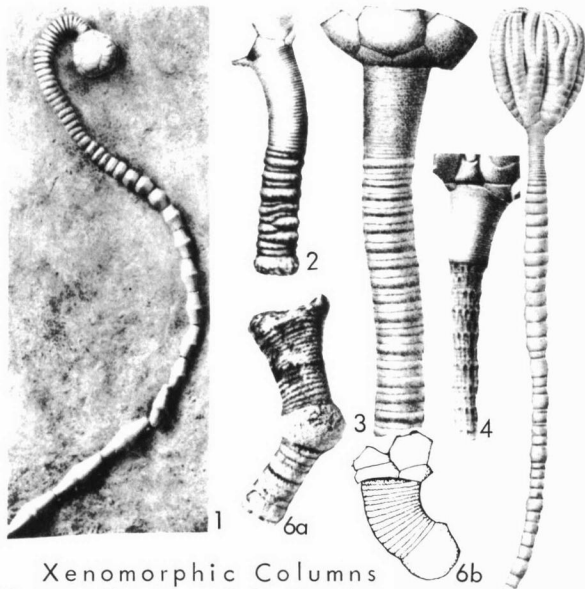
## FIGURES

- 1-3. *Heterostelechus keithi* MILLER, n. sp., from Gunsight Limestone and Wayland Shale Members of Graham Formation, Upper Pennsylvanian, in Texas.—\*1. Type specimen (Gunsight, E 706-14) showing (1a) half articularium with coarse crenulae and moderately wide, uneven areola and (b) median longitudinal section in which claustra, jugula, and spatia are evident, narrow dark lines adjacent to intercolumnal sutures seemingly thin, somewhat modified cavannuli of unknown function,  $\times 3.5$ .—2. Gunsight Limestone specimen (E706-1); 2a, median longitudinal section showing wavy internal sutures,  $\times 3.5$ ; 2b, noditaxis of 8 columnals (nodal at top, internode with 4 small 3IN, 2 slightly taller and wider 2IN, and single relatively large 1IN), coarsely crenulate sutures with intercepts of culmina and crenellae in vertically aligned position,  $\times 7$ .—3. Wayland Shale specimen (E5-51); 3a,b, opposite sides (also with top-and-bottom orientation reversed) of pluricolumnal with noditaxis containing 9 internodals, of which 2 thinnest ones are quartinternodals (4IN),  $\times 3.5$ .
- 4-8. *Preptopremnum rugosum* MOORE & JEFFORDS, n. gen., n. sp., from Wayland Shale Member, Graham Formation, Upper Pennsylvanian, in Texas.—4. Median longitudinal section of specimen (E672-71)

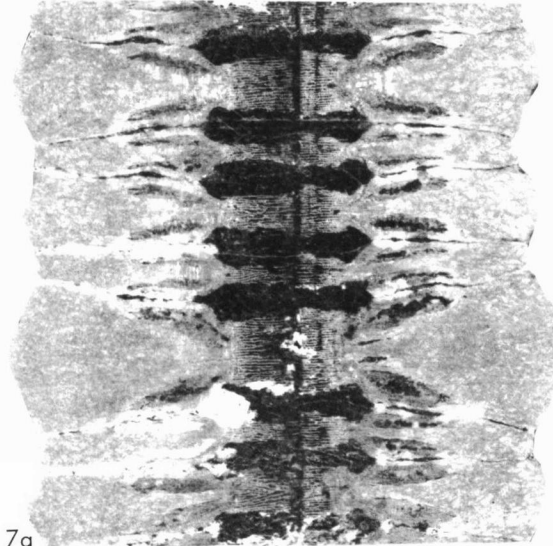
showing typical features of axial canal with intracolumnally placed jugula and claustra and intercolumnally placed spatia,  $\times 2$ .—5. Exterior of well-preserved pluricolumnal (E672-75) having 4 cirri-nodals and showing noditaxes of 4 (nodal + 3 internodals),  $\times 1.7$ .—6. Longitudinal sections of specimen (E706-0) showing well-marked claustra, jugula, spatia, and cavannuli; 6a, section cut in plane slightly removed from median position; 6b, same pluricolumnal sectioned medially; both  $\times 5$ .—7,8. Articularia of columnals (E722-4, E722-25) with crenularia tending to grade into areolae, wide subcircular lumina, each surrounding half-spatium of axial canal floored by claustrum (weathered in 7, well preserved in 8, which shows narrowly pentastellate jugulum bordered by subtriangular jugular ramparts),  $\times 3.5$ ,  $\times 4.5$ .

