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## ONTOGENETIC DEVELOPMENT IN LATE PENNSYLVANIAN CRINOID COLUMNALS AND PLURICOLUMNALS

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## ONTOGENETIC DEVELOPMENT IN LATE PENNSYLVANIAN CRINOID COLUMNS AND PLURICOLUMNS

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

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### ABSTRACT

Crinoid columnals and pluricolumnals from the Wayland Shale and Gunsight Limestone, Late Pennsylvanian, of north-central Texas differ in size and other external and internal features. Growth stages of pluricolumnals not associated with calices are interpreted from the insertion of internodals, relationship between diameter of columnal and number of articular ridges (culmina), and nature of longitudinal sections. Growth characteristics are shown for four types of these pluricolumnals.

## INTRODUCTION

Single crinoid columnals and short segments of crinoid stems (pluricolumnals) are characteristic of many post-Early Ordovician Paleozoic beds. As these skeletal elements are not related readily to the calices commonly used for differentiating crinoid taxa, Paleozoic dissociated columnals and groups of them joined together (pluricolumnals) (MOORE, JEFFORDS & MILLER, 1967, —)<sup>1</sup> have been largely ignored by paleontologists. A few early workers (e.g., GOLDFUSS, 1826-44) recorded dissociated columnals along with other elements in faunas, and some others have described parts of crinoid stems in some detail and classified them either as distinct taxonomic entities or in terms of taxa described from calices (e.g., TIEN, 1926; MOORE, 1939a,b; SIEVERTS-DORECK, 1942; TERMIER & TERMIER, 1949; YELTYsheva, 1956, 1959; STRIMPLE, 1962; STUKALINA, 1966). Other faunal studies include brief mention or description and illustration of a few columnals (e.g., GIRTY, 1915; THOMAS, 1923; VALETTE, 1934; TERMIER & TERMIER, 1958; EASTON, 1962; STRIMPLE, 1963). General features of the nature and development of columnals have been reviewed in some detail by WACHSMUTH & SPRINGER (1897), BATHER (1898 [in 1898-99], 1900), MOORE (1939b, 1952), and TERMIER & TERMIER (1949). The present study does not attempt to summarize these findings for crinoid columnals broadly; rather it is limited to consideration of a small part of the field.

The somewhat fortuitous opportunity to obtain a large collection (several thousand specimens) of columnals from a narrow zone in the Late Pennsylvanian of north-central Texas led us to attempt the application of existing concepts of morphology and ontogeny to columnals. A wide variety of qualitative and quantitative approaches resulted in a few findings that seem to contribute to the basic understanding of stem development as expressed by dissociated

stem parts. These conclusions, however, pertain only to the forms here described and lack the obvious demonstration obtainable in essentially complete stems attached to crowns. The observations here recorded, however, illustrate that 1) attention to dissociated columnals and especially pluricolumnals is not futile, albeit mainly of academic value, and 2) amplification of these studies could increase substantially general understanding of stem development in crinoids.

Dissociated crinoid fragments, essentially all pluricolumnals, occur abundantly on surface exposures of the fossiliferous Wayland Shale and Gunsight Limestone Members, Graham Formation, Cisco Group, Virgilian, Upper Pennsylvanian, in north-central Texas. Crinoid calices from these beds have been described by MOORE & PLUMMER (1940). Most of the available collections are from McCulloch, Brown, and Coleman Counties where the Wayland comprises shale and local thin beds or lenses of argillaceous limestone. This shale was deposited in a relatively shallow nearshore marine environment with changes from place to place and with time in response to proximity to shifting centers of sediment inflow from the east (MARTIN, 1965, 1966). The subjacent Gunsight is slightly more marine generally, but the rubbly shaly limestone from which crinoids were obtained represents depositional conditions approximating those of the Wayland. The faunas and field relationships of these two members suggest that the collections are from beds differing somewhat in facies but not appreciably in age. The nature, distribution, and age of the two members have been discussed by PLUMMER & MOORE (1922), BULLARD & CUYLER (1936), LEE *et al.* (1938), EARGLE (1960), and CRONEIS & TOOMEY (1965). The age, as expressed by the fusulinids, has been reviewed by MYERS (1960) and by KAUFFMAN & ROTH (1966).

## METHODS AND PROCEDURES

Dried samples comprising hand-picked columnals and other fossils, together with "sweepings" of the "lag gravel" of fossils on slightly weathered surfaces and shale for packing, were washed and the fraction retained on a 1/8-inch screen was studied. Smaller-size fractions were examined, however, for juvenile and small adult specimens. Separation of columnals from other fossils and debris is facilitated by picking roughly screened fractions (as those retained on 3/4-, 1/2-, and 1/4-inch screens). Readily distinguished types of columnals, such as speci-

mens described below, were selected and these materials were separated. Columnals having clearly preserved articular or other surfaces were segregated for careful study, and specimens having identifiable but poorly preserved external features were used for sectioning.

Measurements and counts were made using an ocular micrometer in a low-power binocular microscope or a finely scaled caliper. Staining has not been successful in differentiating structures composed of calcite, but staining with Safranin O of the clay matrix filling axial canals facilitates examination. This red stain also tends to increase the contrast between the stained matrix and unstained calcite in photographs because it appears dark when panchromatic film is used.

<sup>1</sup>Literature citations, indicated by names of authors and dates are given in the consolidated list of references for Echinodermata, Articles 8-10, separately published as a Supplement to them.

