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MICROSTRUCTURAL ANALYSIS OF THE CRINOID STEM¹

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ABSTRACT

The microstructure of the crinoid stem of Recent crinoids consists of two different types of stereom. Study of the organization and distribution of these within a stem plate and their ontogenetic development yield functional interpretations of the crinoid stem. Although frequently altered by diagenesis, fossil crinoid stems of the Mesozoic and Cenozoic crinoids are often well enough preserved to permit similar interpretations based upon microstructural analysis.

INTRODUCTION

When a paleontologist studies disarticulated parts of crinoid stems, he necessarily tends to build a parataxonomy and is likely to put skeletal elements of the same species into very different parataxons. He then seeks some method of bringing all parts of one fossil column together again, independent of the variable morphology of the column ossicles. Microstructural analysis is such a method. It is based upon quantitative studies (stereom biometry) and dynamic notions (growth, morphogenesis, functional morphology). Comparison between Recent and fossil crinoid

stems is very important in validating the interpretations.

With this view in mind, a few years ago I selected crinoid stems of Articulata, which are easy to study in the early stages of an investigation (Roux, 1970, 1971, 1974). In this paper I present the principles of microstructural analysis with a few examples. It may be possible to extend some of these results to Paleozoic crinoid columns, but this has to be confirmed by other research.

MICROSTRUCTURE OF THE CRINOID STEM

**OBSERVATIONS ON STEREOM
FOSSILIZATION**

Microstructural study of fossil crinoid ossicles is often difficult because specimens preserved in sediments may be altered. My purpose here is not to describe all possible types of ossicle diagenesis, but it is important to know those aspects that are favorable for observation of fossil stereom,

or, on the contrary, those that make interpretation difficult.

The early stages of diagenesis are very well displayed in specimens from the Eocene London Clay. Near the ossicle surface aragonitic needles grew into the stereom meshes. They are very numerous where the stereom has a thick calcitic meshwork (e.g., growth lines, fulcral ridge). Probably this thick, high, magnesian calcite is unstable and easily altered (Pl. 1, 1, 3, 5). Due to the growth of aragonitic needles, an external

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crust impastes the meshwork and may hide morphological details (Pl. 1,2). This process can be limited to an external crust or the calcite may penetrate the ossicle. Later on, the whole piece (stereom and infilling carbonate) becomes a single crystal of calcite, but a discontinuity often remains between the stereom and the infilling carbonate. This becomes clearly apparent after a slight artificial etching by dilute acid.

When ossicles are buried in mud, some sediment may penetrate into the articular facet and preserve the stereom against diagenetic alteration (Pl. 1,4,6). In some confined environments, framboidal pyrite grows within the stereom and occasionally induces the meshwork to burst (Gaspard & Roux, 1974). When the stereom is preserved, a later oxidation of the pyrite commonly induces a decay of the calcite meshwork and a carbonate crust precipitates at the boundary between ossicle and sediment. Occasionally, ferrous oxides make an internal cast of the stereom (Pl. 2,2,3). Depending on the specimen, the external calcite crust may grow during early or late diagenesis. When it hides the stereom, it has to be removed in order to observe the microstructure of the meshwork.

In spite of the numerous causes likely to destroy the stereom during diagenesis, part of an ossicle is frequently well enough preserved to be useful for a detailed microstructural analysis. However, it is only on rare occasions that fossil stereom can be observed in three dimensions (Pl. 1,5) as in Recent specimens. Usually, it is necessary to cut thin sections across fossil columns either longitudinally (axially or paraxially) or transversely.

MICROSTRUCTURAL ORGANIZATION

Principal Types of Stereom and Their Significance.—The two main stereom types are:

1) A regular meshwork, alpha (α) stereom (Pl. 1,5), which consists of parallel galleries that are penetrated by collagenous fibers, which are parallel throughout the ossicle. They both parallel the axis in the stem. Alpha stereom is found in the areola and crenularium in the majority of the articular facets of stems.

2) An irregular meshwork, beta (β) stereom,

which occasionally has growth lines. When it corresponds to a secondary development of the stereom, it commonly has distinctive character, e.g., very dense little meshes (smooth articular surface of synostosis), or large meshes when stereom grows in the lumen. Syzygial crenularium is made with β stereom.

