MORPHOLOGICAL FEATURES OF CRINOID COLUMNS

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

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

RAYMOND C. MOORE and RUSSELL M. JEFFORDS

ONTGENETIC 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]

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The University of Kansas Paleontological Institute

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

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[Asterisk (*) indicates type species of genera]

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Morphological Features of Crinoid Columns

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 (lateral), 2) shape transversely and longitudinally, 3) intercolumnar 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 Doderlein (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 1915-471]) 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,
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 to minute size, along with waste rock which can be tossed aside (Pl. 1, fig. 1). When the concentrates, with accompanying dust 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 1/4-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 1/4-, 1/2-, and 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. 1/2-inch), intermediate (ca. 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 are entirely surrounded by matrix, as in parts of well cores, will be indeterminable in the future. 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, CIRRALS, AND PLURICIRRALS**

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 cirrals. 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, 2; 2,1). Thus, almost any collection of dissociated crinoid stem parts is certain to contain many columnals and pluricolumnals.

Similarly, a pluricirrals comprises any two or more cirrals joined together. Dissociated cirrals and pluricirrals, 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 pluricirrall, 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 cirrall. 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 epifacial 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 cirrall latera viewed perpendicularly to the axes of these stem parts are mostly quadrilateral, 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 *nodicirral articula (facets)* (Fig. 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: 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 & Jefferds, n. gen., n. sp. (9: Pl. 1, fig. 4-7).

**HOMEOMORPHIC AND HETEROCHRONIC 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...
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. 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 zygocirrals attached to cirrus scars on nodal, petaloid divisions of articulum separated abaxially by narrowly triangular epifacetal areas, very short crenulae nearly surrounding lanceolate arcular 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.

(Fig. 2.)

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.
identical, termed homeomorphic (Fig. 2, 2) (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 articula of all columnals in homeomorphic pluricolumnals generally are substantially identical in their characters, like the readily observed latera; with few exceptions, the articula 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., Diarthrocoeloma *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 pseudo homeomorphic.

**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 articula 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 articula (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 articula 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 articula are divisible into two parts; lumen (pl., lumina), which is the opening in the plane of the articulum of the axial canal that traverses each column longitudinally, and zygum (pl., zygga), which is the entire area of the articulum 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 pentameral 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 comonly 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,a,b). 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 extracetal 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 angularizations 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 synostosial (Fig. 2,3,R). 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.
type of union is defined as symplex (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 crenulae 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 adjoining 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 bifacial articulation). It is confined to some camerate (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 crenulanium 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 fulcrum 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 fulcrum 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 pantametal 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 interradial. 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), subpentagonal 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, 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. X1.
Moore, Jeffords, & Miller—Morphological Features of Crinoid Columns
Moore, Jeffords, & Miller—Morphological Features of Crinoid Columns
Morphological Features of Crinoid Columns

4; Pl. 3, *lb, 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 canals possess varied sorts of intercolumnally located expansions, termed spatia (sing., spatium), and midcolumnally 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 adaxially 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 facetal 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-Pcl8a) and Wayland Shale Member, Graham Formation (2, UKPI-Pcl1001), 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. ×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. ×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, ×3.5.—4. Specimen with nodals lacking cirrus scars (thus distinguished as nudinodals) and nudi-taxis also lacking one tertinternodal, ×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-Pca21a), showing aligned cirrus scars in three rays and lack of scars in other two rays, ×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), ×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
Morphological Features of 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 proxi-

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 one (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 xenomorphic (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 xenomorphic 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 xenomorphic stem parts. A few striking examples of xenomorphic 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 articula—DFR
- epifacet (latus)—E
- epifacial (lateral) index—Ei
- facial (articular)—F
- height (of columnal)—KH
- height index—Hi
- internode (internodal)—IN
- internodal index—INi
- latus (epifacet)—E
- lateral (epifacetal) index—Ei
- luminal—L
- luminal index—Li
- maximum—y
- minimum—x
- nodal—N
- nodal index—Ni
- noditaxis—NT
- periluminal index—Pi
- radius—R
- shape indices, areolar—ASI
- columnal—KSi
- crenularial—CSI
- epifacial (lateral)—ESi
- facial (articular)—FSi
- luminal—LSi
- periluminal—PSi
- zygum—Z
- zygal—ZSi

Determination of columnal indices is simplest in dealing with circular stem parts having articula 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 articula.