9. *Cyclocaudex plenus* MOORE & JEFFORDS, n. gen., n. sp., from Wayland Shale Member, Graham Formation, Upper Pennsylvanian, in Texas; 9a,b, longitudinal sections (E675-1) in median and slightly off-median planes showing adaxially truncate claustra surrounding jugula and intercolumnal spatia which appear quadrangular in cross section; vertical lamination of columnals produced by intersection of growth bands;  $\times 3.5$ .

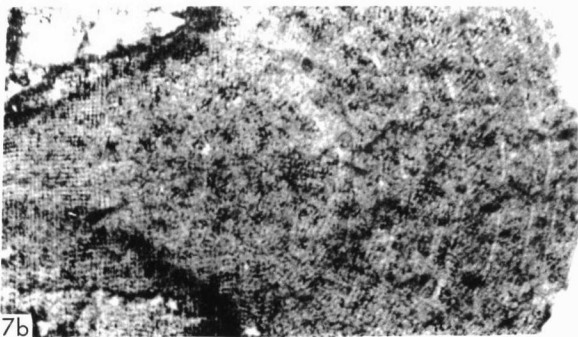




Xenomorphic Columns  
 1. Mespilocrinus. 2-3. Onychocrinus.  
 4-5. Taxocrinus. 6. Nevadacrinus.  
 (1-5, Miss., X0.85; 6, Perm., X1.7)



7a



7b

7. *Preptopremnum \*rugosum*, U.Penn., Texas. 7c



and spatium, can be computed, preferably in terms of ratios of their width to that of the axial canal (or lumen).

For characterization of different specimens, some in-

stances are more important than others. Accordingly, only those judged to be most significant generally are computed.

## MORPHOLOGICAL GROUPS OF COLUMNALS

Inasmuch as consideration of disarticulated skeletal remains of crinoids here is confined to those forming parts of the pelmata, chiefly columnals and pluricolumnals, first objectives in study are segregation of such main stem parts from holdfasts, if present in collections, and cirrals and pluricirrals, if they can be distinguished. Ordinarily, only columnals and pluricolumnals are to be dealt with and these, without meaningless separation of one from the other, are most conveniently divided into groups based on readily visible external characteristics. Transverse shape, features of the articula, relative size and outline of the lumen, and to some extent structural division of stem parts longitudinally serve for recognition of four reasonably clear-cut assemblages. These are designated as 1) **Pentameri**, 2) **Elliptici**, 3) **Cyclici** and 4) **Varii**, names which are almost self-explanatory. The groups do not correspond to recognized subclasses of the Crinoidea, for the Pentameri include representatives of the Camerata, Inadunata, and Articulata; the Elliptici contain stems of crinoids classified in the Camerata and Articulata; the Cyclici and Varii are distributed among all four crinoid subclasses, including the Flexibilia.

### PENTAMERI

Columnals and pluricolumnals of the Pentameri are distinctly fivefold in being pentagonal, quinquelobate, or pentastellate in transverse section and some are physically divided into pentameres by longitudinal sutures. These last include some circular and subcrescentic stems which are placed with the Pentameri because of their division into five segments. Also, stem parts having articula that display a prominent five-petaled or five-rayed pattern of grooves and ridges on the surface surrounding the axial canal are placed in this assemblage.

### ELLIPTICI

The Elliptici include crinoids with elliptical columnals among which the long axis may be little greater than the short one, as well as many with the long axis two or more times greater than the short axis.

The nature of the articulum aids in distinguishing elliptical columnals, for invariably this bears a fulcral ridge coinciding with the long axis and bisecting the

## EXPLANATION OF PLATE 4

### Xenomorphic Crinoid Stems and Sections of Pluricolumnals with Complex Axial Canals

[Asterisks (\*) denote type species of genera]

#### FIGURES

1-6. Xenomorphic crinoid columns,  $\times 1$  (1-5, Springer, 1920; 6, Lane & Webster, 1966).—1. *Mespilocrinus konincki* HALL, Burlington Limestone, Lower Mississippian, in Iowa, showing well-marked differences in columnals of proxistele, mesistele, and dististele regions.—2. *Onychocrinus diversus* MEEK & WORTHEN, also Burlington Limestone in Iowa, showing abrupt change of columnals beneath proxistele portion of stem.—3. *Onychocrinus pulaskiensis* MILLER & GURLEY, from Chesteran, Upper Mississippian, beds in Kentucky.—4. *Taxocrinus colleti* WHITE, from Borden Group, Lower Mississippian, in Indiana.—5. *Taxocrinus communis* (HALL), from Waverlyan beds, Lower Mississippian, in Ohio.—6a,b. *Nevadacrinus \*geniculatus* LANE & WEBSTER, Bird Spring Formation, Lower Permian, in southern Nevada, showing greatly enlarged columnal separat-

