MORPHOLOGY AND EVOLUTION
OF
BLASTOZOAN ECHINODERMS

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ABSTRACT. The new subphylum Blastozoa is proposed for four classes of extinct Paleozoic "pelmatozoan" echinoderms, Eocrinoidea, Parablastoidea, Rhombifera, and Blastoidea, until now included in the subphylum Crinozoa. All blastozoan echinoderms are characterized by small fingerlike food-gathering appendages called brachioles apparently lacking tube feet, respiratory sutural pores or folds, a columnal-bearing stem or irregularly multiplated holdfast, holoperipheral calyx plate growth, and often well-developed pentameral symmetry. Most blastozoans were semipermanently attached upright filter feeders, but a few may have been bottom-living and mobile. The total range of the subphylum Blastozoa is from early Cambrian to late Permian.

The contrast in food-gathering appendages appears to be the most important difference between blastozoan (brachiole-bearing) and crinozoan (arm-bearing) echinoderms. Normal brachioles, unlike crinozoan arms, are usually attached to specialized recumbent ambulacral areas, and are always biserially plated, unbranched, and nonpinnulate. Brachioles are present in all known blastozoans and appear to be relatively conservative structures, showing only minor changes over 350 million years. In addition, because blastozoan ambulacra lack openings to the calyx interior, the brachioles mounted on them may have completely lacked tube feet and extensions of the water vascular system.

Nearly all blastozoan echinoderms have either sutural pores (epispires) that open directly into the calyx interior and probably housed external, soft, papulae-like organs, or sutural folds (pectinirhombs, cataspires, or hydrospires) with thin calcified membranes extending into the calyx interior. Calyx respiratory structures like these are rarely found in crinozoan groups where the tube feet on the arms are the primary respiratory organs. Pentameral symmetry was already present in the ambulacral systems of the earliest known blastozoans, and in later forms it gradually spread to other calyx structures. During the middle Cambrian and earliest Ordovician, respectively, blastozoan eocrinoids and crinozoan crinoids independently developed an almost identical columnal-bearing stem from a more primitive multiplated holdfast.

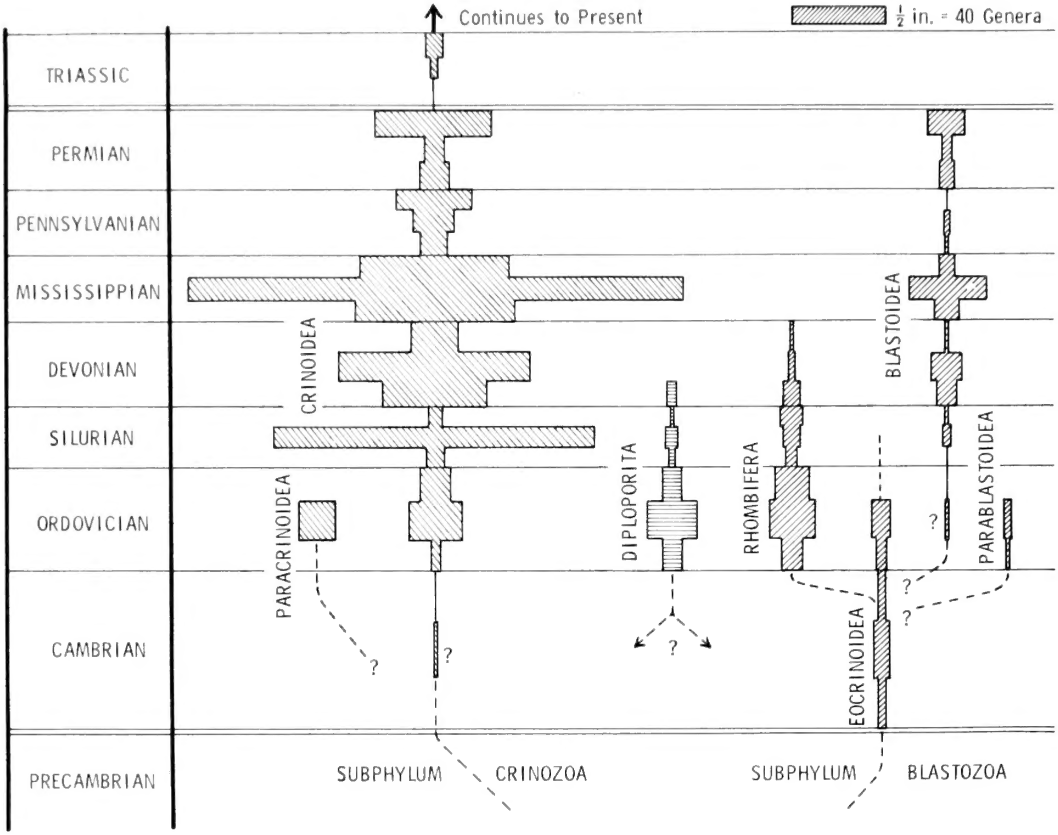
The two smaller and less well-known blastozoan classes, Eocrinoidea and Parablastoidea, were studied in detail during this project. Eocrinoids, with at least 25 genera and 37 species, range from the early Cambrian to the middle Ordovician and are the earliest and most primitive blastozoan echinoderms. The recently erected class Lepidocystoidea (Durham, 1967b) is here rejected, and its members are returned to the Eocrinoidea as a separate order. Parablastoids, with three genera and seven species, are confined to the early and middle Ordovician and apparently represent a short-lived, blastoid-like, experimental stock. The subphylum Crinozoa is here amended and restricted to include only two classes of attached echinoderms with arms, Crinoidea and Paracrinoidea; an additional "pelmatozoan" class, Diploporita, is left unassigned at present. New taxa include four eocrinoid genera and nine species from the Cambrian and Ordovician, one parablastoid genus and five species from the middle Ordovician, and one crinoid(?) genus and species, extending the range of this class back to the middle Cambrian.

Blastozoan echinoderms first appeared in the fossil record in the early Cambrian, and by middle Cambrian times crinozoans were also present. These early representatives of both subphyla were already quite different, especially in their characteristic food-gathering appendages, and it seems likely that these two groups diverged at some time before the beginning of the Cambrian. During the early and middle Paleozoic, blastozoan echinoderms underwent a gradual evolution of more advanced morphologic features, plus a sequential replacement of classes within the subphylum. These blastozoan classes competed with the more successful Paleozoic crinoids during most of the Paleozoic for the role of dominant attached filter-feeding echinoderm. However, the record of blastozoan echinoderms came to a close with the extinction of blastoids during the late Permian invertebrate crisis.

INTRODUCTION

During the past ten years, there has been a marked revival of interest in primitive Paleozoic echinoderms. This has come about both because of new discoveries, especially in the Cambrian and Ordovician, and because of extensive review work dealing with the morphology, taxonomy, and evolutionary history of early echinoderms during preparation of the echinoderm volumes for the Treatise on Invertebrate Paleontology, edited by R. C. Moore. Two of the three echinoderm volumes in this series that review all Paleozoic echinoderms except crinoids have now been published (Vol. U[1 and 2], 1965, and Vol. S[1 and 2], 1967). Since 1962, new discoveries and taxonomic revisions have resulted in the proposal of ten new echinoderm classes (for examples, see Durham and Caster, 1963, and Robison and Sprinkle, 1969), raising the total number of living and extinct echinoderm classes to 21 according to the present Treatise classification. Echinoderms now lead all other phyla in the number of proposed and generally accepted classes, although only four (or five) classes are living today and a total of only about 18,000 living and extinct species have been described.

The older two-subphylum classification of echinoderms that used the names Pelmatozoa and Eleutherozoa was rejected by Fell in the early 1960's (1962: 138; 1963: 490). He suggested that a four-subphylum system, using the names Crinozoa (Matsumoto, 1929), Asterozoa and Echinozoa (Zittel, 1895), and Homalozoa (Whitehouse, 1941), be substituted for it, and this proposal was subsequently adopted for use in the Treatise (Ubaghs, 1967a: S51). This four-subphylum classification is further modified here by the proposal of the new subphylum Blastozoa for four (and possibly five) classes of extinct, brachiole-bearing, Paleozoic attached echinoderms, and the restriction of the subphylum Crinozoa to two (and possibly three) classes of attached echino-



Text-figure 1. Ranges and relative importance of crinozoan and blastozoan classes. Abundance plotted in number of genera (½ inch width = 40 genera). Note that both subphyla begin in the Cambrian and show a similar abundance pattern throughout the Paleozoic, but that crinoids completely dominate the record after the Ordovician. Crinoid and "cystoid" data modified from Moore (1952) and Kesling (1967).

derms with arms. As presently understood, the new subphylum Blastozoa includes the classes Eocrinoidea Jaekel, 1918 (early Cambrian–middle Ordovician, 25 genera), Parablastoidea Hudson, 1907 (early–middle Ordovician, three genera), Rhombifera Zittel, 1879 (early Ordovician–late Devonian, 50 genera), and Blastoidea Say, 1825 (middle Ordovician(?), middle Silurian–late Permian, about 87 genera) (Text-fig. 1). The class Diploporita Müller, 1854 (early Ordovician–early Devonian, 36 genera) may possibly belong either in this subphylum or in the Crinozoa, but cannot be assigned with certainty at the present time because knowledge of the food-gathering appendages is almost completely lacking. The subphylum Crinozoa, as revised here, includes the class Crinoidea Miller, 1821 (middle Cambrian(?), early Ordovician–Recent, about 750 genera) and probably the class Paracrinoidea Regnell, 1945 (early–middle Ordovician, 14 genera) (Text-fig. 1).