Stem parts with elliptical articula 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: \( Ni = \frac{NH}{NTH} \times 100 \). \( Ni + INi = 100 \).

Internodal index (INi).—Ratio of total height of internode (IN) to that of noditaxis (NT) containing it: \( INi = \frac{INH}{NTH} \times 100 \). 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 epifacial index (Fig. 5, Table 1).

Columnal height index (KHi) [also simply termed height index].—Ratio of columnal (K) height (H) to its diameter (KD) \( \times 100 \). \( KHi = \frac{KH}{KD} \times 100 \) (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 (KRx) and long radius (KRY). The height index of such columnals is expressed as \( KHi = \frac{KH}{(KRx + KRy)} \times 100 \) (Fig. 5, G-J).

Articular facet index (Fi) [also simply termed facetal index].—Ratio of total width (diameter) of articular facet (articulum) to that of columnal \( \times 100 \). For circular facets this is expressed as \( Fi = \frac{FD}{KD} \times 100 \) (Fig. 5, A-F). Computation of the facetal index of pentagonal, pentastellate, quadrangular, and elliptical facets requires determination of mean diameter (FRx+FRy) and this may apply to diameter of the columnal as well. For such columnals the index is expressed as \( Fi = \frac{(FRx + FRy)}{KD} \times 100 \), or \( Fi = \frac{(FRx + FRy)}{(KRx + KRy)} \times 100 \) (Fig. 5, G-J). The facetal index of a circular articulum borne by a non-circular columnal is computed as \( Fi = \frac{FD}{(KRx + KRy)} \times 100 \).

Epifacetal index (Ek).—Ratio of two radial intercepts of epifacet to total width (diameter) of columnal \( \times 100 \) (Fig. 5, C-G-I). \( 2ER/KDX100 \), or \( (ERx + ERY)/KD \times 100 \), or \( (ERx + ERY)/(KRx + KRy) \times 100 \), or \( 2ER/(KRx + KRy) \times 100 \).

FACET-PART INDICES

Morphological divisions of columnal articula 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 columnal mean diameters may need to be determined for either or both. For a circular lumen the luminal index is determined as \( Li = \frac{LD}{FD} \times 100 \) (Fig. 5, A-D), or \( \frac{LD}{(FRx + FRy)} \times 100 \) (Fig. 5, G-I). A pentagonal or pentastellate lumen of a circular facet is indicated as \( Li = \frac{(LRx + LRY)}{FD} \) (Fig. 5, E-F), and a noncircular lumen belonging to a noncircular facet is represented by \( Li = \frac{(LRx + LRY)}{(FRx + FRy)} \times 100 \) (Fig. 5, H-I). The sum of luminal and zygal indices must equal 100.

Zygal index (Zi).—Ratio of total width (diameter) of zygm (possibly sum of minimum and maximum radial intercepts) to that of columnal articulum \( \times 100 \) (Fig. 5, A-J). \( Zi = \frac{ZD}{FD} \times 100 \), or \( \frac{(ZRx + ZRY)}{FD} \times 100 \), or \( (ZRx + ZRY)/(FRx + FRy) \times 100 \), or \( \frac{ZD}{(FRx + FRy)} \times 100 \).

Periluminal index (Pi).—Ratio of two radial intercepts of perilumen (possibly PRx+PRy) to total width (diameter) of columnal articulum (possibly FRx+FRy) \( \times 100 \) (Fig. 5, C). \( Pi = \frac{PRx + PRy}{FD} \times 100 \), or \( \frac{(PRx + PRy)}{FD} \times 100 \), or \( (PRx + PRy)/(FRx + FRy) \times 100 \), or \( 2PR/(FRx + FRy) \times 100 \). \( Pi + Ci + Li \) (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). \( Ai = \frac{2AR}{FD} \times 100 \) or \( (ARx + ARy)/FD \times 100 \). 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). \( Ci = \frac{2CR}{(ARx + ARy)} \times 100 \), or \( (CRx + CRy)/FD \times 100 \), or \( (CRx + CRy)/(FRx + FRy) \times 100 \), or \( 2CR/(FRx + FRy) \times 100 \). 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.
Morphological Features of Crinoid Columns