ing proxistele and mesistele regions of stem with articular facets in planes obliquely disposed to each other, thus producing abrupt geniculation of column. 7. *Preptopremnum \*rugosum* MOORE & JEFFORDS, n. gen., n. sp., Gunsight Limestone Member, Graham Formation, Upper Pennsylvanian, in Texas (loc. E706), projection of parts of median longitudinal thin section (E706-0) showing columnals not differentiated into cortical and medullary regions but with distinctive reticulolaminar microstructure of claustra and clearly discernible cavannular openings.—7a. Section showing general relationships, thickest columnal a nodal,  $\times 8.5$ .—7b. Peripheral part of nodal shown in 7a showing honeycomb microstructure and arcuate growth bands,  $\times 42$ .—7c. Section of median region showing claustra, jugula, spatia, and cavannuli,  $\times 42$ .

facet into two ligament fields, and hence termed bifascial. The artacula may be bordered by a rim or may be rimless, but in either type crenulations along the border are weak or absent. Some columnals classified as Elliptici actually are quadrangular in outline, although their articular facets are elliptical. The quadrangular shape is introduced by an angular shift in orientation of the fulcral ridges on opposite facets, a shift that may be as great as 90 degrees.

### CYCLICI

The Cyclici consist of cylindrical stems having subequal circular columnals or circular columnals of very unequal size. In both subgroups the peripheries of

columnals may be smooth and rectilinear, or evenly to asymmetrically convex in longitudinal profile, rounded or angulated, and margins may be modified by projecting tubercles, nodes, or spines. Rarely, sides of circular columnals are concave. Variations are many but all are characterized by regularity in the arrangement of crenulations around edges of their facets.

### VARIII

The Varii contain the varied sorts of stems that do not find a place in the other three main groups, and with them holdfast structures and miscellaneous dissociated plates of all kinds derived from the theca and arms of crinoids.

### CIRRUS FRAGMENTS

The laterally directed appendages of crinoid stems called **cirri** are nearly identical in morphological features to the stems that bear them, as they are composed of homeomorphic articulated segments (called **cirrals**, instead of columnals) having an axial canal. They gradually diminish in diameter away from the stem and taper to a point, which in modern free-swimming crinoids has

the curved form and sharp point of a cat's claw. The cirri are highly mobile, as least in a vertical plane that intersects the axis of the stem or theca, and they serve as tactile organs and for clinging. The articular facets commonly have very short crenulae around the margin. Most, but not all cirrals are circular in transverse section and they tend to have height equal to or greater than width.

### HOLDFASTS

The anchorage structures of stem-bearing crinoids, collectively termed **holdfasts**, are included among disarticulated skeletal remains because they are well known as fossils and nearly all are found alone with little or none of the stem preserved in attached position. Many are discoid, lobate, or digitate incrustations on shells, corals, and other crinoids, and if they lack distinctive

characters, merit little study. Some which do possess easily recognized features have been described and named (MILLER, 1874; SARDESON, 1908; SPRINGER, 1917; FENTON, 1929). The modified distal cirri of some crinoids which serve for fixation of the stalk to the substrate are termed **radicular cirri** or collectively defined as a **radix**. Commonly these holdfast cirri are branched, but some are unbranched.

### SUMMARY

Well-preserved dissociated fossil crinoid remains consisting of discrete columnals and groups of them joined together (pluricolumnals), possibly associated with cirrals and pluricirrals, which are much less common and mostly small in value, can be obtained in very great numbers by bulk-collecting methods. These are found with other fossils weathered from weakly consolidated marine deposits such as shale and shaly or crumbly limestone, brushed or swept together in heaps, and then washed, dried, sieved, and sorted in the laboratory. The abundance and variety of stem parts thus provided for study from many localities are surprising and a majority of them exhibit well-preserved morphological features which allow them to be classified.

The nature of the sides (latera) of pluricolumnals especially guides initial segregation of homeomorphic ones, composed of identical or near-identical columnals,

and heteromorphic specimens containing more or less evidently dissimilar columnals joined together. Individual loose columnals are grouped as well as possible by comparison with the pluricolumnals, using both characteristics of the latera and articular facets (artacula).

Very important are transverse shapes of the columnals and all features of the artacula, including relative size and shape of the lumen and nature of the zygum. Specimens with circular transverse section are readily separated from others of pentagonal or pentastellate form and elliptical stem parts, if present. With rare exceptions, circular columnals possess a crenularium, but its constituent culmina and crenellae may differ widely in number, height, length, prominence, and pattern of arrangement in different groups of specimens. The lumen of circular columnals is also circular very commonly. In very many it is bluntly to sharply pentastellate. In each shape group

every external morphological feature and combinations of them are used for step-by-step classification into divisions and subdivisions. Ultimately this leads to recognition of assemblages which with fair confidence can be judged to represent different fossil crinoid species.