Blastozoan echinoderms have certain distinctive features that can be used to characterize this new subphylum. Nearly all members have small, biserial, food-gathering appendages called brachioles, usually mounted on specialized recumbent ambulacral areas. A columnal-bearing stem, or in some early forms an irregularly multiplated holdfast, is commonly used to attach the calyx to the sea floor. The calyx is usually more or less globular in the many upright attached forms, but modifications to a flattened bilaterally symmetrical calyx and a mobile way of life have apparently occurred several times. Most blastozoan echinoderms have developed characteristic pore- or foldlike respiratory structures on the sutures between the calyx plates. Well-developed pentameral or five-sided symmetry is present in the calyces of many later forms, although it first occurs as far back as the early Cambrian in the ambulacral systems of lepidocystid eocrinoids. The calyx plates show holoperipheral primary plate growth with growth lines on the exterior, and secondary deposits on the interior and scattered parts of the exterior. Finally, there is considerable evidence that all blastozoan echinoderms may have lacked tube feet on their brachioles and ambulacral areas, thus indicating that the water vascular system was much reduced. This last feature, if true, would represent a major difference from crinozoans and most other known echinoderms.

Many paleontologists have studied blastozoan echinoderms since the first blastozoan species, the rhombiferan cystoid *Echinus* (now *Echinosphaerites*) *aurantium,* was described by Gyllenhaal in 1772. The first major grouping of blastozoan echinoderms, the family (now class) Blastoidea was established by Say (1825: 293) to include echinoderms "intermediate between crinoids and echinoids." The class Cystoidea was established in 1846 by von Buch, and during the later half of the 19th century major works on cystoids and blastoids, plus other early echinoderms, were produced by Roemer, Billings, Barrande, Etheridge and Carpenter, and others. Bather (1900) and Jaekel (1899) proposed modified classifications of these primitive echinoderms and described many new forms. Hudson (1907: 119) proposed the order (now class) Parablastoidea for an unusual Ordovician blastoid-like form, and in 1918, Jaekel (1918: 24) proposed the subclass (now class) Eocrinoidea for several genera of early cystoid-like forms that could not be assigned elsewhere. During the first half of the 20th century, major additions to our knowledge of blastozoan echinoderms were made by Foerste, Yakovlev, Chauvel, Hecker, Bassler, Reimann, and Regnell. Since 1950, new discoveries have been made and older genera revised in the eocrinoids by Ubaghs and Robison; in the cystoids by Kesling and Paul, and in the blastoids by Fay, Macurda, and others. All of the information available up to early 1966 has been summarized in Treatise Vol. S(1 and 2) (1967) in chapters by Ubaghs, Durham, Kesling, Fay, Beaver, Macurda, and others.

Several authors, ranging as far back as Burmeister in 1856 and extending up to the recent Treatise volumes (Ubaghs, 1967a: S54), have suggested that there is a fundamental difference between attached echinoderms with arms and those with brachioles (see p. 57). However, until now this distinction has not received any definite taxonomic status, probably because many of the more primitive brachiole-bearing groups, especially in the Cambrian, were so poorly known and because appendages in many groups are not commonly preserved. Recent studies described here, in publications by other authors, and in the Treatise, have given us much additional information on which to base a new class and subphylum classification of these early attached echinoderms.

During work on this project, I studied the preserved morphology and revised the taxonomy of the two smaller and less well-known blastozoan classes, Eocrinoidea and Parablastoidea, using extensive new collections made in the field and a restudy of previously described museum specimens. The much larger blastozoan classes Rhombifera and Blastoidea were not studied in detail during this project for the following reasons: their known morphology and taxonomy have recently been adequately summarized in Treatise Vol. S (1967); they are both being actively studied by other workers at the present time; and the fact that there was not sufficient time to study them in any great detail for a project of this scope. However, short sections describing their known morphology, taxonomy, and evolutionary history have been included in this work for the complete coverage of all blastozoan echinoderms. In addition, short sections on the crinozoan classes Crinoidea and Paracrinoidea and the unassigned class Diploporita are also included here for comparison with known blastozoan classes.

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STUDIED MATERIAL

Collection and Preparation Techniques

Field work. During the summers of 1967 and 1968 I spent approximately ten and a half weeks each summer doing paleontologic field work with an assistant in the Appalachians (1967) and Rockies (1967 and 1968). Localities where described blastozoan and crinozoan echinoderms were collected are listed in a locality index at the end of this report (Appendix 1). During this field work, approximately 108 Cambrian and Ordovician localities were visited, 46 of which yielded blastozoan echinoderms described here.

Preservation and preparation techniques. Three general types of fossil preservation were encountered during this project, each requiring the use of one or more different preparation techniques before the specimens could be studied to best advantage. These were: 1) weathered-out calcite specimens or calcite specimens on a limestone or limy shale slab surface; 2) silicified specimens in a limestone or limy shale; and 3) natural molds, or else partially weathered and/or buried calcite specimens in a shale or siltstone. The most important techniques used for each of these categories are described below.

Calcite echinoderm specimens either on slab surfaces or partially or entirely weathered out from the matrix were encountered at some Middle and Upper Cambrian and many Ordovician localities in the Appalachians and Rockies. When entirely weathered out, specimens usually required very little preparation, which consisted mostly of washing and scrubbing with a soft toothbrush. Specimens imbedded in a slab were initially prepared in the same way. However, some specimens, such as the two large complete types of *Petalocystites ikecanensis* n. gen., n. sp. (Pl. 31, figs. 1–2), were partially covered by a hard limestone matrix, which could be successfully removed only with an S. S. White air abrasive machine using dolomite powder. A few calcite specimens of *Gogia spiralis* preserved in slabs of silty limestone were prepared by using hydrofluoric acid (HF) to dissolve the quartz grains in the matrix. This technique, originally described by Sprinkle and Gutschick (1967: 390), was not completely successful, probably because of the low detrital quartz content in this particular matrix.

Much of the Ordovician blastozoan material collected from the Rocky Mountains was preserved as silicified disarticulated plates in thin to medium-bedded limestones. In contrast, only a single occurrence of silicified Cambrian echinoderms (possible *Gogia* plates in the Carrara Formation of eastern California) was encountered during this project. I extracted these silicified blastozoan plates from the matrix by etching with hydrochloric acid (HCl), or, in a few cases, acetic acid (CH_3COOH), using standard acid techniques (see Cooper and Whittington, 1965: 294–296). A few of the smaller and more delicate plates were strengthened with Glyptal during etching (see Wilson, 1965: 135–136) to aid in their recovery. The silicification seems to be associated with the occurrence of chert nodules in the same or nearby beds, and echinoderm plates are usually among the better silicified fossils, perhaps because of their original porous nature. Silicified echinoderm plates are not especially common in beds with abundant silicified trilobites, but are often extremely abundant in beds with silicified brachiopods.

Because many of the Cambrian eocrinoids studied in this project are preserved as natural molds or in a matrix suitable for making artificial molds by acid etching, latex casting became the most important technique available for the study of these early echinoderms. There are several distinct advantages to this technique. Latex casting replicates the original external surface of the echinoderm, very often with superb detail; when the matrix splits across a natural mold (often flattened), castings of these two halves (called matched counterparts) show both sides of the echinoderm at the same time. Also, if the matrix is suitable for acid etching, latex casting can be used on badly weathered or deeply buried calcite specimens, which are otherwise almost useless. Finally, brachioles and other delicate appendages are often more complete and show better detail when studied by latex casting.

A series of latex casts of the same specimen often shows a "progression" of features and additional appendages covering the exterior surface, since the latex rubber gradually excavates and breaks through to detritus-filled cavities and appendages during repeated castings. The first cast(s) will show the exterior surface without any appendages covering it, since these are still filled with weathering-produced detritus; later casts will show the cleaned-out and broken-through appendages covering this surface (compare Pl. 5, figs. 1 and 2, for an example of this). This increases the amount of information obtainable from a single specimen. In addition, some matched counterpart molds have sediment-filled interiors preserved inside them. Often these are too thin and fragile to use, but sometimes they are found adhering to one side of the external mold when the matrix is split open. This unusual feature produces casts having a "hole" in the outer facing surface through which a portion of the inside surface of the opposite calyx wall can be seen (Text-fig. 2). These partial internal casts are extremely useful for studying internal features of the calyx not visible from the exterior (see p. 23); several lepidocystid examples of this are figured in Plate 3, figures 1–2, and Plate 4, figures 3–4.

The multi-layer latex casting techniques described by Baird (1955: 202) and Rigby and Clark (1966: 392–393) were used during early parts of this study. However, in many cases, these techniques did not produce satisfactory results because of problems with air bubbles and were very time consuming as well. Therefore, a new latex casting technique was developed by experimentation and by using the suggestions of several people, especially those of A. R. Palmer and Porter M. Kier; this technique is described in detail below.