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

<table>
<thead>
<tr>
<th>Columnal Indices</th>
<th>Definition</th>
<th>Measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td>LD / FD = Li</td>
<td>(LRx + Lry = LD) / (FRx + FRy = FD)</td>
<td>Li</td>
</tr>
<tr>
<td>A 3.6 / 20.0 = 18.0</td>
<td>(0.65 + 0.85 = 1.50) / (10.0) = 15.0</td>
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<tr>
<td>B 4.8 / 20.0 = 24.0</td>
<td>(0.85 + 3.75 = 4.60) / (10.0) = 46.0</td>
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</tr>
<tr>
<td>C 1.4 / 18.5 = 7.6</td>
<td>(3.5 + 5.4 = 8.9) / (10.0) = 3.4</td>
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</tr>
<tr>
<td>D 0.4 / 3.6 = 11.5</td>
<td>(4.0 + 5.0 = 9.0) / (10.0) = 22.8</td>
<td></td>
</tr>
<tr>
<td>2PR / FD = Pi</td>
<td>(ARx + ARy = AD) / (FRx + FRy = FD)</td>
<td>Pi</td>
</tr>
<tr>
<td>C 0.3 / 10.0</td>
<td>(3.5 + 5.4 = 8.9) / (10.0) = 3.4</td>
<td></td>
</tr>
<tr>
<td>2AR / FD = Ai</td>
<td>(0.40 + 4.14 = 4.54) / (3.5 + 5.4 = 8.9) / (10.0) = 39.5</td>
<td></td>
</tr>
<tr>
<td>B 3.8 / 20.0 = 15.5</td>
<td>(0.85 + 3.75 = 4.60) / (10.0) = 39.5</td>
<td></td>
</tr>
<tr>
<td>C 6.0 / 18.5 = 32.4</td>
<td>(0.40 + 4.14 = 4.54) / (3.5 + 5.4 = 8.9) / (10.0) = 39.5</td>
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<tr>
<td>D 2.0 / 3.6 = 55.5</td>
<td>(0.40 + 4.14 = 4.54) / (3.5 + 5.4 = 8.9) / (10.0) = 39.5</td>
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<tr>
<td>2CR / FD = Ci</td>
<td>(CRx + CRy = CD) / (FRx + FRy = FD)</td>
<td>Ci</td>
</tr>
<tr>
<td>A 16.4 / 20.0 = 82.0</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
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</tr>
<tr>
<td>B 12.1 / 20.0 = 60.0</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>C 9.0 / 18.5 = 48.7</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>D 1.2 / 3.6 = 33.3</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>2ER / KD = Ei</td>
<td>(FRx + FRy = FD) / (KRx + KRy = KD)</td>
<td>Ei</td>
</tr>
<tr>
<td>A 4.0 / 5.0 = 10.0</td>
<td>(0.90 + 3.20 = 4.10) / (4.0 + 5.0 = 9.0) / (10.0) = 45.6</td>
<td></td>
</tr>
<tr>
<td>B 3.8 / 20.0 = 15.5</td>
<td>(0.90 + 3.20 = 4.10) / (4.0 + 5.0 = 9.0) / (10.0) = 45.6</td>
<td></td>
</tr>
<tr>
<td>C 9.0 / 18.5 = 48.7</td>
<td>(0.90 + 3.20 = 4.10) / (4.0 + 5.0 = 9.0) / (10.0) = 45.6</td>
<td></td>
</tr>
<tr>
<td>D 1.2 / 3.6 = 33.3</td>
<td>(0.90 + 3.20 = 4.10) / (4.0 + 5.0 = 9.0) / (10.0) = 45.6</td>
<td></td>
</tr>
<tr>
<td>KH / KD = KHI</td>
<td>(ERx + ERy = 2ER) / (KRx + KRy = KD)</td>
<td>KHI</td>
</tr>
<tr>
<td>A 16.4 / 20.0 = 82.0</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>B 12.1 / 20.0 = 60.0</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>C 9.0 / 18.5 = 48.7</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
<tr>
<td>D 1.2 / 3.6 = 33.3</td>
<td>(0.80 + 3.75 = 4.55) / (3.5 + 5.4 = 8.9) / (10.0) = 45.5</td>
<td></td>
</tr>
</tbody>
</table>

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 crinoidal 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 (1/1×100=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, zygum, perilumen, areola, and crenularium (Fig. 5, Table 1).