Preparation of longitudinal and transverse sections of pluricolumnals has been found needful for determining significant internal morphological features of specimens, whereas individual columnals rarely, if ever, call for such sections. Polished sections and acetate peels are sufficient generally, but in addition we have made some thin sections and serial sections of crinoid stem parts. In this way the axial canals and associated medullary and cortical parts of columnals have been shown to possess morphological characteristics that vary considerably. Study of them has led to realization of need for terms for designating and describing them. Both external and internal characteristics of crinoid columnals have importance in taxonomic investigations.

## GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CRINOID STEM PARTS

The alphabetically arranged morphological terms applied to crinoid stem parts, including cirri and holdfast structures, incorporate several which are first used and explained in this article. These are distinguished by an accompanying asterisk (\*). A few which are not new but which here are corrected or emended are marked by a canceled equals sign ( $\neq$ ). For example, crenella has long been misused by authors for radially disposed ridges on the articular facets of columnals; in fact, the name signifies small furrow or groove and accordingly we employ the term in this sense. Columnal indices are omitted because they have previously been listed and defined in a section of the paper devoted to them. Terms printed in italics are considered to be usable but less desirable than cited equivalents for them. Some morphological terms for crinoid stem parts used by previous authors but not accepted by us are enclosed within square brackets.

$\neq$ **adcentral crenulae** (of petalodium). Adradial crenulae located near lumen, may merge with perilumen.

$\neq$ **adradial crenulae** (of petalodium). Crenulae located along margin of petal adjacent to interpetal radii and inside periphery of columnal articulum, disposed obliquely or normal to axis of petal.

**ankylosis**. Fusion of columnals (or other skeletal elements), commonly with obliteration of sutures.

\***areola** (pl. **areolae**) (symbol, A). Generally smooth, featureless area of columnal articulum between lumen (or perilumen, if present) and inner margin of crenularium; may be granulose or marked by fine vermicular furrows and ridges.

**articular facet** (of cirral or columnal). *See* articulum.

**articular rim**. Narrow raised border of some columnal artacula.

**articulation** (of cirrals and columnals). Flexible to nearly immovable union of adjoined stem parts effected by ligaments attached to articular surfaces.

\***articulum** (pl., **artacula**) (symbol, F for facet). Smooth or sculptured surface of columnal or cirral serving for articulation with contiguous stem element, may be intercolumnal, intercirral, or

Morphological groups of disarticulated columnals and pluricolumnals having operational value for recognition and classification of fossil crinoids represented by them are four. These are designated as 1) **Pentameri**, characterized by structural or articulum-marked divisions into pentameres, 2) **Elliptici**, with elliptical transverse sections and articular facets bearing a fulcral ridge which divides bifascial ligament fields, 3) **Cyclici**, which are circular transversely and have evenly disposed radial markings on their artacula, and 4) **Varii**, all remaining kinds. These groups are not diagnostic of recognized crinoid subclasses, for the Pentameri include genera of the Inadunata, Camerata, and Articulata; the Elliptici contain forms belonging to both Camerata and Articulata; the Cyclici incorporate representatives of all crinoid subclasses; and the Varii include genera of the Inadunata, Camerata, and Flexibilia.

Morphological terms applied to crinoid stem parts and holdfasts are explained in the following glossary.

nodicirral (between nodal columnal and most proximal cirral); *syn.*, articular facet. All columnal and cirral artacula are divisible into lumen and surrounding area designated zygum.

**axial canal**. Longitudinal passageway penetrating columnals and cirrals, generally but not invariably located centrally; may be single and either simple or complex or multiple (main canal accompanied by smaller accessory canals).

\***axial tube**. Seemingly thin-walled, straight-sided cylindrical passageway within axial canal observed in some exceptionally well-preserved pluricolumnals, its function unknown.

**basilarid**. One of small number of most proximal columnals which seem to be permanently fixed to base of theca, so that newly added columnals are introduced below them, rather than above most proximal columnal (STRIMPLE, 1963).

**bifascial articulation**. *See* synarthry.

**bifascial field**. Generally broad smooth ligament-attachment area on opposite sides of fulcral ridge bisecting columnal articulum, typically developed on elliptical intercolumnal artacula and some nodicirral artacula (e.g., *Isocrinus*, *Austrocrinus*, *Nielsenocrinus*); may be bordered on outer side by articular rim.

\***binodal**. Pair of nodal columnals, with or without distinct intercolumnal artacula and sutures, which share equally in supporting unbranched or branched cirri attached to crenulate or smooth nodicirral artacula (e.g., *Camptocrinus*); called paired nodals by SPRINGER (1926, p. 26).