Observation of the stereom pattern is important in making functional morphological interpretations. Parallel collagenous fibers are inserted on β stereom and go through galleried α stereom (they join two ossicles in such a case) or pass through only α stereom in several ossicles (they take part in the cohesion of many columnals along the stem or from one internodal to another one).

On articular facets, the area of friction between two ossicles is determinable by calcite thickness (crenularium, fulcral ridge, perilumen). Diagenesis makes their identification difficult in fossil columnals (Pl. 2,4).

Disposition of Different Meshworks in Columnals.—Functional morphological needs govern the disposition of the different meshworks in columnals. Starting with a primitive plate with β stereom and a syzygial crenularium (Fig. 1,A), α stereom can develop into two different types of microstructural organization.

1) When β stereom is predominant in the ossicle, it often shows growth lines and α stereom is limited to the crenularium. These articulations are often very strong, but allow only very small movements or no movement at all. Collagenous fibers paralleling the axis are absent or play a secondary part. This type of organization is frequent in distal part of stems.

2) When α stereom predominates, parallel collagenous fibers are important and β stereom is localized in the periphery of the columnal or develops an epifacet. These articulations allow larger movements and are very abundant in the proximal part of stems.

Pentalobate columnals possess both these types of microstructural organization, the first one in interpetaloid areas and the other one in petaloid areas.

The movements of the articulations are favored by a hollowed areola where α stereom is limited to a thin layer over the β stereom area. The calcitic skeleton is thus lightened (Fig. 1,B',C').

When an articulation is modified secondarily to a syzygy or synostosis, parallel collagenous fibers disappear and a stereom becomes useless. In a secondary synostosis (such as the lower joint of distal nodals of Pentacrinidae), the new β stereom with its dense little meshes fills up the interarticular space and anchyloses the articulation. When some areolae undergo later syzygial modification (Fig. 1, D'), a few large parallel fibers are still functional and calcite thickness increases around the lumen of the large parallel galleries. Then, the smooth areola of the original symplexy becomes an irregular syzygial areola.

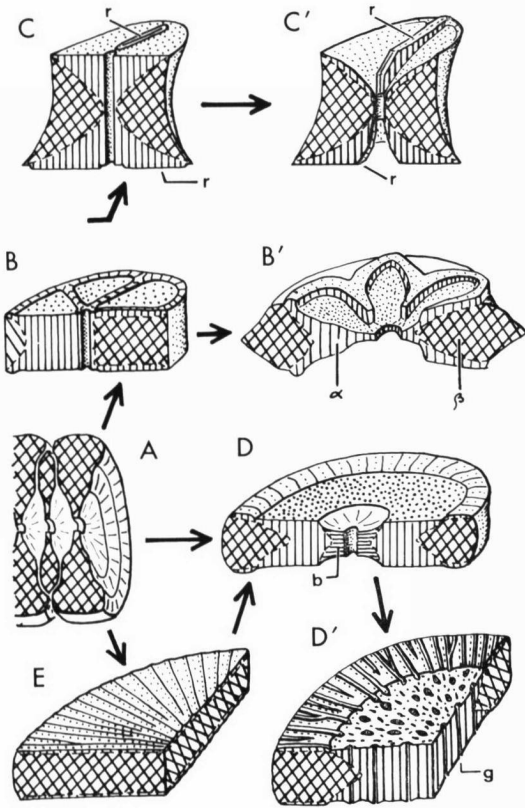


FIG. 1. Main microstructural organizations of crinoid columnals. A, primitive proximal syzygy; B, pentalobate columnals; C, ellipsoid columnals (synarthry); D, multiradiate columnals with an areola; E, multiradiate columnal without areola. B', C', and D' are late ontogenetic stages of B, C, and D. [See B' for α and β stereom representation; b, secondary β stereom with large meshes; g, only large α galleries functional; r, fulcral ridge.] These schematic drawings suppose that columnals are the same feature during growth.

It must be borne in mind that the features of an articular facet and the microstructural organization are the result of changes in the columnal during its growth.