**Columnal shape index (KSi).—**Ratio of minimum columnal radius to maximum radius ×100 (Fig. 5, G-J, Table 1,J). KSi=KRx/KRy×100.

**Epifacetal shape index (ESi).—**Ratio of minimum radius of epifacet (latus) to maximum radius ×100. ESi =ERx/ERy×100.

**Articular (facetal) shape index (FSi).—**Ratio of minimum articular radius to maximum radius ×100 (Fig. 5, G-J, Table 1,J). FSi=FRx/FRy×100. The shape index of all circular columnal articula is 100, whereas that of a broadly oval articulum may be 95 and that of a narrowly elliptical facet 20 or smaller. The shape index of an evenly pentagonal articulum 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 ×100 (Fig. 5,E-F, H-J). LSi=LRx/LRy×100.

**Zygal shape index (ZSi).—**Ratio of minimum radius of zygum to maximum radius ×100 (Fig. 5,E-J). ZSi=ZRx/ZRy×100.

**Periangular shape index (PSi).—**Ratio of minimum radius of perilumen to maximum radius ×100. PSi=PRx/PRy×100.

**Areolar shape index (ASI).—**Ratio of minimum areolar radius to maximum radius ×100 (Fig. 5,E-J). ASi=ARx/ARy×100.

**Crenular shape index (CSI).—**Ratio of minimum radius of crenularium to maximum radius ×100 (Fig. 5,E,G,H). CSI=CRx/CRy×100.

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

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EXPLANATION OF PLATE 3

Longitudinal Sections and Features of Articula and Latera of Crinoidal 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, E706-14) showing (1a) half articulum 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, ×3.5.—2. Gunsight Limestone specimen (E706-1); 2a, median longitudinal section showing wavy internal sutures, ×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, ×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), ×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, ×2.—5. Exterior of well-preserved pluricolumnal (E672-75) having 4 cirri-nodals and showing noditaxes of 4 (nodal + 3 internodals), ×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 ×5.—7,8. Articula 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), ×3.5, ×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, ×3.5.
Moore, Jeffords, & Miller--Morphological Features of Crinoid Columns
Xenomorphic Columns
4-5. Taxocrinus. 6. Nevadacrinus.
(1-5, Miss., X0.85; 6, Perm., X1.7)

7a 4:1% •'
7b 7. Preptopremnum *rugosum, U.Penn., Texas. 7c

Moore, Jeffords, & Miller—Morphological Features of Crinoid Columns
and spation, 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 indices 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.

**ELLIPITCI**

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 fulcrum ridge coinciding with the long axis and bisecting the

**EXPLANATION OF PLATE 4**

Xenomorphic Crinoid Stems and Sections of Pluricolumnals with Complex Axial Canals

[Figures 1-6. Xenomorphic crinoid columns, ×1 (1-5, Springer, 1920; 6, Lane & Webster, 1966).—1. *Mespilocrinus konincki* HALL, Burlington Limestone, Lower Mississippian, in Iowa, showing well-marked differences in columns of proxistele, mesistele, and dististele regions.——2. *Onychocrinus diversus* MEER & 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 separating proxistele and mesistele regions of stem with articular facets in planes obliquely disposed to each other, thus producing abrupt geniculation of column. 7. *Preptopreparatum* *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 reticulolaminate microstructure of claustra and clearly discernible cavannular openings.——7a. Section showing general relationships, thickest columnal a nodal, ×8.5.——7b. Peripheral part of nodal shown in 7a showing honeycomb microstructure and arcuate growth bands, ×42.——7c. Section of median region showing claustra, jugula, spata, and cavannuli, ×42.]
facial. The articula may be bordered by a rim or may be rimless, but in either type crenulations along the border are weak or absent. Some columns 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 columns or circular columns of very unequal size. In both subgroups the peripheries of columns 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 columns are concave. Variations are many but all are characterized by regularity in the arrangement of crenulations around edges of their facets.

**VARI**

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 columns) 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 columns 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-coll ecting 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 (lateral) of pluricolumnals especially guides initial segregation of homeomorphic ones, composed of identical or near-identical columns, and heteromorphic specimens containing more or less evidently dissimilar columns joined together. Individual loose columns are grouped as well as possible by comparison with the pluricolumnals, using both characteristics of the latera and articular facets (articula).