**canal**. *See* axial canal, interarticular radial canal.

\***canalicula** (pl., **canaliculae**). Radially disposed tubular passageway penetrating stereom of middle part of nodal columnal and extending from axial canal to nodicirral articulum, typically associated with four other canaliculae spaced at 72° angles. In some seemingly homeomorphic pluricolumnals each columnal contains five canaliculae which emerge at mid-height of latus as small open pore, or terminate in diminutive nodicirral articulum or pimple-like protuberance (aborted cirrus).

\***cavannulus** (pl., **cavannuli**). Low hollow ring in inner medulla of some columnals girdling axial canal and sloping somewhat inward toward mid-plane of columnal, paired with another on opposite side of mid-plane; may contain delicate, rather open vesicular tissue (function unknown).

[*central area* (BATHER). *See* perilumen, areola.]

[*central canal*. *See* axial canal.]

- \***central nodicirral articulum (or facet)**. Attachment scar of cirrus placed at or very near mid-height of nodal latus and generally facing straight outward (compare infra- and supranodicirral artacula) (=central cirrus-facet, BATHER, 1909).
- cirral**. Single ossicle forming part of cirrus.
- cirral articulum** (pl., **cirral artacula**). Joint face of cirral transverse to axis of cirrus; most proximal cirral articulum is apposed to nodicirral articulum of columnal nodal.
- \***cirrinodal**. Cirrus-bearing nodal (other nodals called nudinodals).
- \***cirripore**. Small circular opening of canalicula approximately at mid-height of columnal latus, commonly accompanied by four others distributed with even spacing around columnal, interpreted as rudimentary type of cirrus structure but of unknown function (e.g., *Mooreanteris*), cirripore-bearing columnal classed as nodal.
- cirrus** (pl., **cirri**). Jointed appendage of crinoid column.  
*cirrus facet, scar, or socket*. See nodicirral articulum (or facet).
- cirrus root**. See radicular cirrus, radix.
- \***claustrum** (pl., **claustra**). Thick or thin inward projection of columnal medulla constricting axial canal, inner extremity acuminate to bluntly rounded, truncate with rabbeted edges, or clavate, composed of dense stereom or showing microstructure of fine annular lamellae subparallel to mid-plane of columnal, with or without intersecting longitudinally disposed lamellae which form microscopic cribwork. Transverse sections of claustra may show pentastellate indentations which are extensions of jugulum and between such indentations inner parts of claustrum may be thickened to form jugular ramparts. [*close suture*. See zygositystosis.]
- column**. Crinoid stalk exclusive of cirri and holdfast structures, composed of ossicles termed columnals.
- columnal** (symbol, K). Individual skeletal component of crinoid column.
- columnal diameter** (symbol, KD). Dimension transverse to longitudinal axis, may be uniform in all longitudinal planes or notably dissimilar in different ones.
- columnal height** (symbol, KH). Dimension in longitudinal plane, generally any such plane, but in comparatively rare columnals with opposite artacula inclined to one another, plane of measurement needs to be specified for definition of minimum, maximum, and mean height.
- \***complex axial canal**. Medial perforation of crinoid column characterized by successive alternating constrictions (jugula) produced by adaxial annular projections (claustra) of columnals and intercolumnal expansions (spatia).
- \***cortex**. Peripheral substance (stereom) of columnal or cirral next to latus, rather clearly distinct from medulla or grading into it; substance of columnals with undifferentiated cortex and medulla referred to simply as stereom.
- ≠**crenella** (pl., **crenellae**). Groove or furrow between culmina of columnal or cirral artacula (commonly misapplied by previous authors to ridges).
- \***crenula** (pl., **crenulae**). Any adjoined couple of ridge (culmen) and groove (crenella) on columnal or cirral articulum.
- \***crenularium** (pl., **crenularia**) (symbol, C). Portion of columnal and cirral artacula occupied by crenulae.
- \***crenulate suture**. Wavy line of contact between symplectically articulated columnals or cirrals; may appear in both external and internal sutures.
- cryptosymplectic articulation**. See cryptosymplexy.
- cryptosymplexy**. Weakly marked symplectic union of contiguous columnals or cirrals.
- cryptosynarthrial articulation**. See cryptosynarthry.
- cryptosynarthry**. Weakly marked synarthrial union of contiguous columnals (unknown in cirri).
- \***culmen** (pl., **culmina**). Ridge between adjoining pair of crenellae on columnal or cirral artacula (same as crenella of previous authors).
- \***discoid holdfast**. Subcircular, depressed, upwardly convex to crateriform plated structure with interior supported by radial walls, base plane or somewhat concave for cementation to foreign object such as shell, central articulum on upper surface for attachment of most distal columnal of crinoid stalk (e.g., *Lichenocrinus*, *Aspidocrinus*).
- distal**. Applied to crinoid columns, direction away from theca toward holdfast or free lower extremity of stalk; applied to cirri, direction away from column toward free extremity.
- dististele**. Distal region of crinoid column.
- divergence of fulcral ridges** (symbol, DFR). Azimuthal angular difference in orientation of fulcral ridges on opposite artacula of synarthrially joined columnals.  
[*division series*. See taxis.]  
[*encrusting root*. See discoid holdfast.]
- \***epifacet** (symbol, E). Extrafacetal surface (latus) of columnal, which may be considerably extended; term not used for straight- or nearly straight-sided columnals and inappropriate for application to most cirrals.  
[*epizygal*. Equivalent to nodal in crinoid columns (BATHER, 1909) but misnomer, since distal articulum of nodals is not a surface of syzygial articulation.]
- facet**. (articulum) (symbol, F). Surface of columnal or cirral transverse to longitudinal axis, serving for articulation with contiguous skeletal element; on side of nodal comprises nodicirral articulum for attachment of cirrus.
- facetal rim**. Narrow raised border of columnal or cirral articulum.
- floor** (of petal in petaloid columnal articulum). Generally smooth, plane or gently concave median area of petal, bordered by short crenulae; equivalent to areola.
- \***fossula** (pl., **fossulae**). Radially disposed groove somewhat larger and longer than crenellae on apposed artacula of binodal, extending from columnal lumen to center of nodicirral articulum; morphologically equivalent to half-canalcula.
- fulcral ridge**. Linear elevation on columnal articulum, invariably located on long axis of elliptical ones and separating bifascial ligament fields; facilitates differential movement in directions normal to ridge. Fulcral ridge may be interrupted by lumen or continuous around it and may be simple or variously modified. Some nodicirral artacula (on latus of nodals) and apposed articulum of most proximal cirral bear fulcral ridges.
- growth-index line**. Graphic plot of selected dimensions of crinoid skeletal elements in graded series of specimens differing in size or number of elements considered.
- height** (of columnal or cirral). See columnal height.
- \***heteromorphic** (column or pluricolumnal). Sequent columnals dissimilar, some consisting of nodals and others of internodals, latter commonly divisible by order of their intercalation into prim-, second-, tert-, and quartinternodals or higher-rank ones. Nodals and internodals may be clearly distinguishable along sides of axial canal, as seen in longitudinal sections, but not in views of columnal latera.
- holdfast**. Any anchorage structure at and near distal extremity of crinoid column, commonly discoid or rootlike (radicular) but may be bulbous or shaped like grapnel (e.g., *Ancyrocrinus*).
- \***homeomorphic** (column or pluricolumnal, cirrus or pluricirral). Composed of identical or essentially identical skeletal elements. Pluricolumnals from different parts of xenomorphic crinoid columns may be homeomorphic within themselves but dissimilar when compared with one another.  
[*hypozygal* (columnal). Internodal adjoining distal extremity of nodal (BATHER, 1909), considered inappropriate term because articulation of nodal and this internodal is not syzygial.]
- infracentral nodicirral articulum (or facet)**. Cirrus attachment scar located below mid-height of nodal latus, generally directed obliquely downward and outward. In dissociated pluricolumnals (excepting those derived from a few genera of stalked Articulata) infra- and supracentral nodicirral artacula are not distinguishable because proximal and distal extremities are indeterminate (=infracentral cirrus-facet, BATHER, 1909).