Cementex No. 600 latex rubber (Cemen-

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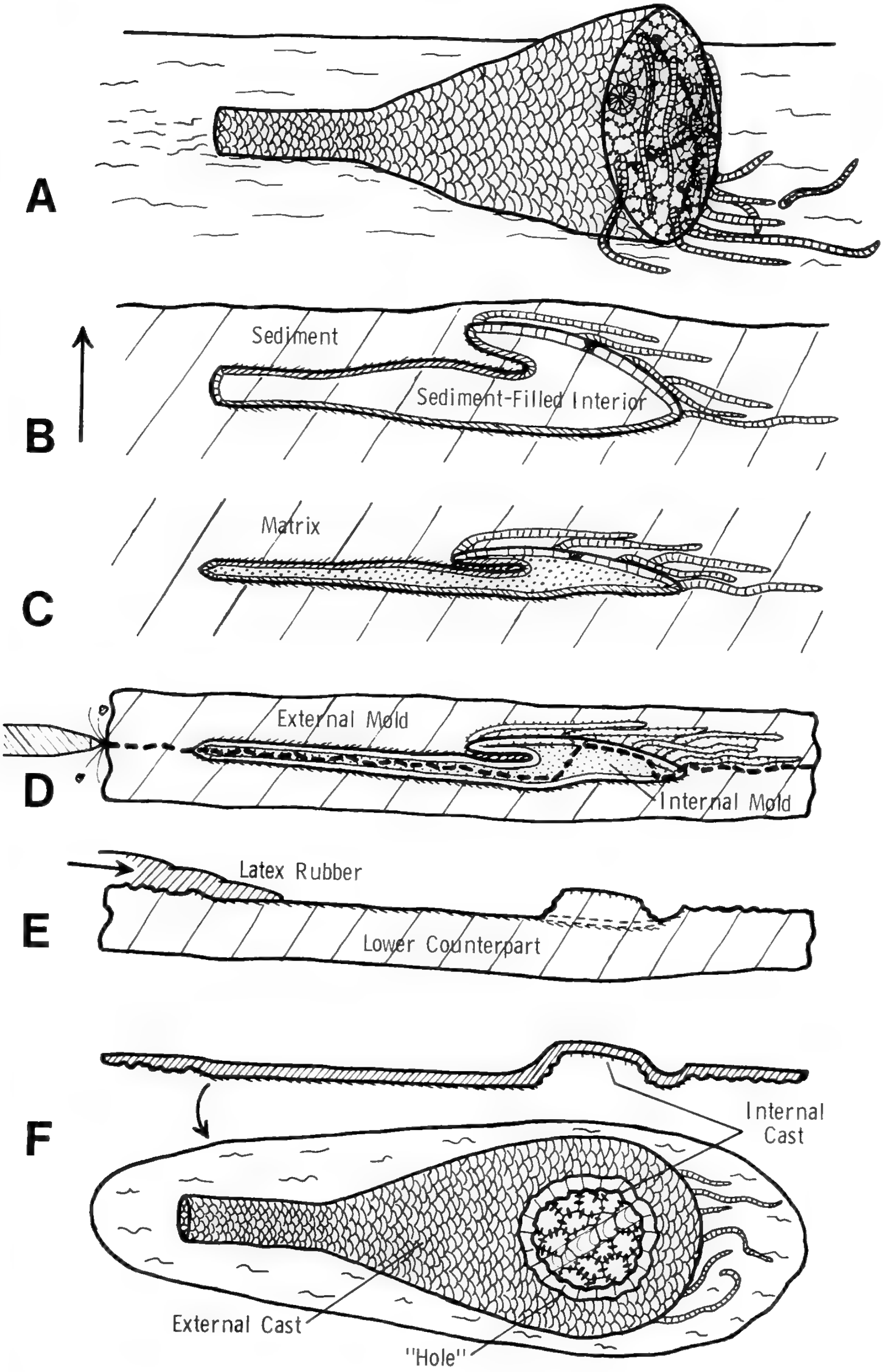
Text-figure 2. Development of natural mold preservation in an early Cambrian lepidocystid. A, dead lepidocystid torn loose from its attachment and lying on sea bottom. B, buried specimen with sediment filling the calyx interior; note that the original top orientation (arrow at left) is recorded by settling of the relatively rigid oral surface over the more flexible calyx. C, lepidocystid crushed flat by diagenesis of surrounding sediment with formation of an internal mold. D, slab containing the lepidocystid weathers at outcrop with leaching out of original calcite in the echinoderm; when broken open with chisel, break travels irregularly through hollow specimen, leaving part of internal mold attached to one counterpart. E, bottom counterpart mold is cast with latex rubber. F, side and front views of resulting latex cast showing lower surface of specimen with "hole" where interior of upper surface shows through; note lack of openings under ambulacrum in center of "hole."


A
B
Sediment
Sediment-Filled Interior
C
Matrix
D
External Mold
Internal Mold
E
Latex Rubber
Lower Counterpart
F
Internal Cast
External Cast
"Hole"

tex Co., New York City) was used during most of this work. A small amount of black India ink was added to a 16–20-ounce container of liquid latex until the color turned dark gray; the resulting black latex casts showed excellent contrast when smoked white with ammonium chloride (NH_4Cl) for study or photography. The liquid latex was then carefully thinned with water to a consistency approximating runny pancake batter and left tightly covered overnight for the elimination of any air bubbles resulting from this mixing. Each specimen to be cast was cleaned by using a soft toothbrush and soap and water to remove any adhering weathered material from the mold. It was then allowed to soak in a pan of clean water for at least half an hour (sometimes overnight) before casting. The specimen was then removed and the excess water blown off; this wet-and-blow procedure was repeated again with either plain water or a brushed-on dilute solution of Tamol, a commercial wetting agent (Rohm and Haas Co., Philadelphia), which aided latex spreading and penetration in a few cases. The specimen was then blown off again to produce a very damp, but not soaking wet, surface; the latex was then applied from a dripping spatula and the specimen tilted slightly to allow the slow spreading of a single layer of latex 1/16 to 1/8 inch thick. The specimen was then set aside on a flat surface to dry, and examined at 10–15-minute intervals for 1) air bubbles, which were broken with a needle, 2) thin spots over raised areas on the specimen, and/or 3) depressions where the latex was being sucked into overhangs or cavities, both of which were covered with an additional drop or two of latex on the partially dry surface. The cast was then allowed to dry for about 36 hours, or longer if there were deep excavations or overhangs where the latex was over 1/8 inch thick. After drying, these latex casts were carefully peeled off the specimens by using a small brush dipped in alcohol to aid in the separation. The casts were then washed to clean off any adhering matrix, trimmed with a pair of fine scissors, dried, and numbered before being filed away in air- and light-tight boxes. Sequential casts of a single specimen (or of matched counterparts of the same specimen) were sequentially numbered (A1, A2, . . . ; B1, B2, . . .) and stored together. Usually between 5–50 latex casts could be poured in a single session of one to four hours, and I estimate that, using this method, I made a total of 800–1000 latex casts during the course of this study. Latex casts made almost five years ago are still in excellent condition, although a few are beginning to change color from black to amber brown.

This casting technique was further aided by preliminary work on difficult or broken specimens. Since many of these eocrinoids are flattened by compaction in the plane of the bedding, the best counterparts for casting are those produced by splitting the specimen along the bedding plane to produce two matched flat molds with little relief. However, most specimens split apart in the field are rarely this perfect, and many are broken into several pieces or have partial overhangs where the break has diverged from the plane of the specimen. These overhangs must be carefully split off and reattached to the other counterpart, and broken specimens carefully glued back together into two complete counterparts by the use of Duco cement or some other type of non-water-soluble glue. The holotype of *Kinzercystis durhami* (Pl. 4, figs. 1–2) was brought back in 11 pieces, and glued back together to form two nearly perfect counterparts.

Many specimens of *Gogia* from the Rocky Mountains were preserved either as badly weathered or completely buried calcite specimens in a shaly or sandy matrix. As preserved, these specimens are almost useless for study, but can be prepared by first etching away the rest of the original calcite plates with hydrochloric acid (HCl) to produce an artificial mold, and then casting the mold with latex rubber. Often the calyx plates must be uncovered or excavated with a fine chisel or pin and the brachioles traced along their length so that the acid can dissolve away the remaining plate material. A. R. Palmer was apparently the first person to use this preparation method on Cambrian echinoderms (see Robison, 1965: 359); a before-and-after comparison of a specimen prepared by him is shown in Plate 7, figs. 1–2. While using this technique, I discovered that the latex does not adhere well to a freshly etched specimen, because of acid residues left in the matrix. This can be corrected by soaking the etched specimen in water for a day or two before casting; this produces excellent results often equalling or surpassing those from natural molds (see Pls. 7, 8, 14, and 19).

Terminology and Orientation Terms

Many of the orientation terms used in describing the primitive echinoderms studied in this project are identical to those used by Fay (1961b: 8–9) for more advanced blastoids. The most important of these terms are defined below, along with numerical ratios and their abbreviations used in some of the taxonomic descriptions. Specific terminology for various parts of the calyx and its appendages is introduced in the general morphology sections dealing with these structures (pp. 12–49).

Most primitive attached echinoderms consist of a large globular or flattened *calyx* containing most of the visceral material of the animal, erect food-gathering appendages (*brachioles* or *arms*) branching off the upper side of the calyx (*summit*) as oriented in life, and an attachment appendage (*holdfast* or *stem*) on the lower side (*base*). *Adoral* (or *oral*) refers to any direction toward, or any region near, the mouth; *aboral*, any direction away from, or any region far from the mouth. Similar pairs of orientation terms (*admedial, abmedial; adsutural, absutural*; etc.) have similar "to-and-from" meanings. *Posterior* and *anterior* refer to any direction or region toward or near the anal opening, and away or far from the anus, respectively. *Exterior* and *interior* refer to the outside and inside (enclosed) surfaces of the calyx, respectively. In terms of appendages of any type, *proximal* is the direction or region toward or near the point of attachment to the calyx; *distal* is the direction or region away or far from this attachment point.

Ambulacral areas have a special set of orientation terms. *Radial* refers to a line (and its extension to the base of the calyx) running from the mouth out along the center of any ambulacrum (or food groove leading to a group of brachioles); *interradial* (sometimes *interambulacral*), to a line (and its extension) running midway between two radii. In an echinoderm with well-developed pentameral symmetry, there are five radii, each partially occupied by an ambulacrum, and five interradii between them. When a specimen of this type is viewed from the oral side with the anal opening (or hydropore) oriented toward the observer, the five ambulacra (and radii) are customarily designated as follows, starting with the upper anterior one opposite the anus and proceeding clockwise, as "A," "B," "C," "D," and "E." Therefore, the anal opening (usually) lies in the "CD" interradius, and the other interradii are designated by similar two-letter combinations from their bounding radii.

Length usually (but not always) refers to the longest dimension of a structure; *width*, to the intermediate; and *height*, to the shortest dimension. In terms of calyx dimensions, length refers to the calyx size in the adoral-aboral direction; width (or diameter in globular specimens), to the intermediate dimension perpendicular to the length; and height (in flattened specimens), to the shortest dimension perpendicular to the length. The ratio between the length and width of a calyx is designated as the "L/W ratio." The *vault* (sometimes *oral surface* or *summit* when it projects laterally) of a calyx is the portion of the length occupied by ambulacral areas (or their projections on the length); the *pelvis* includes the remainder of the length below the vault. The ratio between the length of the vault and the pelvis of a calyx is designated as the "V/P ratio."