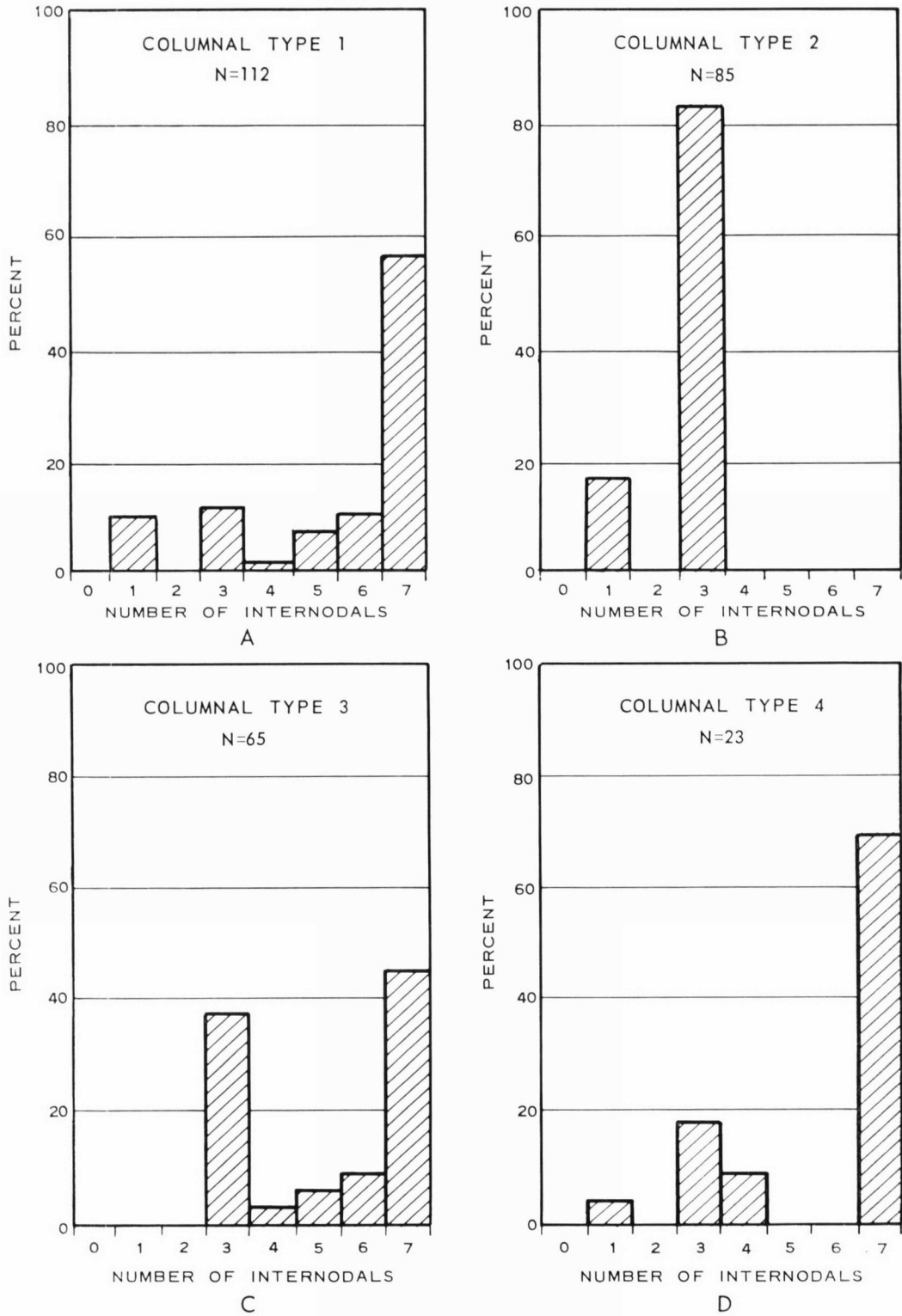


FIG. 1. Percentages of pluricolumnals having 1 to 7 internodals in noditaxes in columnal (pluricolumnal) types 1, 2, 3, and 4.

Surface ornamentation and other features such as the geometric distribution of cirrus facets are especially difficult to study, describe, and illustrate for the cylindrical columnals. A plan view is obtained, therefore, by rolling a specimen on a flat surface of self-hardening pottery clay, putty, dental plastic, or similar material (Pl. 1, fig. 7).

Polished surfaces have been adequate for examination of most longitudinal sections, although detailed analysis of some internal structures is aided by thin sections. Crystallographic orientation other than for the c axis, as indicated by traces of cleavage planes on transverse sections, differs from columnal to columnal but will require further analysis before significant results are available.

## GENERAL ONTOGENY OF CRINOID STEMS

Many workers have indicated specialized developmental features of stems in particular genera and groups of crinoids; the discussion here, however, is limited to a general plan that seems very common among late Paleozoic stems and is described by several crinoid specialists. These columnals mainly comprise two types, nodals that are inserted at the base of the calyx as the stem lengthens and internodals that are inserted in cycles between the nodals at differing distances below the calyx. The youngest part of the stem, therefore, is adjacent to the calyx, and attachment scars on calices need not approach in diameter the diameter of the large (i.e. mature) dissociated columnals observed commonly. Nodals may, and commonly do, bear cirri, low nodes, or pores and generally are larger (in height and diameter) than internodals, although nodals and internodals may be similar in the

full adult stage. Nodals near the calyx are in contact with one another and just below may be separated by only one internodal; then two thinner secondary internodals appear, one each side of the first internodal. Subsequently, successive cycles of internodals may be added, representatives of each cycle separating the earlier internodals. The theoretical number of internodals for successive growth stages then would be 0-1-3-7-15-.... Differences between nodals and internodals and between cycles of internodals generally suggest the development stage represented by a segment of stem. As is indicated later, other measures of growth suggest that rate of insertion of internodals differs for different types of stems and that stem maturity for any single type may not be expressed adequately by merely noting the number and cycles of internodals.

## MORPHOLOGIC TERMINOLOGY

As used in this paper, individual stem ossicles are termed **columnals**, in accordance with custom, and groups of columnals joined to one another are called **pluricolumnals**. (8).<sup>1</sup>

<sup>1</sup> Boldface numbers (8,9) refer to accompanying papers published as Echinodermata, Articles 8 and 9. Morphological terms are explained in the glossary included in Article 8.

The terms mature (or adult) and immature (or juvenile) as applied to dissociated crinoid columnals are measurably subjective at the present stage of knowledge, but tentative use of the terms is necessary to facilitate description. A **juvenile** of one form (type 1 described later), for example, is interpreted as a small specimen with a diameter of approximately 4 to 5 mm., about 35 articu-

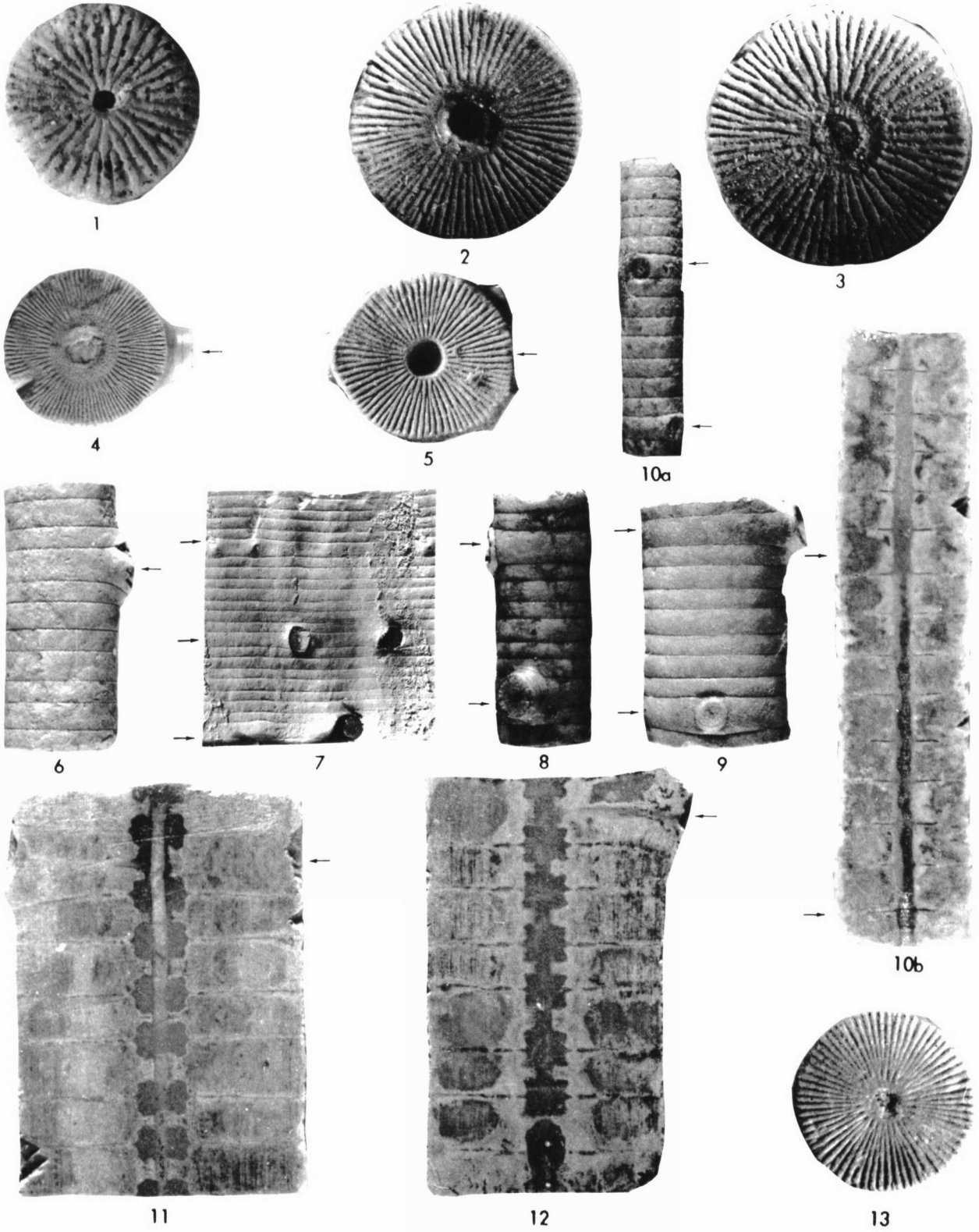
## EXPLANATION OF PLATE 1

Columnal (pluricolumnal) type 1 (*Cyclocaudex plenus* MOORE & JEFFORDS) from the Wayland Shale showing changes from juvenile to mature specimens in the articular facet, relationships of nodals and internodals, and axial canal. [Additional illustrations of this species are given in Echinodermata Art. 8-9.]