MICROSTRUCTURAL ASPECTS OF ONTOGENETIC DEVELOPMENT

Stereom Growth.—The stereom grows from many growth centers or from growth lines parallel to the external surface of the columnal. The growth unit is a succession of meshes from the smaller to the larger one (Pl. 1,4). The subdivision of the larger meshes gives rise to one or two new mesh series. Dichotomy is not a general rule. The threshold of division is variable with different areas and growth stages (Fig. 2). Usually, the radial component of growth is more important than the axial one. Thus, the main biometrical analysis of the stereom is made along a radial line (radial biometrical graph) on an articular facet or a transverse section through the stem.

A radial biometrical graph is irregularly serrated (Fig. 2). When growth centers are very numerous with clear thresholds of mesh division, the graph shows several stages that are easy to observe on fossil specimens (Fig. 3). Comparison between radial biometrical graphs of β stereom and α stereom is very important for interpretations in pentalobate columnals because the former is often more independent of functional morphological needs than the latter.

Growth centers are present in α and β stereom, growth lines only in β stereom.

Microstructural Evolution During Columnal Growth.—The ontogenetic development of columnals is recorded in the stereom; this can be studied by microstructural analysis. A radiograph through a Recent xenomorphic stem (Pl. 2,1) and many observations on fossil columnals confirm the unmodified preservation of the microstructure of the early growth stages of the ossicle. Transverse selections from the articular facet to the midline of the ossicle show several microstructural organizations resulting from morphological changes during columnal growth.

If changes in columnal morphology are important, a study of microstructural organization reveals the ontogenetic relations between several facet features (Fig. 4, 5). This has to be com-

pared to distal syzygies of a stalk, which are the most likely to show changes in form (Fig. 5,C,D). When the rate of morphological change is low, it is necessary to make a biometrical study of the stereom to reveal growth stages (Fig. 3).

During the microstructural evolution of a columnal, the functional morphological adaptation of α stereom is in progress. When a perilumen functions as an axial pivot, strong parallel collagenous fibers are localized around it and allow larger movements of the articulation with strength concentrated toward the center of the facet. In this light, Middle Jurassic *Extracrinus*

columnals have an α stereom that is more advanced than that of the *Pentacrinus*, and the Lower Jurassic *Extracrinus* (*Seirocrinus*) *subangularis* has a stem in which proximal or young columnals show a primitive α stereom similar to that of *Pentacrinus*. Isocrinid columnals (Fig. 3) are useful in demonstrating that the biometrical characteristics of the stereom have a taxonomic significance in addition to functional morphological interpretations. Comparison between proximal biometrical graphs of several species or genera can be helpful in establishing some phylogenetic relationships.