- [*infranodal*. Internodal adjoining distal face of nodal (CARPENTER, 1884).]
- [*interarticular pore* (CARPENTER). See interarticular radial pore.]
- interarticular radial canal**. Small radially directed passageway formed by apposed radial grooves on petaloid articularia of some columnals (e.g., *Isocrinus*); not identical to canal produced by apposed fossulae on binodal articularia.
- interarticular radial pore**. Small opening at outer extremity of interarticular radial canal.
- internodal** (symbol, IN). Columnal intercalated between any pair of sequent nodals, invariably lacking cirri; classifiable by order of generation as prim-, secund-, tert-, and quartinternodals, etc. Seemingly homeomorphic pluricolumnals may be demonstrated by longitudinal sections to contain nodals and internodals and thus actually are heteromorphic.
- internode** (symbol, IN). Entire succession of internodals between any pair of sequent nodals.
- internal suture**. Line of contact of apposed columnals or cirrals inside of their latera, as seen in longitudinally cut or in weathered specimens.
- joint**. Connection between any pair of contiguous columnals or cirrals (as well as between various other ossicles of crinoid skeleton).
- [*joint face* (BATHER). See articulum.]
- \*jugular rampart**. Localized thickened adaxial part of claustrum bordering jugulum.
- \*jugulum** (pl., *jugula*). Localized constriction of axial canal produced by approximated adaxial edges of claustrum, may be longitudinally very short to moderately tall and transversely circular or pentagonal to strongly pentastellate.
- latus** (pl., *latera*). Surface of crinoid columnal or cirral exclusive of articular facets, equivalent to epifacet.
- loose suture**. Line of contact between somewhat readily movable columnals or cirrals (as well as between other skeletal elements).
- lumen** (pl., *lumina*) (symbol, L). Open space approximately in plane of columnal or cirral articulum comprising intercept of axial canal, generally located centrally, highly variable in size and shape, surrounded on all sides by zygum.
- \*medulla**. Part of columnal girdled on outward side by cortex, from which it is distinguished by differences in microstructure if discernible at all, may be divided into well-defined or indistinctly bounded inner (adaxial) and outer (abaxial) portions and may consist solely of substance of claustrum, remainder of columnal then being classed as thick cortex.
- mesistele**. Intermediate part of crinoid column between proxistele and dististele regions, doubtfully distinguishable in pluricolumnals.
- nodal** (symbol, N). Columnal of heteromorphic crinoid stalk generally distinguished by diameter and height greater than in other columnals and typically by presence of nodicirral articularia on its latus.
- \*nodicirral articulum (or facet)**. Scar or socket on latus of nodal for attachment of cirrus.
- \*noditaxis** (pl., *noditaxes*) (symbol, NT). Nodal combined with all internodals of contiguous internode, in most fossil pluricolumnals arbitrarily taken as internode on either side of nodal, because proximal and distal directions are not determinable, but in extant stalk-bearing crinoids and some fossil forms (e.g., *Isocrinus*) internode on proximal side of nodal is reckoned to compose noditaxis because making of this internode follows that of nodal next below it.
- noncrenulate suture**. Straight or curved nonwavy line of contact between contiguous columnals or cirrals.
- \*nudinodal**. Nodal lacking nodicirral articularia on its latus.
- oblique suture**. Line of contact between contiguous columnals not perpendicular to longitudinal axis of column (e.g., distal suture of enlarged columnal in abruptly bent stalk of *Nevadocrinus* and *Lampidocrinus*).
- ossicle**. General term applicable to columnal, cirral, or other single skeletal element of crinoid.
- pelma** (pl., *pelmata*). Entire crinoid stalk with attached cirri and holdfast structure, if present.
- pentamere**. Fifth part of columnal or pluricolumnal, may be discrete or laterally ankylosed with other fifths.
- \*perilumen** (pl., *perilumina*) (symbol, P). Raised inner border of columnal articular zygum, surrounding lumen as rim or tubular field with smooth, granulose, tuberculate, or vermiculate surface. Internally, perilumen of some columnals corresponds to dense inner medulla, which is very distinct from reticulate to spongy outer medulla between areolae and possibly part of crenularia of opposite articularia.
- ≠ **peripheral crenulae** (of petaloid columnal articularia). Crenulae along abaxial border of petal, generally reaching margin of articulum next to columnal latus.
- ≠ **perradial crenulae** (of petaloid columnal articularia). Crenulae insinuating adradial crenulae along inner borders of petals (e.g., *Balanocrinus*).
- petal**. One of five main lobate divisions of petaloid columnal articulum (petalodium).
- petalodium**. Pentalobate, petal-shaped arrangement of short crenulae typically developed on articularia of some stalked crinoids (e.g., *Isocrinidae*, *Pentacrinidae*).
- \*pluricirral**. Two or more cirrals attached to one another.
- \*pluricolumnal**. Two or more columnals attached to one another.
- proximal**. Applied to crinoid columns, direction toward attachment with theca; applied to cirri, direction toward attachment with nodal.
- proximale**. Noncirriferous topmost columnal with or without ankylosed portion of dorsal cup, generally distinguished by enlargement and permanent attachment to base of cup (e.g., *Bourgueticrinus*).
- proxistele**. Proximal region of crinoid column near theca, generally not clearly delimited from mesistele. Dissociated columnals and pluricolumnals are rarely identifiable as belonging to proxistele.
- \*pseudocirrus**. Unsegmented sideward projection from columnal resembling cirrus in having axial canal but very irregular in form and distribution.
- \*pseudohomeomorphic**. Crinoid column with perfect or near-perfect homeomorphic appearance externally but internally possessing internodals which do not reach stem periphery (e.g., *Dianthicoeloma*).
- quartinternodal**. Internodal belonging to fourth order of intercalation.
- \*rabbet**. Channel or groove along suture between adjoined columnals (or other skeletal elements) formed by beveling of their edges.
- radial canal** (of petaloid columnal articulum). Radially disposed tubular passageway in apposed articularia of contiguous petaloid columnals formed by matched radial grooves between petals, extending to periphery but not reaching lumen (e.g., *Isocrinus*) (*syn.*, interarticular radial canal).
- radial groove** (of petaloid columnal articulum). Narrow space between adjacent petals of petaloid columnal articulum.
- radial pore** (of petaloid columnal). External opening of radial canal (*syn.*, interarticular radial pore).
- radial ridge groups** (of petaloid columnal articulum). Various types of perradial culmina on petaloid columnal articularia, gable-shaped, alternating, or confluent-rectilinear.
- radial space** (of petaloid columnal articulum). Narrow to broadly triangular space between adjacent petals of petalodium with base of triangle on columnal periphery and apex near lumen (e.g., *Pentacrinites*).
- radicle**. See radicular cirrus.
- radicular cirrus**. Individual branch of radix.
- radix**. Rootlike holdfast at distal extremity of crinoid column, adherent to foreign objects or with its branched or unbranched