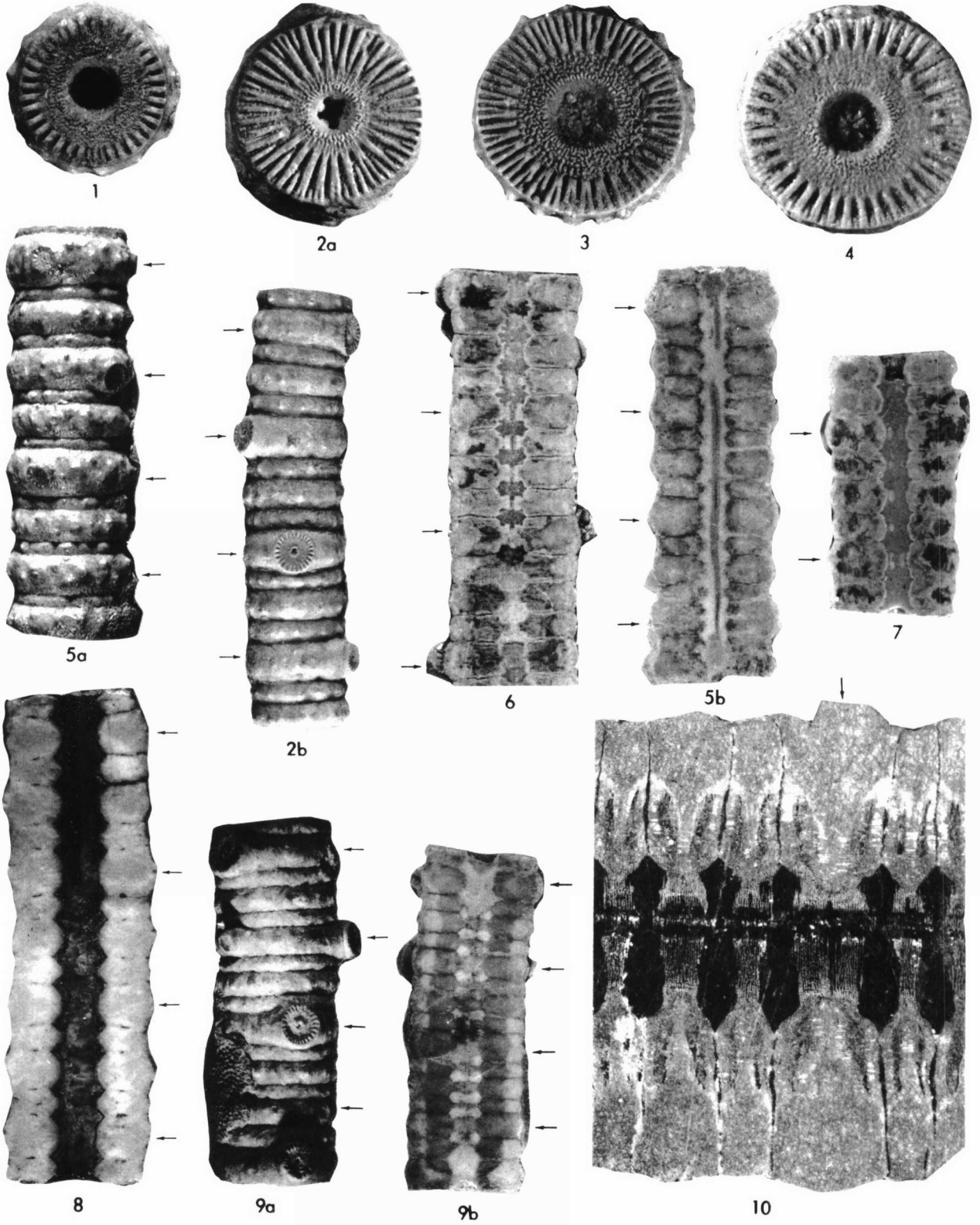
### FIGURE

1. Juvenile specimen (E 705-51) from locality E 705 having a few articular ridges and a small lumen,  $\times 8$ .
- 2-5, 13. Articular surfaces showing increase in number of articular ridges as the diameter increases.—2-3. Specimens (E 733-21, 22) from locality E 733,  $\times 6$ .  
—4. Specimen (E 732-33) from locality E 732,  $\times 2$ .  
—5. Specimen (E 722-10) from locality E 722,  $\times 4$ .  
—13. Specimen (E 705-9) from locality E 705,  $\times 4$ .
6. Exterior of specimen (E 5-103) from locality E 5 showing very finely crenulate suture,  $\times 2$ .
7. Impression of stem segment in clay showing distribution of cirrus scars and other nodal markings,  $\times 1$ .
- 8-9. Specimens from locality E 732 showing internodals

- alternating in thickness between nodals bearing cirrus scars,  $\times 2$ .—8. Specimen (E 732-57) having 6 internodals.—9. Specimen (E 732-29) having 7 internodals.
10. Juvenile specimen (E 722-12) from locality E 722 having 7 internodals; 10a, exterior,  $\times 2$ ; 10b, axial section showing simple tubular axial canal,  $\times 4$ .
- 11-12. Axial sections of mature specimens showing complex axial canal resulting from medial projections of columnals,  $\times 4$ .—11. Specimen (E 675-1) from locality E 675 showing very rarely occurring tube in axial canal.—12. Specimen (E 5-59) from locality E 5, showing evident effect of weathering on axial structures near base of section.



Jeffords & Miller – Ontogenetic Development in Late Pennsylvanian Crinoid Columnals



Jeffords & Miller – Ontogenetic Development in Late Pennsylvanian Crinoid Columnals



lar ridges, a small opening (1-2 mm.) for the axial canal (lumen), a smooth interior of the axial canal, any number of internodals up to 7, and 5 or fewer cirrus scars but generally not exceeding 4. An **adult** of the same form is interpreted to be a specimen approximately 12 mm. in diameter with about 110 ridges (**culmina**, 8) on **articular facets (articula)**, a large opening for the axial canal (4-5 mm.), and medial columnal projections (**claustra**, 8) developed in the axial canal. Commonly stem segments of mature columnals have a full development of internodals (as 3 or 7) and nodals and internodals are or tend to be equal in diameter and height. Mature (i.e., large) specimens generally have distinctive features that facilitate recognition of types; increasing difficulty is encountered as attempts are made to classify smaller and smaller specimens.

TERMIER & TERMIER (1949) recognized four regions (ages) of stems—**first age** near the calyx where columnals are not appreciably ornate and lack cirri; **second age** below the point where internodals are being inserted and where nodals are larger than in the first age and may be ornate and bear cirri; **third age** where insertion of internodals has ceased and nodals and internodals approach an identical size; and **fourth age** which includes the somewhat irregular portion of the stem serving to fix the crinoid to the substrate. The dissociated pluricolumnals with which we are concerned here show no indication of the “root” portion. The fragments, also, are not readily classifiable into the other three “ages”; rather they show a gradual

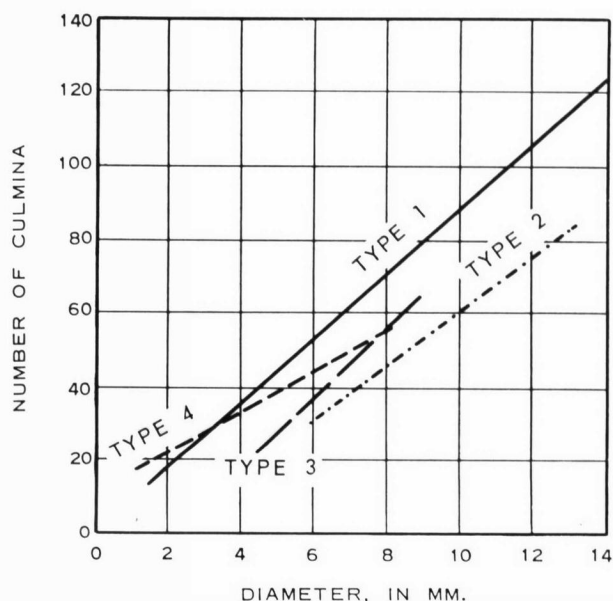


FIG. 2. Comparison of growth-index lines—relationship of columnal diameter to number of culmina—for columnal (pluricolumnal) types 1, 2, 3, and 4.

development to a relatively constant mature stage (“third age” of TERMIER & TERMIER). Columnals and segments from different parts of stems of the same taxa may differ

### EXPLANATION OF PLATE 2

[Type species of genus indicated by asterisk (\*)]

Columnal (pluricolumnal) type 2 (*Preptopremnum \*rugosum* MOORE & JEFFORDS) from the Wayland Shale (fig. 1-9) and Gunsight Limestone (fig. 10) showing changes from juvenile to mature specimens in the articular facet, relationships of nodals and internodals, and axial canal. [Additional illustrations of this species are given in Echinodermata Art. 8-9.]