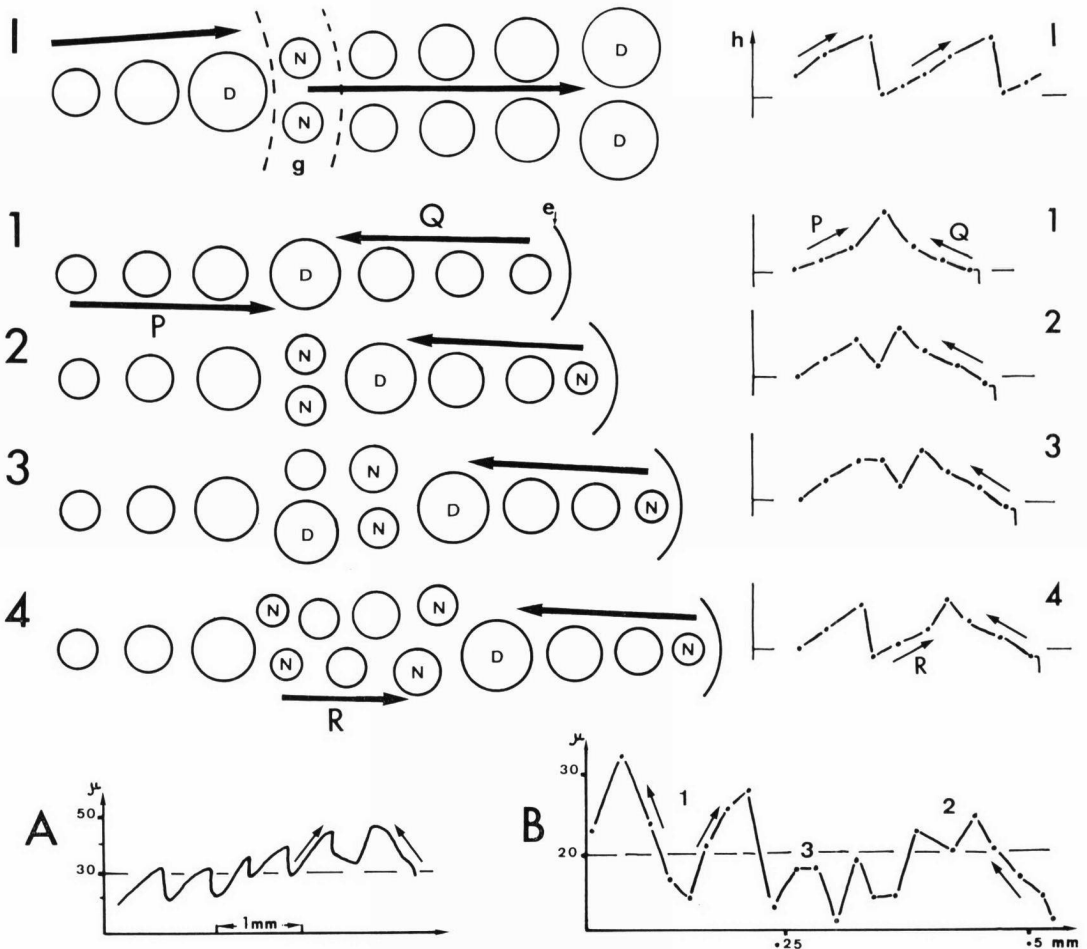


FIG. 2. Stereom growth and interpretation of biometrical graphs. I, β stereom with growth lines; A, radial biometrical graph of the β stereom of Jurassic *Apiocrinites* columnal; B, radial biometrical graph of the α stereom of a young columnal of Recent *Annacrinus*; 1, 2, 3, 4, growth centers development near a stem surface (e). [P and Q, first growth centers, the growth of P is stopped after 2, Q is always active after 4; R, new growth center; D, mesh at the threshold of subdivision; N, new mesh; g, growth line.] See Roux, 1971, for further detail.