I have defined the length of a brachiole as the long dimension from its proximal attachment point to its distal tip; the width, as the dimension perpendicular to length across the adoral food groove "face"; and the height, as the third dimension perpendicular to the other two along the side of the brachiole. This is somewhat different from the orientation terminology used for brachioles and brachiolar plates by Fay and Reimann (1962: 30, 34–35) (see also Sprinkle and Gutschick, 1967: 397; Text-fig. 6I), but seems to be more satisfactory. The ratio between the length of a brachiole (BR) and the length of the calyx (C) is designated as the "BR/C length ratio." The ratio between the number of brachiolar cover plates (BCP) and the number of brachiolar plates (BP) is designated as the "BCP/BP ratio."

The length of a holdfast or stem is defined as the dimension between the attached proximal end and the extreme distal tip. The width (usually the same as the diameter) of a holdfast or stem is the dimension across the appendage perpendicular to the length. The ratio between the length of the holdfast (HF) and the length of the calyx (C) is designated as the "HF/C length ratio." The ratio of the length of a holdfast (or stem) and its width is defined as the "holdfast (stem) L/W ratio."

The length of an epispire or sutural pore is the dimension running across the suture from one absutural end to the other on the two plates; width is the dimension of the epispire along the suture. The ellipticity (or elongation) of an epispire is usually measured by its "epispire L/W ratio."

Several other measurements, such as the number of "calyx plates per side" (of the calyx), the number of "holdfast plates per ½ circumference" (of the holdfast), and the number of "epispires per calyx plates" are self-explanatory; the first two measurements are usually close to half the true total number of plates in the calyx and around the holdfast circumference, respectively. In all numerical values, the range includes the lowest and highest observed and acceptable measurements or ratios, while the average is the mean value for the measurement or ratio for all of the acceptably complete specimens measured.

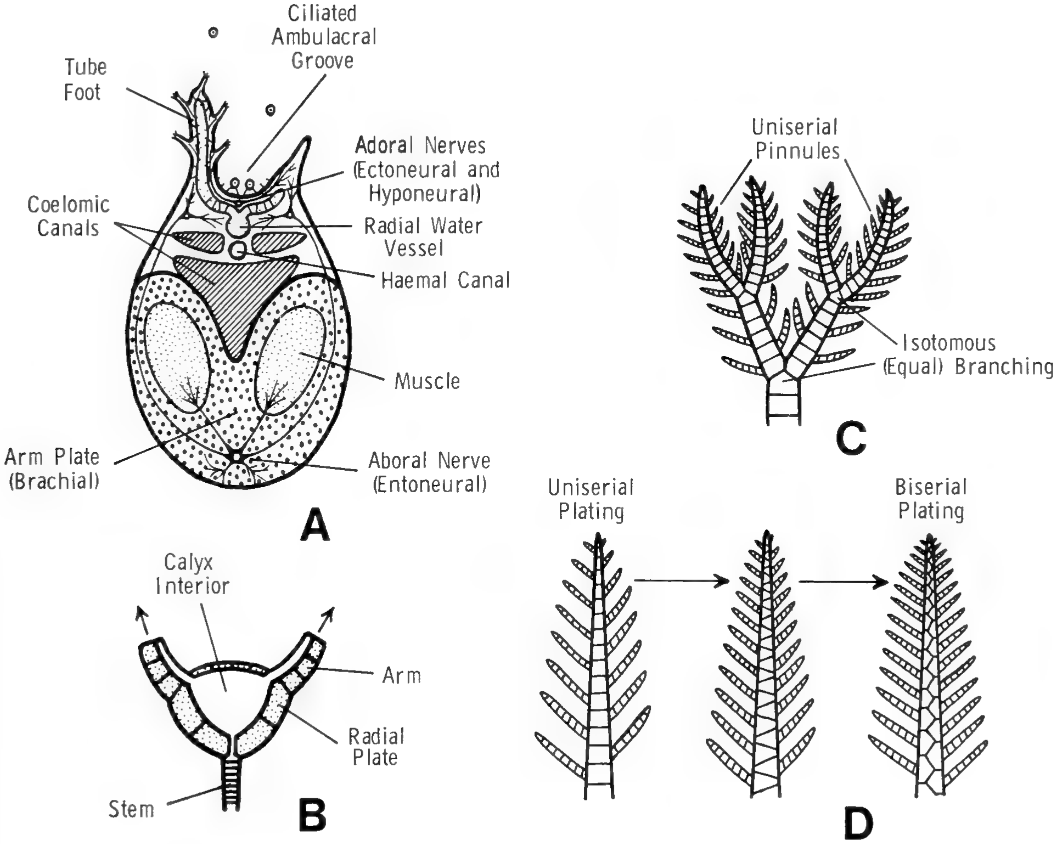
MORPHOLOGY OF BLASTOZOAN ECHINODERMS

Introduction

Blastozoan echinoderms have certain characteristic features that can be used to distinguish them from crinozoan forms. These features include 1) major calyx systems, such as food-gathering appendages and ambulacra, respiratory structures, and attachment appendages, 2) the way in which both the calyx plates and entire calyx grow, and the way in which various calyx systems are organized into pentameral or other types of symmetry, and 3) special features such as the possibility that all blastozoan echinoderms may have lacked ambulacral tube feet. These major features are reviewed in the following sections with emphasis on the morphology of these structures, the similarities and differences shown by blastozoan and crinozoan echinoderms, and the evolutionary changes shown by these features in blastozoan forms through time. Short sections are also included wherever possible on the functional morphology of these structures and their possible use in interpreting the paleoecology of these extinct blastozoan echinoderms.

Ambulacral System and Food-Gathering Appendages

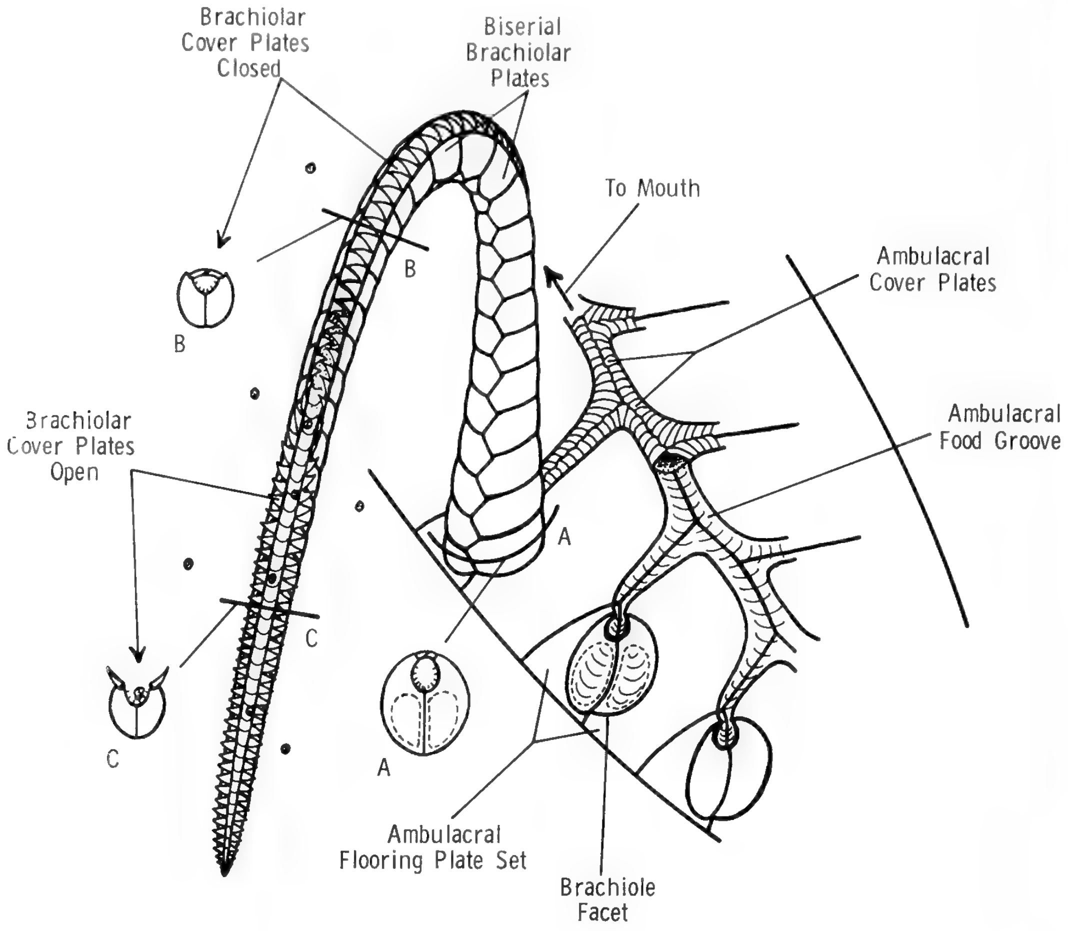
The contrast in food-gathering appendages appears to be the most important



Text-figure 3. Arm structures in living and fossil crinoids. A, cross section through brachial plate in the arm of a living crinoid showing development of ambulacral tube feet and presence of water vascular, coelomic, haemal, and nerve canals from the calyx. B, cross section through a crinoid calyx showing how arms continue the aboral plating of calyx and how coelomic systems extend out from the calyx interior to the arms by way of the radial facet. C, diagram showing a simple type of crinoid arm branching (isotomous). D, generalized diagram showing how some fossil crinoids developed biserial plating in their arms from more primitive uniserial plating. Notice that the number of pinnules per arm increases, but that these pinnules remain uniserial. Fig. A adapted from Ubaghs (1967a) and Nichols (1962).

difference between crinozoan (arm-bearing) and blastozoan (brachiole-bearing) echinoderms, and is the primary feature used at present to separate these two subphyla. This marked difference in food-gathering appendages was already present in the earliest representatives of both subphyla in the early and middle Cambrian. Therefore, if these two food-gathering systems had a common origin, then this divergence probably took place at some unknown time back in the late Precambrian. This is one of the reasons why I have given these two groups of echinoderms equal subphylum rank.