#### FIGURE

- 1, 3-4. Articular surfaces showing increase in numbers of crenulae with increase in diameter of columnal,  $\times 4$ .—1. Juvenile specimen (E 5-200) from locality E 5.—3. Mature specimen (E 5-201) from locality E 5.—4. Mature specimen (E 722-25) from locality E 722 showing rarely preserved plate structure in axial canal.
2. Mature specimen (E 672-31) from locality E 672; 2a, articular showing fine adaxial projections of culmina,  $\times 4$ ; 2b, side view of pluricolumnal showing cirrus scars on nodals and three internodals in each noditaxis,  $\times 2$ .
5. Mature specimen (E 672-1) from locality E 672,  $\times 2$ ; 5a, exterior showing first- and second-order internodals between nodals; 5b, longitudinal section showing effect of weathering along axial canal.
6. Longitudinal section (E 672-71) from locality E 672 showing complex axial canal constricted by medial axial projections (claustra) of columnals,  $\times 2$ ; thickness of columnals differs with order of insertion, sutures typically somewhat irregular.
7. Longitudinal section of mature specimen (E 672-52) from locality E 672, probably weathered,  $\times 2$ .
8. Longitudinal section of juvenile specimen (E 5-72) from locality E 5 showing relatively simple and wide axial canal,  $\times 4$ .
9. Mature specimen (E 672-45) from locality E 672,  $\times 2$ ; 9a, exterior; 9b, longitudinal section.
10. Negative print of thin section of mature specimen (E 706-0) from locality E 706 showing rarely preserved axial structures and peculiar appearance of adaxial portions of columnals,  $\times 10$ .

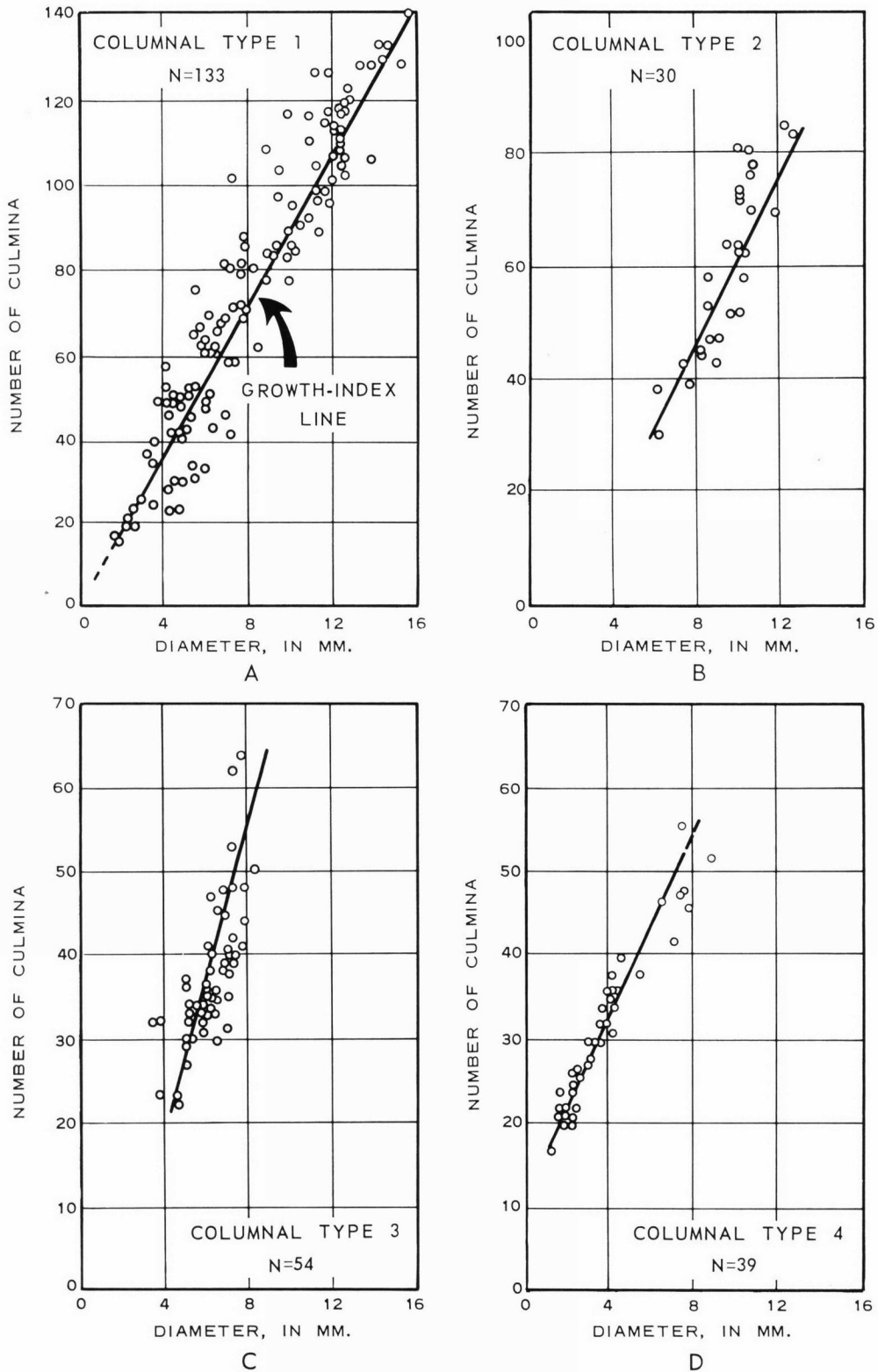


FIG. 3. Relationship of diameter of columnal to number of culmina (counted at periphery) in columnal (pluricolumnal) types 1(A), 2(B), 3(C), and 4(D). Growth-index lines drawn by inspection.