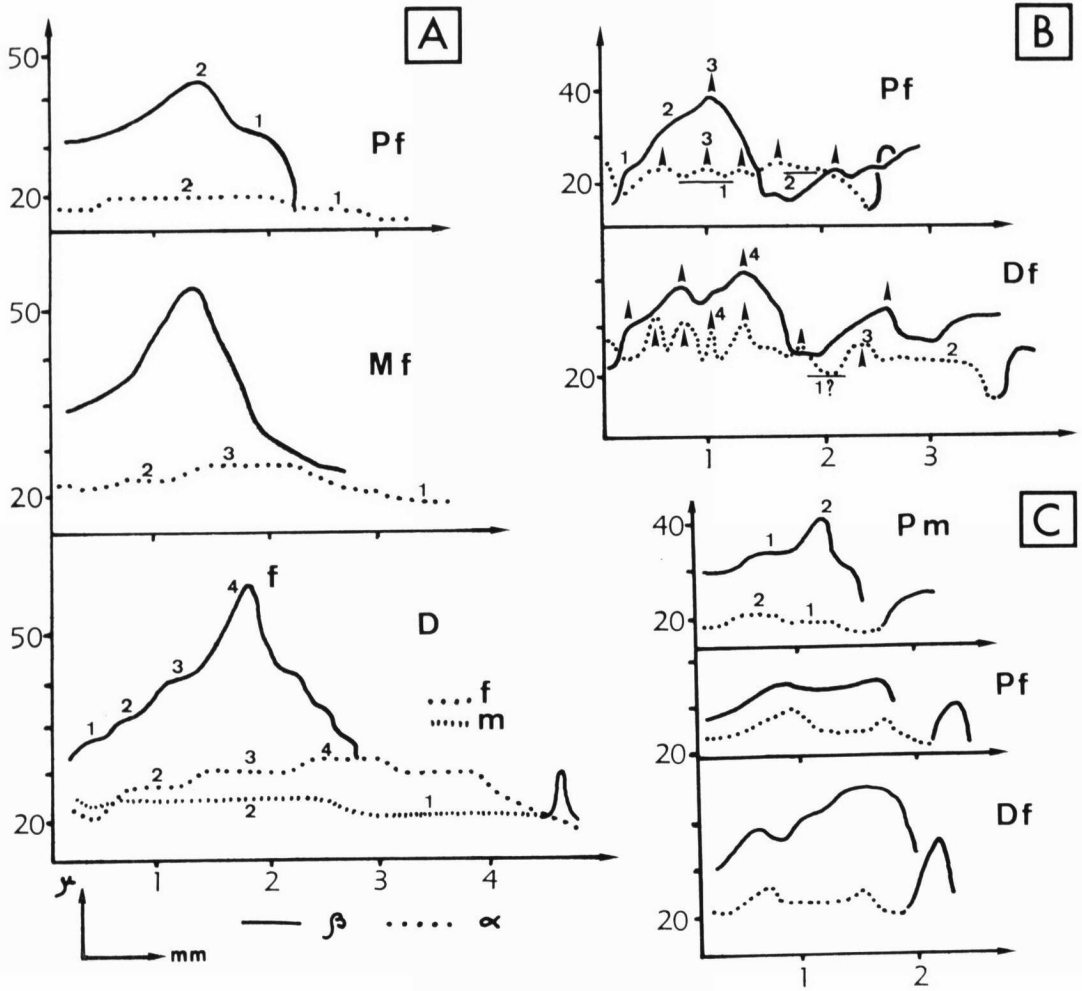


FIG. 3. Radial biometrical graphs of isocrinid columnals. A, *Pentacrinus tuberculatus* Miller; B, *Extracrinus (Seirocrinus) subangularis* (Miller); C, *Balanocrinus subteres* (Münster); [P, proximal; M, median; D, distal; f, articular facet; m, near the median section; numbers indicate growth stages; arrows indicate big growth centers]. Note the most important taxonomic characteristics in distals.

CONCLUSIONS

Microstructural analysis of crinoid columnals provides detailed information on the ontogeny and morphogenesis of crinoid stalks. This is a valuable complement to the macroscopic studies of morphological features of crinoid columns (Moore *et al.*, 1968). Such analyses will be extended to other echinoderms. Macurda (1973)

has tried an interesting comparison between crinoid, ophiuroid, and blastoid stereom. However, the most important consequence of microstructural analysis of the stereom concerns the study of the ontogeny of the skeletal parts of fossil echinoderms which are usually disarticulated and isolated in the sediments.

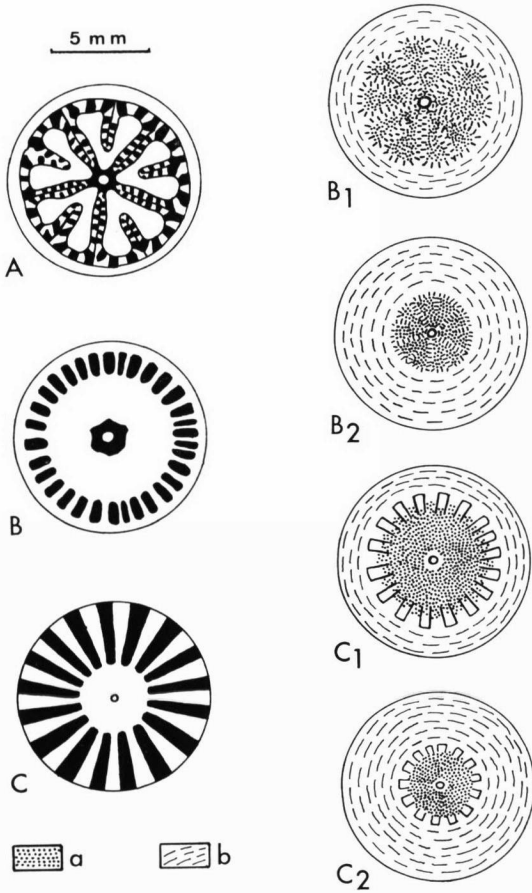
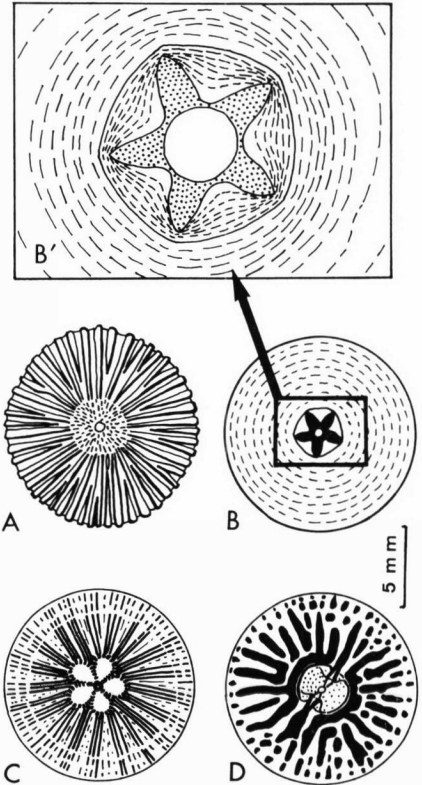