Arm-bearing crinozoan forms are represented in the modern echinoderm fauna by the articulate crinoids (subclass Articulata), while there are no known living blastozoan echinoderms. Therefore, we have relatively good information about both the hard- and soft-part morphology in modern crinoid arms, and by comparing fossil with living forms, fair information for fossil crinoids and other crinozoans, but we have much less information about the



Text-figure 4. Generalized diagram of brachiole morphology in an advanced blastozoan (rhombiferan cystoid or blastoid); note constant biserial plating of brachiole without branching or additional appendages, enlargement and change in shape near proximal attachment end and opening of brachiolar cover plates distally for feeding (cross sections A, B, and C), mounting of each brachiole on a two-plate set of ambulacral plates, and lack of openings to calyx interior at the brachiole facet or along the ambulacral food grooves to the mouth.

soft-part morphology in the brachioles of extinct blastozoans. Since there appear to be major morphological differences and probably also major functional differences between these two types of food-gathering systems, observed features in one system cannot be compared with similar features in the other with any real certainty. This problem must be kept in mind in the following sections in which I have outlined major similarities and differences between these two food-gathering systems.

In terms of observed hard-part morphology (Text-fig. 3B-D), crinozoan arms are relatively large, heavily plated, erect, endothecal food-gathering appendages. The term "endothecal" means that they are direct evaginations of the calyx wall (Ubaghs, 1967a: S55). Arms in crinoids are often branched, and in three of the four subclasses have characteristic smaller uniserial appendages called pinnules attached to them, usually one per arm plate. From the evolution of early crinoids, it appears that the calcified arm plates (brachials) were primitively uniserial, and in some evolutionary lines have been secondarily modified to a biserial plating arrangement, probably to increase the number of pinnules per arm (Text-fig. 3D). Crinoid arms are usually attached to characteristic calyx plates called radials, and appear to continue the plating from the aboral portion of the calyx. The ambulacral food groove for each arm is located on the adoral side of the arm and its pinnules, and is usually protected by a biserial set of tiny, articulating cover plates.

Like crinozoan arms, blastozoan brachioles are long, erect, plated, food-gathering appendages with a food groove on the adoral side protected by tiny covering plates (Text-fig. 4). In contrast to arms, however, they are relatively small, lightly plated, exothecal food-gathering appendages usually mounted on specialized recumbent ambulacral areas (see Text-fig. 4). Normal brachioles are always biserially plated and unbranched, and have no smaller plated appendages attached to them (Text-fig. 5A-I). Because they are exothecal, brachioles are mounted on plates of the ambulacral system usually overlying the actual calyx wall, and unlike arms, these appendages are not an evagination or continuation of this calyx wall (Ubaghs, 1967b: S476). A few flattened eocrinoids have partially modified the alternate biserial plating found in normal brachioles; these are discussed below as a special case. Brachioles are usually found attached on the oral surface or summit to specialized ambulacral support plates, which probably represent modified calyx or oral surface plates. While early eocrinoids have only slightly modified calyx plates supporting the brachioles, the ambulacral plating in more advanced blastozoans has become more highly organized with either one ambulacral plate in a biserial ambulacrum supporting each brachiole, as in parablastoids (Text-fig. 6B), or a set of two ambulacral plates in a biserial ambulacrum, as in rhombiferan cystoids and blastoids (Text-fig. 6A, C). In many advanced blastozoan forms, this ambulacral system with its attached brachioles extends down over an appreciable part of the calyx, either overlying other calyx plates (Text-fig. 6A), lying between them (Text-fig. 6B), or lying in an elongate sinus in one plate (Text-fig. 6C). In a few blastozoan forms, the ambulacral system has been extensively modified into an erect, moveable, armlike arrangement; this is discussed as the second special case below.

There also appear to be several major functional differences between arms and brachioles. In terms of soft-part morphology in crinoid arms, both the coelomic