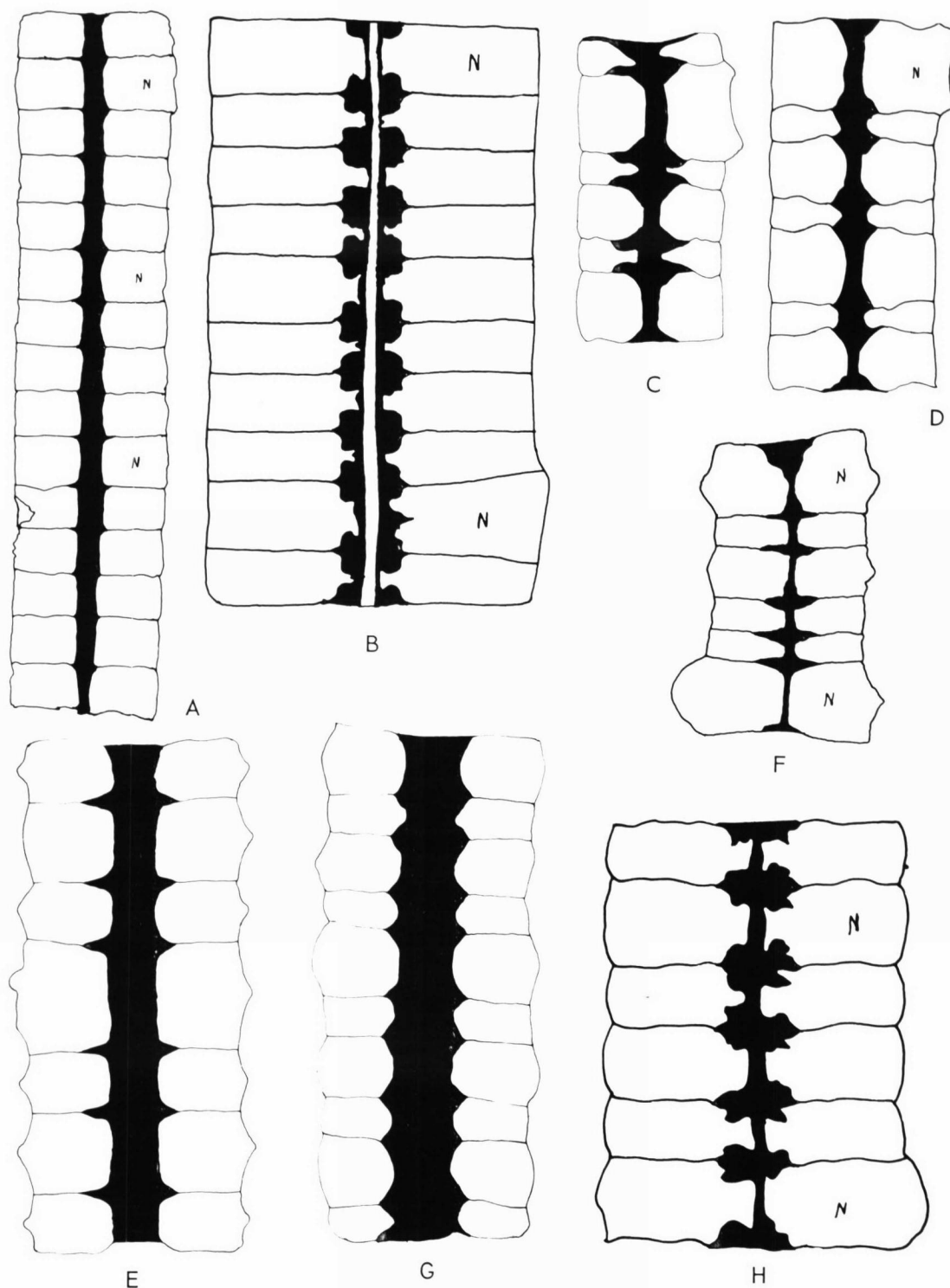


FIG. 4. Median longitudinal sections showing nature of axial canals in juvenile and mature pluricolumnals. *A, B.* Columnal (pluricolumnal) type 1; juvenile ( $\times 4$ ) and mature ( $\times 4$ ). *C, D.* Columnal (pluricolumnal) type 3; juvenile ( $\times 6$ ) and mature ( $\times 4$ ). *E, F.* Columnal (pluricolumnal) type 4; juvenile ( $\times 6$ ) and mature ( $\times 5$ ). *G, H.* Columnal pluricolumnal) type 2; juvenile ( $\times 6$ ) and mature ( $\times 4$ ).

notably so that only comparable fragments can be compared directly.

Crinoid literature contains only a few comments on the detailed growth features of stems (GRANT, 1963, p. 138). Thus, the general discussion by LANE (1963) of Mississippian stems extending as much as 970 mm. below the calyx and ranging in diameter 1 inch below the calyx from 2.5 to 18.0 mm. is notable for indicating possibilities for further study using existing collections.

Terms here applied to morphologic features of columnals and stem segments are basically from MOORE (1939b,

1952) and MOORE, JEFFORDS, & MILLER (1967). General descriptive terms serve to supplement the technical terms at this time. The discussion for each of the four types of columnals includes description and illustration of the insertion and development of internodals (Fig. 1), of the most readily observed growth-stage indicator which is the relationship of the number of articular ridges to the diameter (Fig. 2, 3), and changes with growth in features of both the articular facet and longitudinal section (Fig. 4).

## CHARACTERISTICS OF CRINOID COLUMNALS AND PLURICOLUMNALS

General morphologic features serving to differentiate four readily recognizable types of columnals and interpreted growth relationships are described below. The initial description pertains to the mature pluricolumnals; the nature of immature ones is considered in the following discussions of growth. For continuity and clarity each of four types of columnals is treated separately, but graphs showing growth or relationships are grouped to emphasize similarities and differences. Numerical data are plotted as scatter diagrams. An approximate **growth-index line** is drawn by inspection for the diameter-culmina relationship. This visual representation of data facilitates observation of relationships; more refined statistical treatment is practicable (and may be warranted if many comparable studies are reported) but mere numerical values for such growth series are not easily evaluated by most paleontologists. Because measurements of size and other features differ markedly, depending on the developmental stage, and because few columnals and pluricolumnals even in a large collection have essentially the same dimensions, the amount of individual variation generally

has not been determined. Moreover, minor errors caused by specimen distortion, undetected removal of some peripheral parts of articular surfaces, and inaccurate measurements result in a spread of the points on the graphs. Reliable and consistently reproducible measurements of the lumen, for example, are obtainable for only a very few of thousands of specimens.

Axial longitudinal sections of pluricolumnals from the Wayland and Gunsight collections show many features that facilitate recognition of the types of columnals (pluricolumnals) and comprise significant morphological characteristics of crinoids. Although TERMIER & TERMIER (1949) concluded that longitudinal sections of the axial canal of stem segments have little systematic importance, our studies suggest that data on the axial canal and surrounding columnals are sufficiently complex and consistent to have value fully equal to those observable on articular and latera (8). PHILIP (1961) illustrated longitudinal sections of lower Paleozoic stem segments that he interpreted as mature and juvenile specimens. Other features of this growth subdivision are not illustrated.