FIG. 4. Microstructural evolution of columnals of *Encrinurus lilliformis* Lambert (Triassic). At the left, morphology of facets; at the right, microstructural organization of transverse sections. [A, proximal; B, median; C, distal; B₁, C₁, sections near the facet; B₂, C₂, sections near the median plane; a, α stereom; b, β stereom.]



ellipsoidal synarthry to multiradial morphology.

FIG. 5. A, *Millericrinus milleri* Schlotheim, Jurassic, articular facet of a distal columnal; B, transverse section of A showing the pentalobate organization of the young columnal; C, distal columnal of *Austinocrinus* (Cretaceous) showing an evolution from pentaradial to multiradial morphology; D, distal secondary syzygy of Recent *Monachocrinus*, which shows an evolution from

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EXPLANATION OF PLATES

PLATE 1

Stem plates of fossil Isocrinida and Millericrinida.

FIGURE

- 1,3,5. Details of a columnar facet of *Democrinus londonensis* (Forbes) from the London Clay of Copenhagen fields (British Museum Natural History, E 427).—1. General view of the corroded fulcral ridge (*r*), $\times 200$.—3. Enlargement of the same showing aragonitic needles, $\times 750$.—5. Enlargement of the well-preserved *a* stereom, $\times 900$. Compare with Pl. 2,4-7.
2. A columnal facet with a corroded fulcral ridge (*r*) and an external calcitic crust (*e*), *Conocrinus thorenti* d'Archiac, Eocene, southern France, $\times 150$.
4. Detailed view of a columnal facet showing a series of meshes radiating from a growth center, *Encrinus granulosus* Münster, Triassic, Saint Cassian, Southern Alps, $\times 900$.
6. Detailed view of an arcola in which the sediment has preserved the stereom against diagenetic recrystallization, *Encrinus lilliformis* Lambert, same locality as preceding fig. 4, $\times 300$.

PLATE 2

Stem plates of Isocrinida and Millericrinida.

FIGURE

1. Positive of a radiograph of the upper part of the stem of a Recent *Monachocrinus recuperatus* Clark (Paris Museum Natural History, Thalassa, W 425), showing microstructural characteristics of proximal columnals, which are still present in the older mesistele columnals, $\times 6$.
- 2,3. Fossilization of a columnal with an internal cast (ferrous oxide) of *a* stereom (detailed in 3), and a later calcitic crust on the facet (*e*), *Balanocrinus pentagonalis* Goldfuss, Jurassic, black shale in eastern France, $\times 150$ and $\times 600$, respectively.
4. Articular facet of a median columnal of *Encrinus lilliformis* Lambert, Triassic, Saint Cassian, Southern Alps, with a diagenetic external crust (*e*) and the thick calcite of the perilumen (*p*), which functions as part of an axial pivot of the articulation, $\times 15$.