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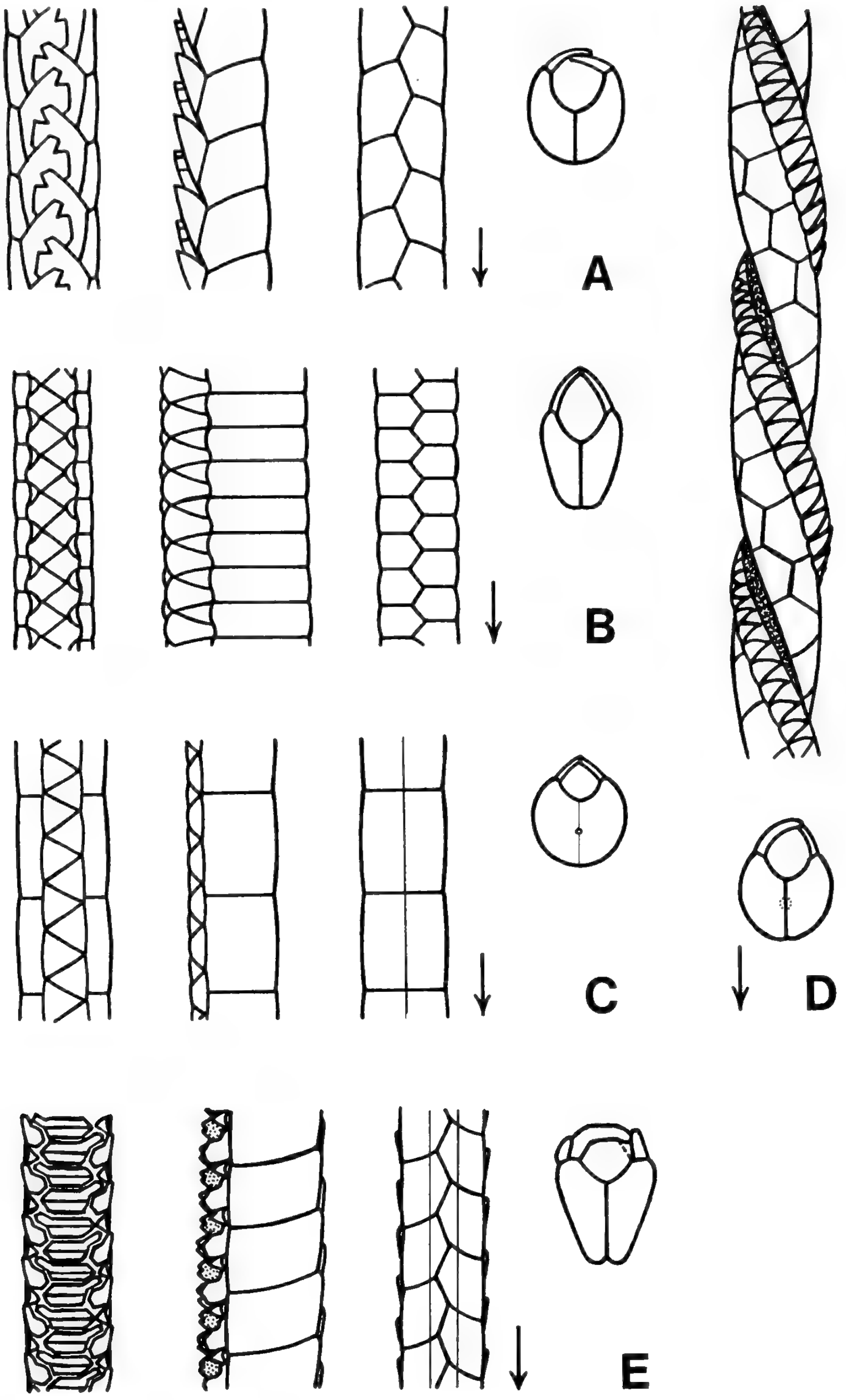
Text-figure 5. Brachiole morphology in blastozoan echinoderms. Each brachiole shown in adoral, side, aboral, and cross sectional views; arrow points to calyx attachment. A, brachiole from the eocrinoid *Kinzercystis durhami* n. gen., n. sp., early Cambrian, Pennsylvania; note serrated distally imbricate cover plates, one per brachiolar plate. B, very large brachiole from the eocrinoid *Nolichuckia casteri* n. gen., n. sp., late Cambrian, Virginia; note two types of high domed cover plates. C, modified brachiole from an undescribed rhipidocystid eocrinoid, middle Ordovician, Maryland (based on drawings kindly supplied by J. Wyatt Durham who is studying this form); note apparent "uniserial" brachiolar plating with a suppressed, almost invisible medial suture. D, spiralled brachiole from the eocrinoid *Gogia spiralis*, middle Cambrian, Utah; note left-handed spiral and slightly asymmetrical cover plates. E, brachiole from the rhombiferan *Cheirocrinus anatiformis*, middle Ordovician, New York; note three types of cover plates. F, asymmetric brachiole ("pinnule") from the arm of the rhombiferan *Caryocrinites ornatus*, middle Silurian, New York; note asymmetric brachiolar plates (cover plate arrangement inferred). G, normal and "abnormal" brachioles from the parablastoid *Meristoschisma hudsoni* n. gen., n. sp., middle Ordovician, Tennessee; note size and shape of normal brachiole vs. enlargement and irregular plating of abnormal one. H, highly ornamented brachiole from an unidentified globular blastoid, middle Mississippian, Crawfordsville, Indiana; note overlapping spines and lateral keels. I, brachiole from the blastoid *Costaloblastus sappingtonensis*, early Mississippian, Montana (from Sprinkle and Gutschick, 1967); note rounded-triangular shape and flush cover plates.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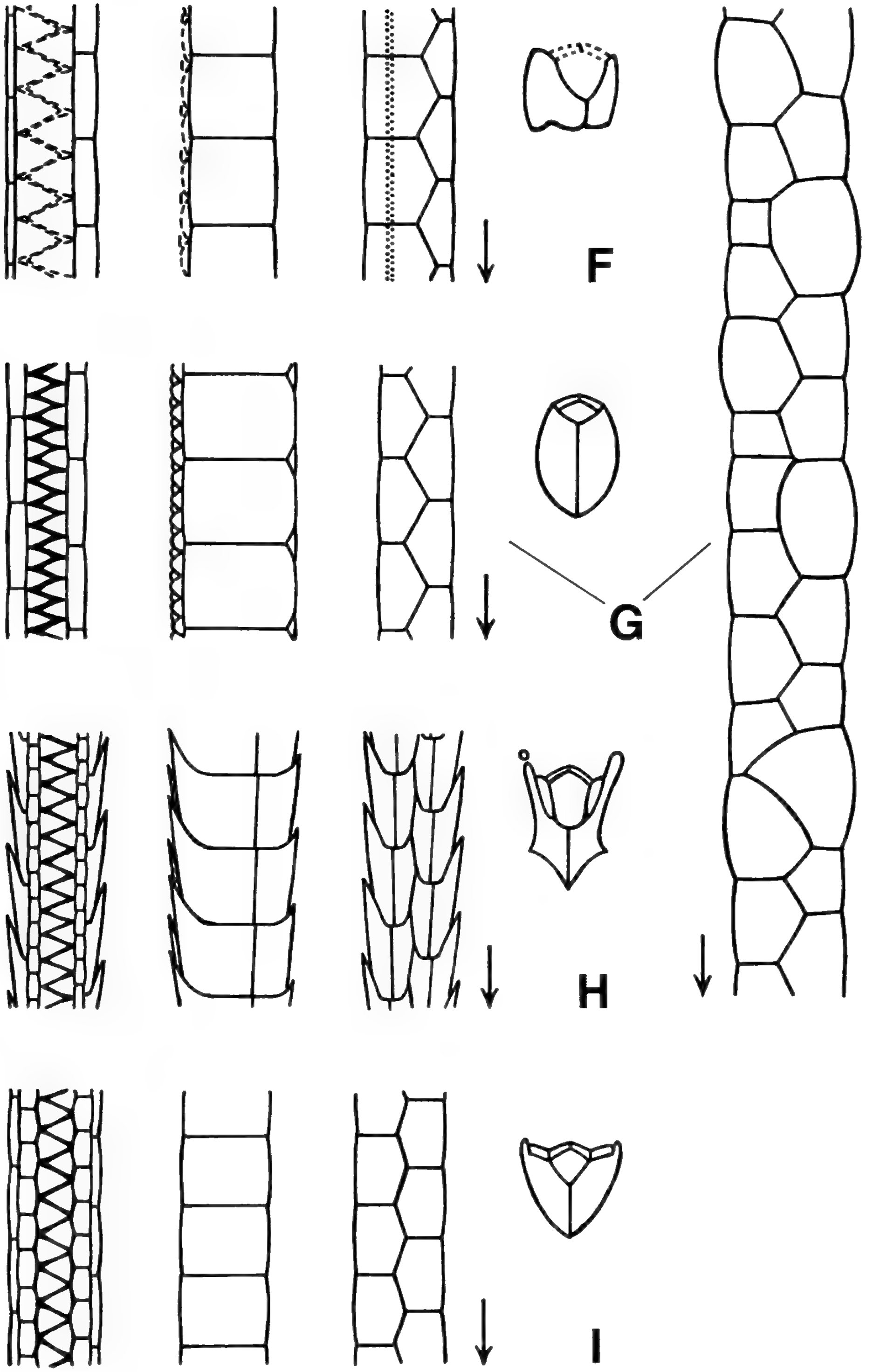
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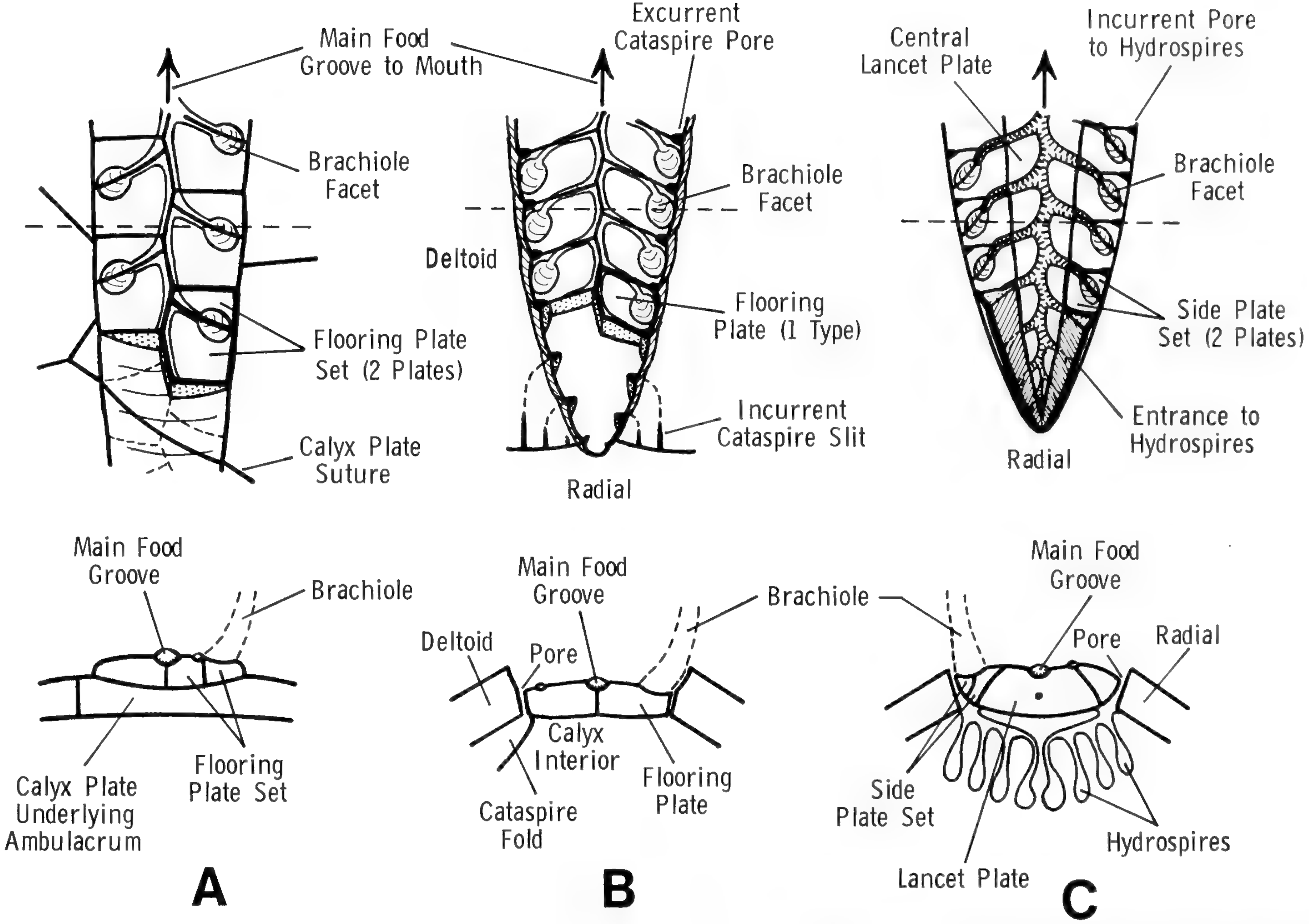


Text-figure 6. Ambulacral morphology in advanced blastozoan echinoderms. A, ambulacrum in a rhombiferan cystoid showing biserially arranged flooring plate sets (two plates) mounted on depressed calyx plates, with each set bearing a single brachiole. B, ambulacrum in a parablastoid showing only one type of flooring plate in a biserial arrangement directly overlying the calyx interior. Note that each brachiole is also sutured against edge of adjacent deltoid and that cataspires have excurrent pores between flooring plates. C, ambulacrum in a spiraculate blastoid showing central lancet plate, two types of lateral side plates in sets, each one bearing a brachiole, incurrent pores to hydrospires between side plate sets, and lobes and sockets for cover plates along main and side food grooves.

cavities and the water vascular system (hydrocoel) with its tube feet are continued out onto the arms (Text-fig. 3A). Crinozoan forms have tube feet in the ambulacra, both on the arms and on the numerous attached pinnules, and these tube feet represent the major feeding, respiratory, and sensory organs in crinozoans. Becauses these major coelomic systems continue out from the calyx interior, there is a prominent opening through which these systems pass out to the arm at the radial facet, where each arm is attached to the calyx (Text-fig. 3B). The nervous system, including both the aboral (entoneural) and the two adoral nerve systems (ectoneural and hyponeural), also extends out to the arms. In many crinoids the entoneural system has its major canal penetrating the brachial (and pinnular) plates of the arm (Text-fig. 3A), and apparently controls the ligaments and muscles that move the arm. Canals for the two adoral systems are located above the arm plates near the bottom of the overlying food groove (Text-fig. 3A).

By comparison, blastozoan brachioles may have lacked the radial water vessels and tube feet altogether. This radical difference is discussed in the next major section below (pp. 21–27). A canal through the brachiolar plates of some early eocrinoids (see Text-fig. 9) may represent a nerve canal for the control of movement of the brachiole. However, this canal is probably the hyponeural or deeper adoral and not the entoneural or aboral canal as in crinoids, since ambulacra and brachioles do not continue the aboral plating of the calyx as in crinoid arms, but do extend outward from the mouth, where the adoral nerve systems are centered. Thus, there are major differences between crinozoan arms and blastozoan brachioles both in hard-part morphology and in the functional soft-part systems present.

When traced back to their earliest occurrence in the Cambrian, these two types of food-gathering appendages do not appear to converge toward each other, but are already quite distinct at their first appearance. Therefore, it is difficult to determine whether these two food-gathering systems have a common origin (that is, whether they are partially or completely homologous), or were derived from separate sources. If they did have a common origin, then even before their first appearance in the preserved fossil record these systems had diverged considerably in morphology and probably also in function.