extensions buried in sediment.  
 [*rebate* (BATHER, 1909). See *rabbit*.]  
 [*root*. See *radix*.]  
**rim**. See *articular rim*.  
**secundinternodal**. Internodal belonging to second order of intercalation.  
**simple axial canal**. Single medial passageway in crinoid column with straight or weakly angulated walls.  
**\*spatium** (pl., *spatia*). Localized widening of columnal axial canal opposite interarticular sutures.  
**supracentral nodicirral articulum (or facet)**. Cirrus attachment scar located above mid-height of nodal *latus*, generally directed obliquely outward and upward. (=supracentral cirrus-facet, BATHER, 1909).  
 [*supranodal* (CARPENTER, 1884). Internodal adjoining proximal articulum of nodal.]  
**suture**. Line of articular contact of columnals, cirrals, or other skeletal elements viewed from outer side (external) or seen in sections (internal).  
**symplectic articulation**. See *symplexy*.  
**symplexy**. Ligamentary articulation of columnals or cirrals in which culmina and crenellae of apposed artacula interlock, marked by crenulate sutures, mobility of articulation slight.  
**synarthrial articulation**. See *synarthry*.  
**synarthry**. Ligamentary articulation of columnals, proximal cirral on nodicirral articulum (and between some other skeletal elements) in which apposed artacula bear fulcral ridges aligned with one another and each articulum has relatively broad bifascial ligament fields next to fulcral ridge, marked by smoothly even sutures, mobility in direction normal to axes of fulcral ridges considerable.  
**synostiosal articulation**. See *synostosis*.