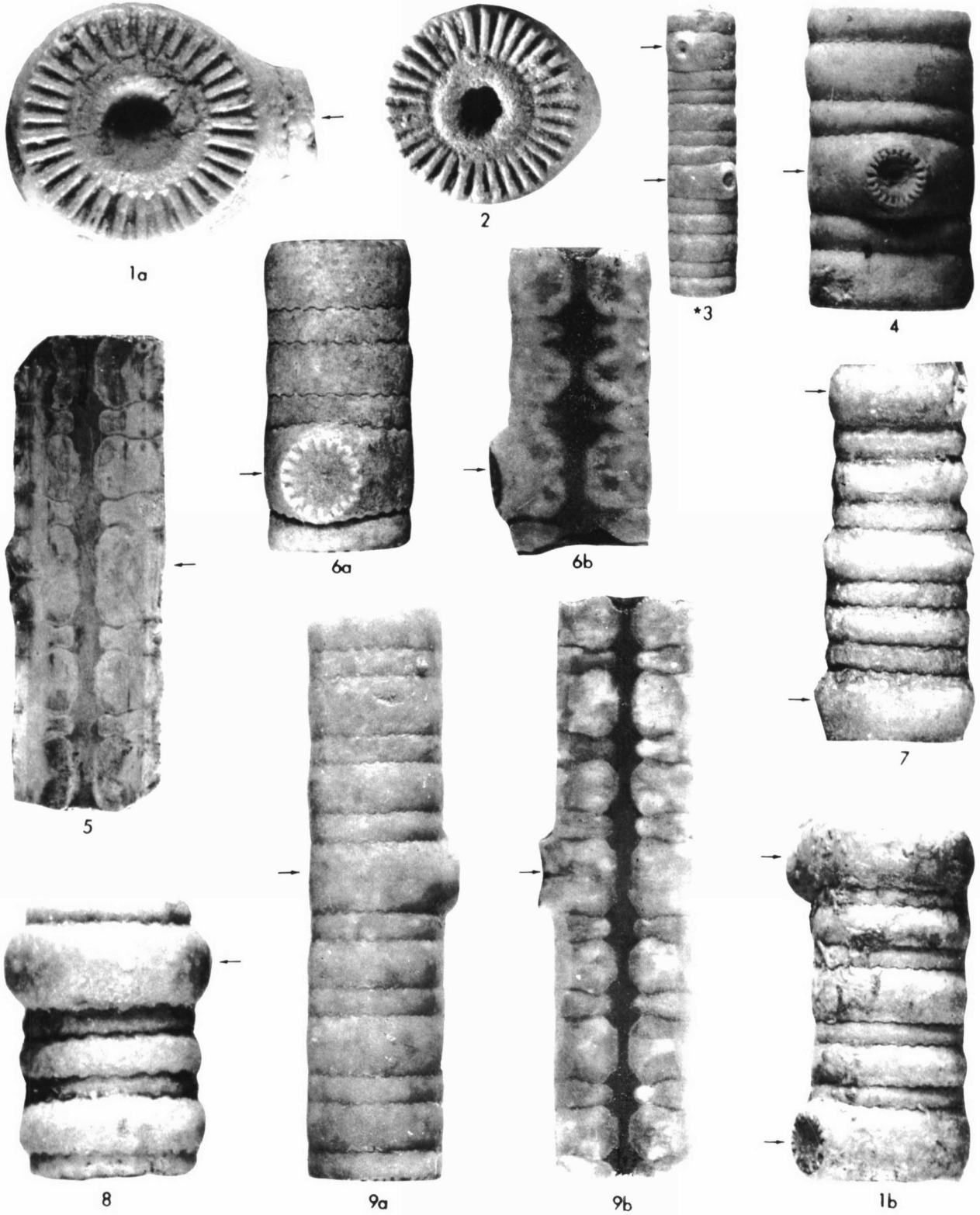
### EXPLANATION OF PLATE 3

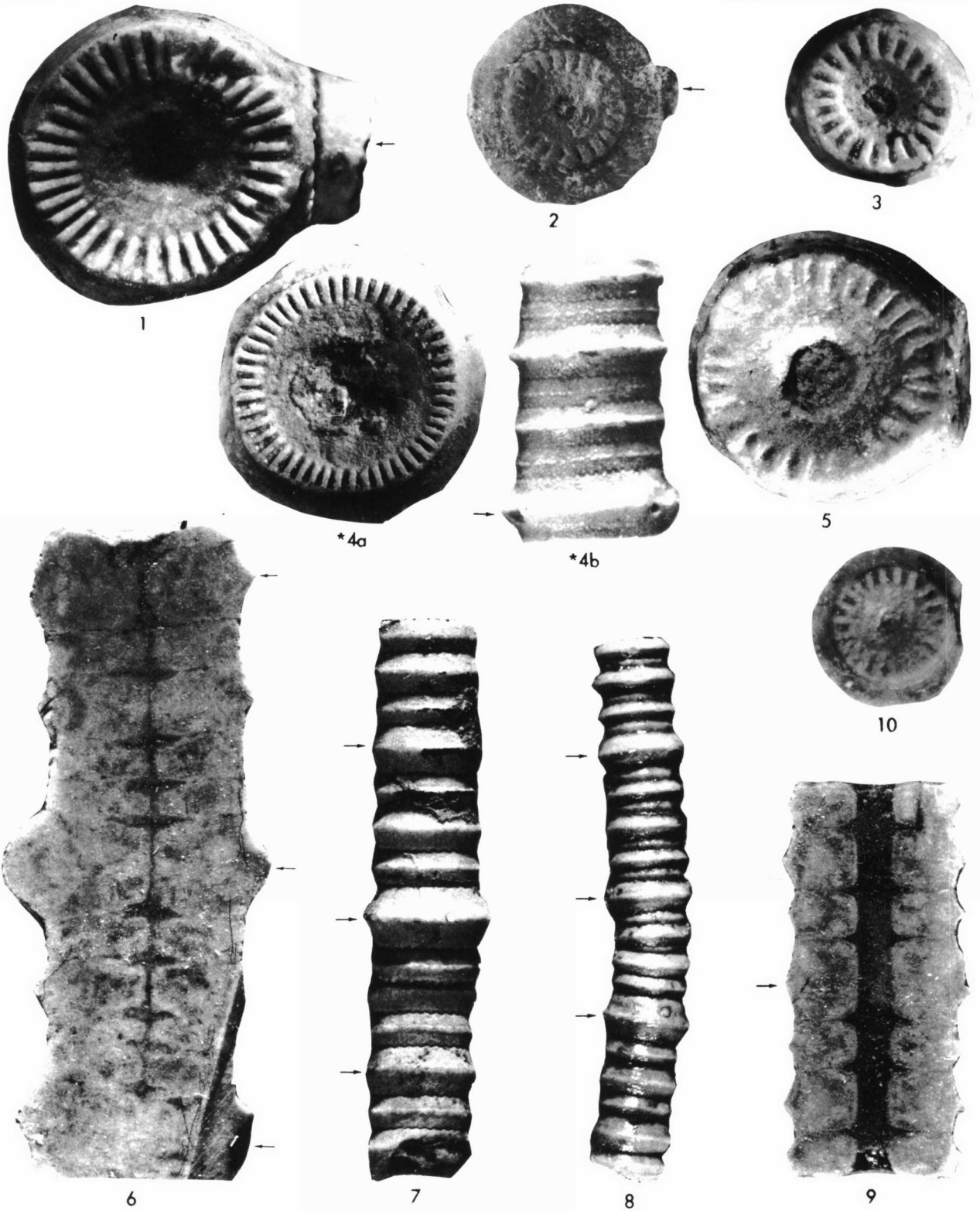
[Type specimen indicated by asterisk (\*)]

Columnal (pluricolumnal) type 3 (*Heterostelechus jeffordsi* MILLER) from the Wayland Shale showing articular surfaces, nodals and internodals, and axial canal. [Additional illustrations of this species are given in Echinodermata Art. 9.]

#### FIGURE

1. Mature specimen (E 5-16) from locality E 5; 1a, articular surface of nodal showing one cirral plate and short peripheral ridges alternating with long coarse ridges for a total of 40 ridges (culmina) at periphery,  $\times 6$ ; 1b, pluricolumnal consisting of 2 nodals and 7 internodals differing in thickness according to order of insertion,  $\times 4$ .
2. Articulum of juvenile specimen (E 672-28) from locality E 672 having 30 culmina,  $\times 6$ .
- \*3. Type specimen (E 672-26) from locality E 672 having 5 internodals in each noditaxis,  $\times 2$ .
4. Exterior of specimen (E 732-101) from locality E 5 showing cirrus facet,  $\times 4$ .
5. Axial section of mature specimen (E 675-2) from locality E 675 showing squeezed outline of most recently added internodals,  $\times 4$ .
6. Juvenile specimen (E 705-95) from locality E 705,  $\times 6$ ; 6a, exterior; 6b, longitudinal section.
- 7-8. Exteriors of juvenile specimens (E 705-360, 88) from locality E 705.—7. Internodals differ in thickness,  $\times 6$ .—8. Note small button-like cirrus indication in center of nodal which is second columnal from top,  $\times 10$ .
9. Mature specimen (E 733-1) from locality E 733,  $\times 4$ ; 9a, exterior; 9b, longitudinal section showing characteristic suture pattern for this columnal type.





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Because weathering very commonly affects preservation of delicate axial structures and this weathering is not evident from the exterior, about ten sections were found necessary on the average to obtain representation of unweathered features. Sections of mature pluricolumnals here described have either smooth to slightly ribbed axial

canals or have medial lateral projections from columnals (claustra) into the axial canals. Rarely preserved and little understood features include an axial tube (?passageway with calcified wall enclosing extension of chambered organ, nerves, etc.) (Pl. 1, fig. 10) and lamellar plates of adaxial parts of claustra adjoining jugula (Pl. 2, fig. 11).

## COLUMNAL (PLURICOLUMNAL) TYPE 1 (*Cyclocaudex plenus* Moore & Jeffords)

Figures 1,A; 2,A; 3; 4,A,B; 5,A,B; Plate 1, figures 1-13

Relatively large columnals rather low in relation to width (diameter), circular in outline, and straight to very slightly concave or convex on longitudinal exterior. Articular facets characterized by small circular lumen (slightly subpentalobate in exceptionally preserved specimens) and straight, long, and rather fine ridges that extend from periphery to or near to the lumen. Nodals (commonly bearing 1 or 2 circular cirrus scars) and internodals equal in diameter; equal in height in mature stage but unequal in immature stage. The large diameter, long culmina, and straight longitudinal profile distinguish this form.