Brachioles appear to have been extremely conservative appendages after their first appearance in the early Cambrian. There are almost no major changes in morphology between brachioles in early Cambrian eocrinoids and those of Mississippian blastoids. Text-figure 5 shows a series of brachioles in eocrinoids, parablastoids, rhombiferan cystoids, and blastoids. There are small differences in the plating arrangement, ornament, and number and arrangement of cover plates in these appendages, but the overall plating features seem to be very similar in all four classes. If tube feet were lacking, brachioles probably operated as filter-feeding appendages that used either ciliary action or a combination of ciliary action and mucus secretion. The ambulacra supporting the brachioles do show gradual evolution to more highly developed types, probably to increase the number of brachioles and to give them better support. The two-plate ambulacral sets in rhombiferan cystoids and blastoids may have been evolved independently, but seem to represent the most successful ambulacral supporting system ever evolved by blastozoan echinoderms because this system is present in all members of these groups and was never appreciably modified.

Brachioles and ambulacra seem to be strongly coordinated in their growth. As new ambulacral plates (or sets of plates) are added, usually at the aboral end of an ambulacrum, a new brachiole is inserted on these newly formed plates. These new ambulacral plates appear to be "budded off" the previously formed ambulacral plates in the few rhombiferan cystoids and blastoids that I have examined for ambulacral growth features. In blastoids, parablastoids, and some other blastozoans, the formation of new ambulacral plates is closely coordinated with surrounding calyx plate growth, since the space for these new ambulacral plates is provided by the lengthening of the ambulacral sinus by growth along the sutures between the adjacent deltoid and radial (or bibrachial) plates. Ambulacral plates appear to grow laterally at a moderate rate, since ambulacra in most advanced blastozoan echinoderms show a gradual increase in width adorally. In contrast, the brachioles mounted on these ambulacral plates appear to grow to their normal length and width quite rapidly, since partially grown, immature brachioles are rarely found at the end of an ambulacrum, even in specimens with undisturbed and well-preserved brachioles. I have observed immature brachioles in only three blastozoan echinoderms; these are figured in Plate 9, figs. 1–3; Plate 39, fig. 23; and Text-figure 30. During this rapid growth of a new brachiole, new brachiolar and cover plates are apparently budded off in a distal direction to form a normal biserial arrangement. Later changes in the brachioles are probably minor, although the periodic, inflated, irregularly plated brachioles in the older portions of the ambulacra of *Meristoschisma hudsoni* (see Text-fig. 39) may by an exception to this.

There are three modifications of this erect brachiole-recumbent ambulacrum food-gathering system that are considered as special cases here. One of these is represented by the strongly modified brachioles evolved by some flattened Ordovician eocrinoids such as *Rhipidocystis,* probably *Batherocystis,* and partially in *Petalocystites* n. gen. The normal biserial alternate arrangement of brachiolar plates is modified in these genera to a biserial opposite arrangement with partial fusion (Text-fig. 5C), thus giving a uniserial appearance. However, the suture between these two sets of brachiolar plates is only partially suppressed and shows up on weathering or during observation of the crystallography of the transversely sectioned brachiole (J. Wyatt Durham, personal communication, 4 August 1967). This brachiole modification first occurs at the proximal end of the brachioles as shown by the intermediate genus *Petalocystites* n. gen. (see Text-fig. 31B). These eocrinoid genera represent the only group in which this change from normal to modified brachioles has been documented. However, a similar change may possibly have occurred in the evolution of diploporan cystoids, but this has not been completely investigated because of the rarity of appendages in this class.

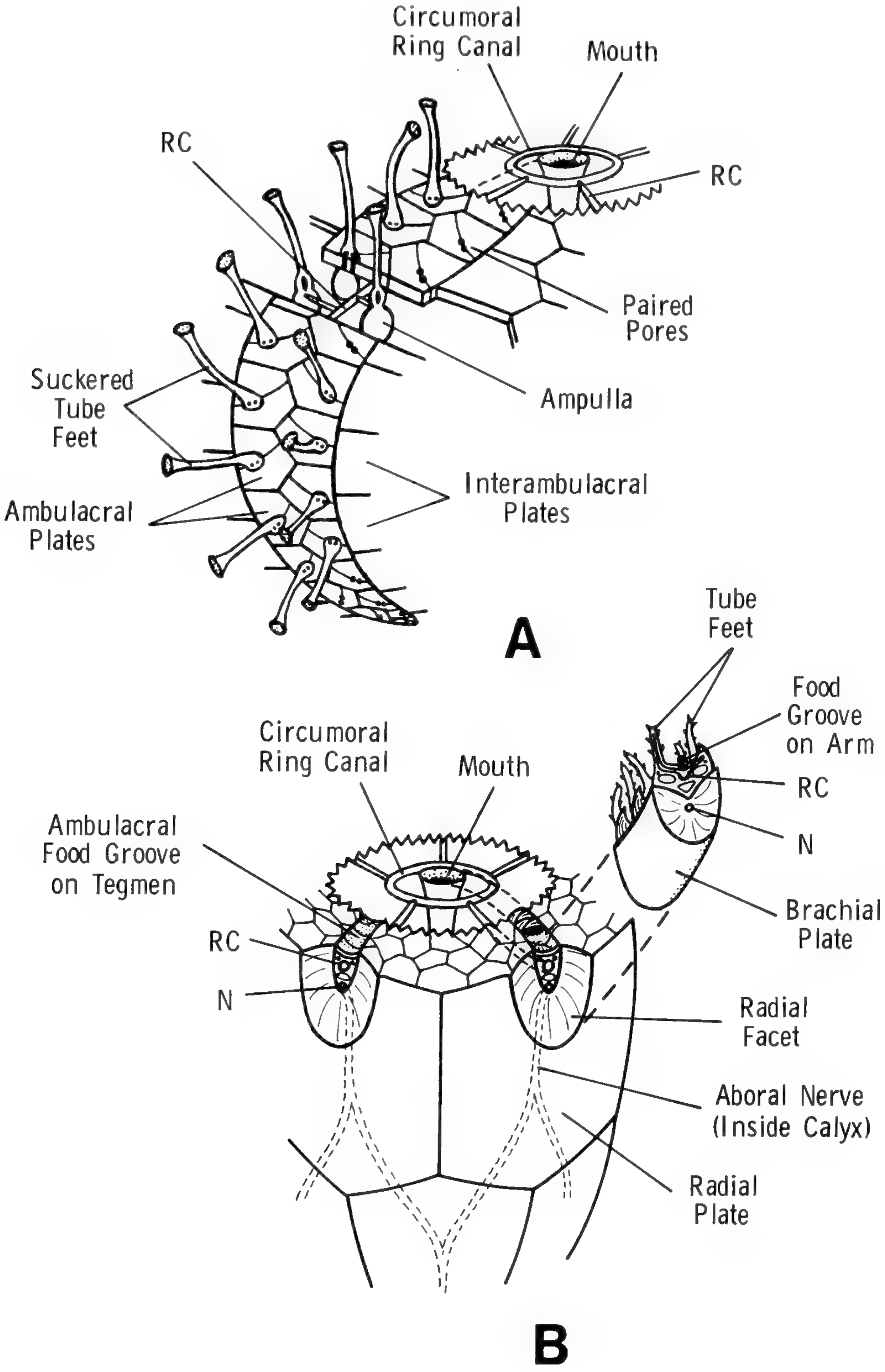
The second major change in the food-gathering system of blastozoan echinoderms involves the modification of the usual recumbent ambulacra with erect brachioles to an erect armlike ambulacrum with pinnulelike brachioles attached to it. This has probably occurred independently in at least one eocrinoid (*Trachelocrinus*) and in a group of rhombiferan cystoids including *Caryocrinites* and closely related genera. Changes similar to this are found in other classes such as the paracrinoids (see p. 185); an example of the opposite change, from erect arms to recumbent ambulacra in the crinoid *Hybocystites,* is discussed on page 23. This modification of ambulacra to an armlike system has been studied in detail only in the Silurian rhombiferan genus *Caryocrinites* for which well-preserved material with appendages was available (Sprinkle, 1968: 210 and in preparation). This genus shows little modification of either the ambulacral plates or the biserial brachioles, except that the brachioles are slightly asymmetrical in order to fold in tightly against a central protective crest (Text-fig. 5F). Apparently, this change represents a crinoidlike modification of the ambulacral system to produce armlike appendages perhaps better adapted to certain types of filter feeding (Sprinkle, 1968: 210). However, this modification apparently was not completely successful in blastozoans and never became a dominant arrangement, perhaps because tube feet may have been lacking.

A third, rather minor, change involves the unusual spiralled brachioles found in three species of the middle Cambrian eocrinoid genus *Gogia*. Spiralled brachioles are unknown in other blastozoan echinoderms except for one instance in which a single spiral is present in one brachiole of another *Gogia* species (*G. palmeri* n. sp., Pl. 16, fig. 6), which otherwise always has straight brachioles. This change involves little structural modification of the brachioles, and they appear to be normally plated except for a slight asymmetry in the brachiolar cover plates in one of these species (Text-fig. 5D). All known specimens of these three species have spiralled brachioles, and the brachioles are always spiralled in a left-handed direction. This direction of spiralling was derived from the standard electrical engineering "left-hand-rule-of-thumb"; if the thumb of the left hand points distally along a brachiole, then the curled fingers of that hand show the direction of spiralling distally. Each brachiole in a specimen has about the same spiral wavelength, although this may slightly decrease distally, and is usually lower in smaller specimens. In two of these species (*G. granulosa* and *G. spiralis*), spiralling begins very near the proximal attachment point, but in the third (*G. guntheri* n. sp.), spiralling is "delayed" with an appreciable straight region at the proximal end of the brachiole before the spiralling abruptly begins. These features, as well as the fact that there is no disturbance of the sediment around these brachioles, imply that this spiralling was very likely present during life and is not a post-mortem death feature.