Very important are transverse shapes of the columns and all features of the articula, 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 columns 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 columns 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 sec-
tions and serial sections of crinoid stem parts. In this
way the axial canals and associated medullary and cor-
tical parts of columnals have been shown to possess mor-
phological characteristics that vary considerably. Study
of them has led to realization of need for terms for design-
ating and describing them. Both external and internal
characteristics of crinoid columnals have importance in
taxonomic investigations.

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 penta-
meres, 2) Elliptici, with elliptical transverse sections and
articular facets bearing a fulcrum ridge which divides bi-
fascial ligament fields, 3) Cyclici, which are circular tran-
versely and have evenly disposed radial markings on
their articula, and 4) Varii, all remaining kinds. These
groups are not diagnostic of recognized crinoid sub-
classes, for the Pentameri include genera of the Inadunata,
Camerata, and Articulata; the Elliptici contain forms be-
longing to both Camerata and Articulata; the Cyclici in-
corporate 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.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CRINOID STEM PARTS

The alphabetically arranged morphological terms ap-
plied 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 (=). For example, crenel 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 em-
ploy 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.

=adcentral crenulae (of petalodium). Adradial crenulae located
near lumen, may merge with perilumen.
=adradial crenulae (of petalodium). Crenulae located along mar-
gin 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), com-
monly 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 vermicu1ar furrows and ridges.
articular facet (of cirral or columnal). See articulum.
articular rim. Narrow raised border of some columnal articula.
articulation (of cirrals and columnals). Flexible to nearly im-
movable union of adjoined stem parts effected by ligaments
attached to articular surfaces.
*articulum (pl., articula) (symbol, F for facet). Smooth or sculpt-
ured surface of columnal or cirr al serving for articulation with
contiguous stem element, may be intercolumnal, intercirral, or
nodicirral (between nodal columnal and most proximal cirral);
*zyn., articular facet. All columnal and cirr al articula are
divisible into lumen and surrounding area designated zyyum.
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 pas-
sageway within axial canal observed in some exceptionally well-
preserved pluricolumnals, its function unknown.
bas.alid. 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 (STIRLING, 1963).
binodal. Pair of nodal columnals, with or without distinct inter-
columnal articula and sutures, which share equally in support-
ing unbranched or branched cirri attached to crenulate or
smooth nodicirral articula (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 nodicular 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 articula) (=central cirrus-facet, BATHER, 1909).

cirral. Single ossicle forming part of cirrus.

cirral articulum (pl., cirral articula). Joint face of cirral transverse to axis of cirrus; most proximal cirral articulum is opposed to nodicirral articulum of columnal nodal.

*cirrinodal. Cirrus-bearing nodal (other nodals called nudinodals).

cryptosynarthry. Weakly marked synarthrial union of contiguous cryptosymplexy.

cryptosymplexy. Azimuthal angular difference in orientation of fulcral ridges on opposite articula of synthetically joined columnals.

distal. Applied to cirrals or columnals, direction away from theca toward holdfast or free lower extremity of stalk; applied to cirri, direction away from columnal toward free extremity.

distitele. Distal region of columnal.

divergence of fulcral ridges (symbol, DFR). Azimuthal angular difference in orientation of fulcral ridges on opposite articula of synthetically joined columnals.

division series. See taxis.

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 cirri.

epizygal. Equivalent to nodal in cirrals (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 than crenella on apposed articula of binodal, extending from columnal lumen to center of nodicirral articulum; morphologically equivalent to half-canalicular.

fulcral ridge. Linear elevation on columnal articulum, invariably located on long axis of elliptical ones and separating bifacial ligament fields; facilitates differential movement in directions normal to ridge. Pulcular ridge may be interrupted by lumen or continuous around it and may be simple or variously modified. Some nodicirral articula (on latus of nodals) and apposed articulum of most proximal cirrals 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). Segment columns dissimilar, some consisting of nodals and others of internodals, latter commonly divisible by order of their intercalation into prim., secnd., 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 lata.

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*).

*homomorphic (column or pluricolumnal, cirrus or pluricirrall. Composed of identical or essentially identical skeletal elements. Pluricolumnals from different parts of xenomorphic crinoid columns may be homomorphic 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 articula are not distinguishable because proximal and distal extremities are indeterminate (=infracentral cirrus-facet, BATHER, 1909).