Pluricolumnals of this sort, identified as belonging to *Cyclocaudex plenus* MOORE & JEFFORDS, n. gen., n. sp., (9), are very abundant in the collections and average 10 articulated columnals. The number of internodals in a noditaxis is 7 for more than half of the specimens (Fig. 1,A). The diagram suggests that internodals are inserted rapidly through the third order. Both second-order internodals are introduced simultaneously, but those of the third order are added somewhat irregularly. The diameters of all columnals in a single segment are essentially equal. The height of columnals is greatest for nodals and progressively less for the first-order internodal, second-order internodals, and third-order internodals. In large (ma-

ture) pluricolumnals the heights of nodals and different orders of internodals become the same or nearly so.

The number of culmina is relatively uniform for specimens of the same type having the same diameter; moreover the number increases more or less directly with the diameter (Fig. 2,A). The ridges were counted at the periphery where increases through bifurcation and insertion of short ridges are recorded but very short ridges may be partly to completely destroyed by weathering and bifurcations close to the periphery are difficult to recognize. Counts made of the inner edges of the culmina near the lumen provide data only on the longer ridges and are not closely related to diameter.

In columnal (pluricolumnal) type 1, the graph of the diameter against number of culmina (Fig. 2,A) reflects what is interpreted as a definite growth pattern represented by the approximate isometric growth-index line drawn through the points. Identification of type-1 pluricolumnals in the collections is relatively easy for the medium-sized to large specimens and seems reasonably reliable down to the smallest stems for which data are plotted.

The scatter of points about the growth-index line (Fig. 2,A) may reflect the inclusion of three distinct but closely similar biologic entities in type-1 pluricolumnals.

### EXPLANATION OF PLATE 4

[Type specimen indicated by asterisk (\*)]

Columnal (pluricolumnal) type 4 (*Cyclocrista martini* MILLER) from Wayland Shale, showing changes juvenile to mature specimens in the articular, relationships of nodals and internodals, and axial canal. [Additional illustrations of this species are given in Echinodermata Art. 9.]

#### FIGURE

- 1-3, 5, 10. Articular of juvenile columnals from locality E 734,  $\times 3$ .—1. Nodal (E 734-201) having weathered axial canal and first cirral plate.—2. Specimen (E 734-400) showing few culmina, small lumen, and wide keel.—3. Specimen (E 734-73).—5. Nodal (E 734-402).—10. Specimen (E 734-401) showing broad keel.
- \*4. Type specimen (E 5-16) from locality E 5; 4a, articular showing greater number of culmina in mature individuals,  $\times 6$ ; 4b, pluricolumnal,  $\times 4$ .

6. Longitudinal section of mature specimen (E 5-14) from locality E 5 showing narrow axial canal with intercolumnal expansions (spatia),  $\times 6$ .
- 7-8. Exterior of juvenile pluricolumnals (E 734-301, 306) from locality E 734 showing keeled latera,  $\times 6$ .
9. Longitudinal section of juvenile specimen (E 734-300) from locality E 734 showing relatively wide axial canal which is straight-sided except for expansions at small intercolumnal spatia, but wedge-like projections between columnals similar to those in mature specimens (fig. 6),  $\times 6$ .

This is suggested also by the longitudinal profiles, which consistently for pluricolumnals, are straight, concave, or convex.

For articular surfaces, growth (increasing diameter) is reflected by progressive enlargement of the lumen, slight expansion of the area between the lumen and the axial ends of the culmina, and multiplication of culmina (Pl. 1, fig. 1-5, 13).

The diameter of nodals in this form (which is essentially equal to the diameter of all columnals in a pluricolumnal) is related in only a broad and ill-defined way to the total height of the noditaxis (Fig. 5,A), the num-

ber of internodals (Fig. 5,B), and the number of cirrus scars.

The relationship of length of the culmina to diameter in type 1 columnals (pluricolumnals) is highly variable because the axial portions lack consistency even for a single specimen.

Longitudinal sections of mature pluricolumnals of this form have a rather wide axial canal and claustra extend from the medial portion of the columnals (Fig. 4,B). Juvenile pluricolumnals, on the other hand, have an axial canal with slight indentations at the junctions of columnals; claustra are lacking (Fig. 4,A).

## COLUMNAL (PLURICOLUMNAL) TYPE 2

### (*Preptopremnum \*rugosum* Moore & Jeffords)

Figures 1,B; 2,B; 3; 4,G,H; Plate 2, figures 1-10

Stem circular with rounded longitudinal profile; exterior finely granulose and bearing scattered low tubercles. Articular surface with coarse ridges or alternating coarse and finer short ridges confined to peripheral band; large circular lumen. Nodals and internodals subequal in diameter but nodals distinctly higher. The typical beaded appearance of columnals in pluricolumnals and the low tubercles characterize this form, which is recognized as belonging to *Preptopremnum \*rugosum* MOORE & JEFFORDS, n. gen., n. sp. (9), type species of the genus.

A maximum of three internodals occur in noditaxes (8) of this form; only segments bearing first-order or first- plus second-order internodals were observed (Fig. 1,B). Both the second-order internodals seem to have been introduced essentially simultaneously. The marked preponderance of pluricolumnals having three internodals

in noditaxes suggests that a complete set of internodals is introduced very rapidly just below the calyx. The nodals clearly are higher than the internodals which decrease in height according to order of insertion (Fig. 4,G).

The number of culmina is somewhat less exactly related to the diameter than in type 1 (Fig. 2,B) and culmina are fewer; the growth-index line (plotted line expressing rate of growth), however, is nearly parallel to that for type-1 columnals (Fig. 3). The articular facets of small specimens have stout culmina nearly reaching the lumen and generally alternating with short culmina; in maturity the culmina are confined to about a third of the radius (Pl. 2, figs. 1-4).

Longitudinal sections of mature specimens have a complex axial canal with broad claustra restricting the opening (Fig. 4,H). Juvenile specimens, however, have only a blunted axial tapering of the columnals (Fig. 4,G).

## COLUMNAL (PLURICOLUMNAL) TYPE 3

### (*Heterostelechus jeffordsi* Miller)

Figures 1,C; 2,C; 3; 4,C,D; 5,C; Plate 3, figures 1-9

Relatively slender columnals, outline circular, sharp keel at mid-height; sparsely ornamented by nodes and granules. Articular facet bears narrow peripheral band of very coarse and straight culmina and small to medium-sized lumen that is circular to pentalobate (in exceptionally preserved specimens). Nodals bear cirrus scars located closer to one articular facet than the other away from mid-height, many cirri incompletely developed; internodals decrease in angulation, height, and diameter with order of insertion. The sharp keel on latera of the columnals is distinctive. These pluricolumnals are typical examples of stem parts belonging to *Heterostelechus jeffordsi* MILLER, n. sp. (9).

Stages with one or two internodals were not noted;

specimens are, however, only moderately abundant. Specimens having three internodals are common (Fig. 1,C) and insertion proceeds rapidly to an observed maximum of seven internodals. Articular ridges are moderately abundant as related to columnal diameter (Fig. 2,C). These ridges increase in length slightly with increase in columnar diameter (Fig. 5,C).

In longitudinal section (Figs. 4,C,D) columnals differ in height according to their sequence in origin and are modified axially. Small internodals of mature specimens have a characteristic "salt shaker" outline, whereas these are more wedge-shaped in juveniles. The broadly rounded axial outline of the larger internodals and nodals also is distinctive.