**synostosis**. Ligamentary articulation of columnals (and some other skeletal elements but not observed in cirrals) in which apposed artacula are essentially plane and devoid of sculptured features, attached short ligament fibers allowing small movement in all directions.

[**syzygial articulation**. See *syzygy*.]

[**syzygy**. Ligamentary articulation of brachials and some thecal plates but not observed in columnal or cirrals in which culmina or less well-defined ridges of one articulum are apposed to corresponding elevations of other articulum and crenellae or ill-defined depressions of apposed artacula to each other. This term has been misapplied by many previous authors to crinoid columnals, especially articulation of nodals with next-distal internodals.]

**taxis** (pl., *taxes*) (symbol, T). Differentiated linear series of skeletal elements such as nodal combined with adjacent internodal series, primibrach and other brachial series in arms, row of anal plates in sac, etc.; see *noditaxis*; *syn. division series*.

[*terminal stem plate* (EHRENBERG, 1929). See *discoid holdfast*.]

**tertinternodal**. Internodal belonging to third order of intercalation.

**xenomorph column**. Crinoid stalk containing dissimilar sorts of columnals in proxistele, mesistele, and dististele regions, but dissimilarity excluding contrast between homeomorphic and heteromorphic pluricolumnals, either or both of which may be represented in the xenomorphic differentiates of the stalk.

**zygocirral**. Most proximal segment of cirrus, articulating with cirrus scar on nodal columnal (cirrinodal).

**zygosynostosis**. Articulation differing from *synostosis* in occurrence of calcareous deposits which reduce mobility nearly or quite to zero.

**zygum** (pl., *zyga*) (symbol, Z). All of columnal or cirral articulum surrounding lumen.

## LOCALITY DESCRIPTIONS AND REFERENCES

Localities from which fossils illustrated in this paper were collected are described in the Supplement which follows *Echinodermata*, Article 10.

Also, publications cited in this paper are included in the consolidated list of references given in the above-mentioned Supplement.