*crenella (pl., crenellae). Groove or furrow between culmina of columnal or cirral articula (commonly misapplied by previous authors to ridges).

*crenula (pl., crenulae). Any adjoined couple of ridge (culmen) and groove (crenula) on columnal or cirral articulum.

crenularium (pl., crenularia) (symbol, C). Portion of columnal claustrum (pl., claustra). Thick or thin inward projection of cirrinodal.

cirrus (pl., cirri). Jointed appendage of crinoid column.

cirrus facet, scar, or socket. See nodicirral articulum (or facet).

cirrus root. See radicular cirrus, rachis.

*claustrum (pl., claustra). Thick or thin inward projection of columnal medulla constricting axial canal, inner extremity acumenate to bluntly rounded, truncate with rabbetted 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 pustellate indentations which are extensions of jugulum and between such indentations inner parts of claustra may be thickened to form jugular ramps.

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 articula 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 alternate 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 articula (commonly misapplied by previous authors to ridges).

*crenula (pl., crenulae). Any adjoined couple of ridge (culmen) and groove (crenula) on columnal or cirral articulum.

crenularium (pl., crenularia) (symbol, C). Portion of columnal and cirral articula occupied by crenulae.

crenulate suture. Wavy line of contact between symplectically articulated columnals or cirrals; may appear in both external and internal sutures.

cytopsysemptic articulation. See cryptopsysemphy.

cryptopsysemphy. 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 articula (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, Aspidoerinus*).

distal. Applied to cirrals or columnals, direction away from theca toward holdfast or free lower extremity of stalk; applied to cirri, direction away from columnal toward free extremity.
Morphological Features of Crinoid Columns

*nudinodal. Internodal adjoining distal face of nodal (Carpenter, 1884).
*interarticual pore (Carpenter). See interarticual radial pore.
interarticual radial canal. Small radially directed passageway formed by apposed radial grooves on petaloid articula of some columnals (e.g., *Isocrinus*); not identical to canal produced by apposed fossulae on bidental articula.
interarticual radial pore. Small opening at outer extremity of interarticual radial canal.
internodal (symbol, IN). Columnal intercalated between any pair of sequent nodals, invariably lacking cirri; classifiable by order of generation as prox., secund., tert., and quarterinternodals, 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 insude 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 (Baither). 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 pentestellate.
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 articula 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 nonway line of contact between contiguous columnals or cirrals.
*nudinodal. Nodal lacking nodicirral articula on its latus.
oblique suture. Line of contact between contiguous columnals not perpendicular to longitudinal axis of column (e.g., distal suture of enlarged column in abruptly bent stalk of *Nevadacrinus* and *Lampidicrinus*).
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.
*peritelynum (pl., peritelynum) (symbol, P). Raised inner border of columnal articular zygym, surrounding lumen as rim or tabular field with smooth, granulose, tuberculate, or verrucose surface. Internally, peritelynum 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 articular.
*peripheral crenulae (of petaloid columnal articula). Crenulae along abaxial border of petal, generally reaching margin of articulum next to columnal latus.
*peripheral crenulae (of petaloid columnal articula). Crenulae insoucating adradial crenulae along inner borders of petals (e.g., *Balatoserinus*).
petal. One of five main lobate divisions of petaloid columnal articulum (petalodium).
petalodium. Pentalobate, petal-shaped arrangement of short crenulae typically developed on articula of some stalked crinoids (e.g., *Isocrinidae, Pentaetarcinidae*).
*pluricirral. Two or more cirrals attached to one another.
*pluricolummal. Two or more columns attached to one another.
proximal. Applied to crinoid columns, direction toward attachment with theca; applied to cirri, direction toward attachment with nodule.
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., *Bourguetiscrinus*).
proxistele. Proximal region of crinoid column near theca, generally not clearly delimited from mesistele. Dissociated columns and pluricolumnals are rarely identifiable as belonging to proxiostele.
*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., *Dianthicodoma*).
*quartinternodal. Internodal belonging to fourth order of intercalation.
*rabbit. 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 articula of contiguous petaloid columnals formed by matched radial grooves between petals, extending to periphery but not reaching lumen (e.g., *Isocrinus* (syn., interarticual 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., interarticual radial pore).
radial ridge groups (of petaloid columnal articulum). Various types of perradial culmina on petaloid columnal articula, 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
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.