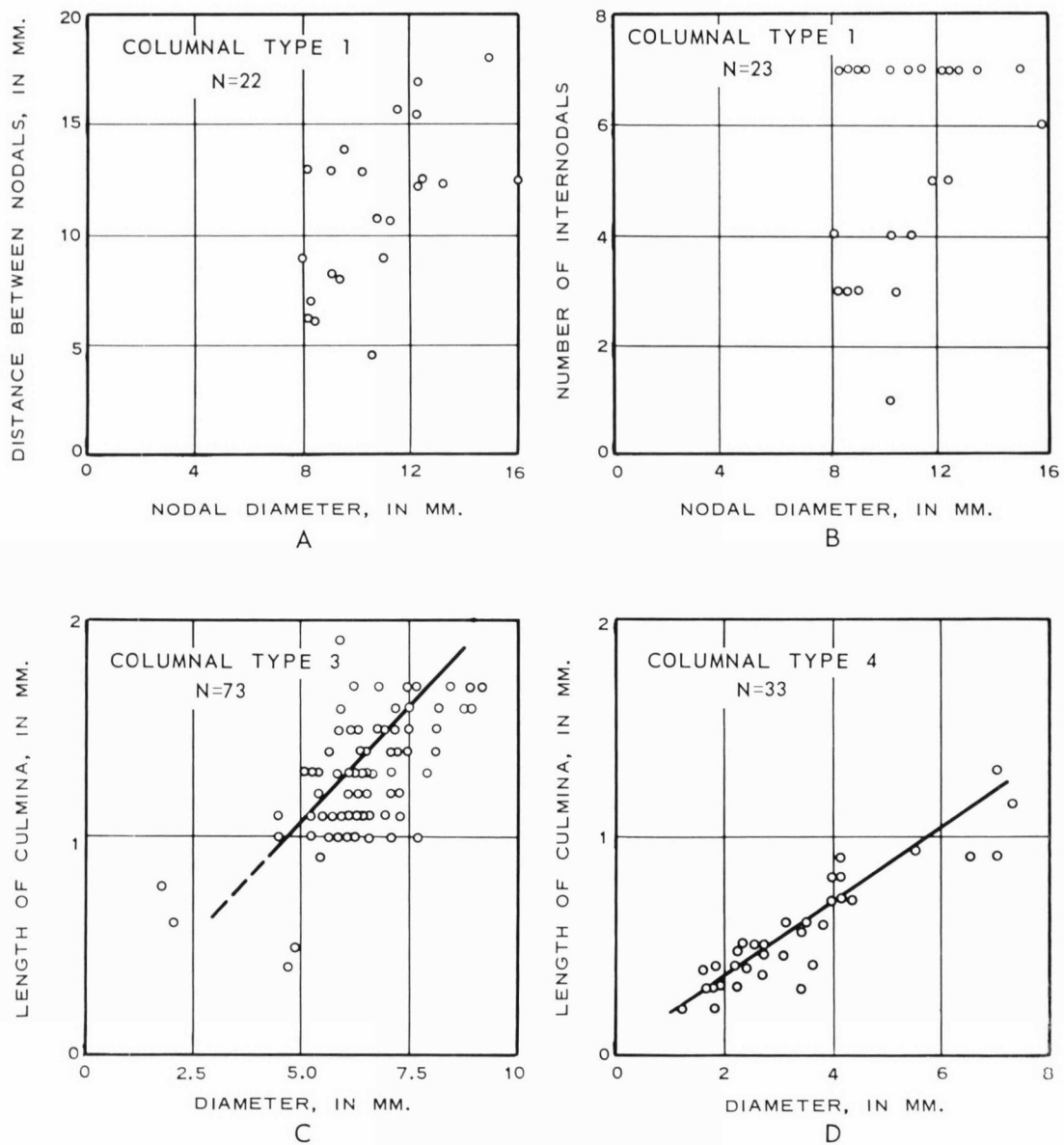


FIG. 5. Relationship of diameter of nodals to distance between nodals and number of internodals in noditaxes in columnal (pluricolumnal) type 1 and to length of culmina in columnal (pluricolumnal) types 3 and 4.

**COLUMNAL (PLURICOLUMNAL) TYPE 4  
 (Cyclocrista martini Miller)**

Figures 1,D; 2,D; 3; 4,E,F; 5,D; Plate 4, figures 1-9

Slender stems comprising circular columnals gently rounded in longitudinal profile. Articula bearing coarse short peripheral culmina that tend to bifurcate; lumen large and circular. Nodals (bearing one to three off-center cirrus scars or undeveloped cirrus indications) and internodals subequal in diameter but former distinctly higher. This type resembles type 2 in the rounded longitudinal profile and differences in height and diameter of

each cycle of internodals. It differs in the lack of tubercles and in the nature of features seen in longitudinal section. Type-4 pluricolumnals belong to *Cyclocrista martini* MILLER, n. sp. (9).

About 70 percent of the stem segments have 7 internodal columnals in noditaxes (Fig. 1,D); seemingly internodals were inserted very rapidly through the third order. Culmina are moderately numerous and increase

markedly with increases in columnal diameter (Fig. 2,D). The ridges are almost as long on small as on large specimens (Fig. 5,D).

As seen in longitudinal section (Fig. 4,E,F), mature specimens have blunt axial margins of columnals with

claustra projecting into the axial canal between columnals. In juvenile segments, the canal is even-sided (simple) except for wedge-shaped indentations at the axial margins of columnals.

## CONCLUSIONS

This analysis of four specific types of columnals (pluricolumnals) from the Late Pennsylvanian Wayland Shale and Gunsight Limestone indicates that growth stages can be interpreted for relatively short crinoid-stem segments not associated with dorsal cups.

A preferred maximum number of internodals was observed for each type (Fig. 1), and the rate at which cycles of internodals are inserted seems to differ from type to type. Although the number of columnals between nodals theoretically should be 1, 3, 7, etc., the two second-order internodals may not be introduced simultaneously and this is true also for the third-order internodals. Consequently, some internodal sequences contain 2, 4, 5, or 6 columnals. In the collection studied, some small specimens interpreted as juveniles have the same number of internodals as large specimens interpreted as mature. Also, the distance between nodals (i.e. total height of noditaxes) and the number of cirrus scars have no consistent relationship to columnal diameter (Fig. 5).

The increase in number of culmina with increase in columnal diameter (Fig. 2,3) is judged to be a practical basis for estimating growth. This relationship based on readily identified specimens also aids in assigning small or juvenile columnals to a particular columnal type.

Features visible on longitudinal axial sections provide essential information for differentiation of columnal (pluricolumnal) types (Fig. 4). In the materials here reviewed, juvenile specimens have a simpler axial canal than mature specimens. The complex patterns observable in the axial canal result primarily from medial axial projections of columnals (claustra) that locally constrict the canal.

Some rarely encountered and as yet unexplained structures noted in longitudinal sections (Pl. 1, fig. 10; pl. 2, fig. 11) may occur only in exceptionally preserved material. They may represent, however, very rare fossilization of the soft anatomy as has been noted by CASEY (1960, p. 270) for mollusks.

Nodals have been designated as of first- or second-order by TERMIER & TERMIER (1949). Nodals (as recognized by exterior or interior indications of cirri) in the Wayland and Gunsight collections are not so separable although some nodals do differ irregularly in thickness and diameter. A suspicion that the first internodal might develop cirri at maturity and thus lead to the appearance of two orders of nodals was investigated insofar as the relatively short pluricolumnals permitted. No substantiation of this concept was obtained, and no regular alternation in size was observed for nodals. Seemingly, therefore, TERMIER & TERMIER (1949) may have designated nodals as "first-order nodals" and the first-order internodals as "second-order nodals."

Inasmuch as the Late Pennsylvanian columnals and pluricolumnals studied change markedly with growth in size and in nature of articular facets and longitudinal sections, comprehensive analyses of such specimens need to take such growth into account. It is observed also that weathering removes details of the axial canal and lumen in a large proportion of these columnals. Although studies on numerous short pluricolumnals such as this can provide a considerable insight into the morphology and growth of crinoid stems, major guidance in these studies would result from similar analyses of long stem segments attached to calices such as the exceptional material recorded briefly by LANE (1963).

## LOCALITY DESCRIPTIONS AND REFERENCES

Localities from which fossils described and illustrated in this paper are listed with those pertaining to Echinodermata, Articles 8 and 9, given with descriptions in the following Supplement.

Also, publications cited in this paper are included in the consolidated list of references for Echinodermata, Articles 8-10, in the separately paged Supplement which follows.

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