It is not clear how these unusual spiralled brachioles were used in feeding. Unlike many other blastozoan echinoderms that probably lived in low current velocity conditions and held the brachioles horizontally outward to catch the near-vertical rain of food particles, these three species of *Gogia* may have lived under more turbulent (or variable current) conditions and fed by holding the spiralled brachioles nearly vertically to catch horizontally moving food particles or to create advantageous eddies.

Were Ambulacral Tube Feet Absent in Blastozoans?

One of the more fundamental and intriguing problems involved with the new subphylum Blastozoa concerns the possibility that all blastozoan echinoderms may have completely lacked ambulacral tube feet. The four (or five) living echinoderm classes all have well-developed tube feet in their ambulacral areas, serving as the external projections of the highly developed water vascular system. From the development of pores in or between the ambulacral plates, the presence of tube feet has been inferred for several early echinoderm classes, including early Cambrian helicoplacoids (Durham, 1967a: 100) and middle Cambrian edrioasteroids (Sprinkle, unpublished). In addition, soft tube feet are actually preserved in some specimens of the middle Ordovician echinoid *Bothriocidaris* (see Durham, 1966: 372), and also appear to be present on an unusual crinoid(?) from the middle Cambrian Burgess Shale (see p. 177). Thus, a highly developed water vascular system with ambulacral tube feet has been a fundamental feature of most echinoderms throughout their entire known history, and is usually cited as one of the two or three basic defining characteristics of the phylum (Hyman, 1955: 3, 702; Nichols, 1962: 14, 1968: 211; Ubaghs, 1967a: S4). However, several direct and indirect lines of evidence strongly suggest that all blastozoan echinoderms, from their first appearance in the early Cambrian, lacked tube feet in their


Circumoral Ring Canal
Mouth
RC
RC
Paired Pores
Ampulla
Suckered Tube Feet
Interambulacral Plates
Ambulacral Plates
A
Tube Feet
Food Groove on Arm
Circumoral Ring Canal
Mouth
Ambulacral Food Groove on Tegmen
RC
RC
N
N
Brachial Plate
Radial Facet
Aboral Nerve (Inside Calyx)
Radial Plate
B

ambulacral areas and had the water vascular system, if present, much reduced.

The strongest line of evidence involves the relationship between the radial water vessels bearing the tube feet and the plated calcite endoskeleton. With the exception of arm-bearing crinoids, most living and fossil echinoderms having a tightly sutured, rigid, globular skeleton have a "closed system" of internal radial water vessels sending off tube feet that individually pass through the ambulacral plates in single or double pores. Thus, there are pores or sets of pores through or between the ambulacral plates along the entire length of the ambulacrum (Text-fig. 7A) as in echinoids, fossil helicoplacoids and edrioblastoids, some heavily plated holothurians, and some fossil edrioasteriods. In crinoids and some other crinozoan echinoderms with arms, the radial water vessels are internal in the calyx but each one extends out to the "exterior" through a large opening at the radial facet and then lies in soft tissue beneath the ambulacral food groove and above the calcified arm plates, sending off projecting tube feet along the entire length of the arm (Text-fig. 7B). This arrangement, sometimes called an "open system" of radial canals, is present even in the few fossil crinoids that had lost some of the arms and instead developed recumbent ambulacra (like those found in most blastozoans) extending down over the calyx plates. In the middle Ordovician inadunate crinoid *Hybocystites*, the two recumbent ambulacra show a prominent opening leading from the food groove into the calyx interior at the adoral edge of the radials (Text-fig. 8). This opening, which was apparently for the normal passage of the radial canal and other nervous and perihemal systems, is similar in location and size to the openings on the radials bearing the three remaining arms. Therefore, in heavily plated echinoderms with a well-developed water vascular system and tube feet, either the tube feet pass through the skeleton by a series of pores from the internal radial water vessels, or the radial water vessel passes out through an opening in the skeleton from the calyx interior and then sends off projecting tube feet. The radial canals never follow the food grooves all the way to the mouth (a completely external arrangement); they always enter the calyx at some earlier point.

Blastozoan echinoderms appear to have lacked ambulacral tube feet because there are *no* observable openings where the radial water vessel or its tube feet could have extended out onto the exterior surface of the ambulacrum from the calyx interior. One of the earliest blastozoan echinoderms and some of the latest and most advanced ones show this feature best. *Kinzercystis durhami* n. gen., n. sp., an eocrinoid from the early Cambrian of Pennsylvania, now represents one of the earliest known blastozoan echinoderms with ambulacra and true brachioles. A counterpart of one of the paratypes of this new taxon, MCZ 582B, shows a portion of the inside of the oral surface, including a nearly complete ambulacrum (Text-fig. 2; Pl. 6, figs. 6 and 8) through a large "hole" in the calyx wall. The depressed external food groove of this ambulacrum is represented on the inside of the calyx by a ridge made up of slightly modified oral surface plates. The sutural epispires between these plates gradually disappear near this ambulacral ridge, and there are no openings through the oral surface wall beneath this ambulacrum or

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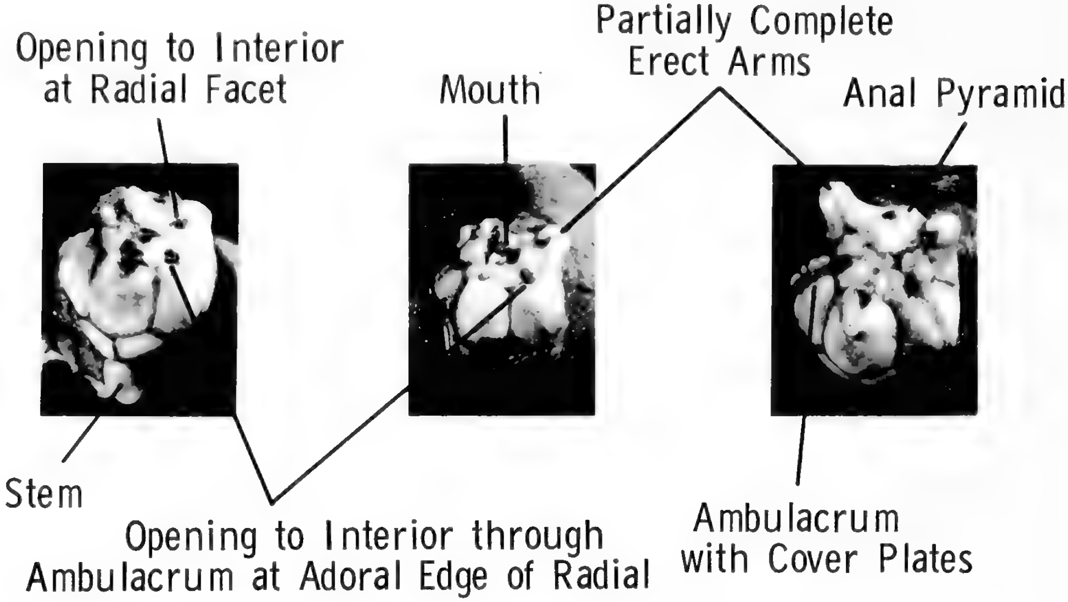
Text-figure 7. Closed and open water vascular systems. A, "Closed system" of radial canals in an echinoid in which each radial water vessel remains internal and sends tube feet individually to exterior through pores (in this case paired) in the overlying plates. B, "Open system" of radial canals in a crinoid in which each radial water vessel extends out to an arm from the calyx interior through a large opening at the radial facet and then sends off numerous tiny tube feet; note that ambulacral food groove diverges from radial canal at edge of the tegmen. N—major nerve canal; RC—radial canal.



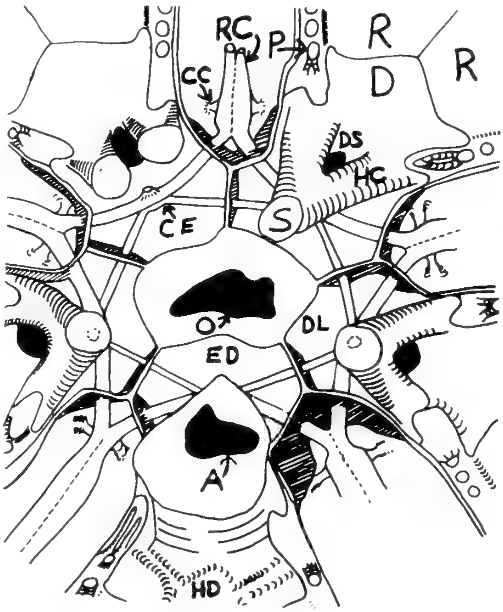
Text-figure 8. Oblique "EA" view of three well preserved specimens of the middle Ordovician crinoid *Hybocystites* from Kirkfield, Ontario (USNM S2048). This crinoid has modified two of its arms into recumbent ambulacra similar to those in most blastozoans, but has still retained the opening from the calyx interior out to the ambulacral groove at the adoral edge of the radial for the radial water vessels and other coelomic canals. Specimens photographed wet.

its brachioles (Pl. 6, fig. 6). The ambulacrum can be traced almost to the point on the exterior where it enters the oral pyramid; again on the interior of the calyx, no openings to the exterior are present here. Therefore, there were apparently no openings in *Kinzercystis* for the passage of a radial water vessel or tube feet from the calyx interior to the external ambulacral tract. If internal radial water vessels were present, they could have opened to the exterior only through the numerous interradial epispires between the oral surface plates, which probably housed small respiratory papulae.

Many rhombiferan cystoids, parablastoids, and nearly all blastoids show this same lack of openings to the interior of the calyx in their more highly developed ambulacral areas. Blastoids, which are perhaps the best known of these more advanced blastozoans, are considered here in detail because the ambulacral structures are well known, and because an internal system of canals, inferred by some authors to be the water vascular system, is present.

In thin sections of the ambulacra of many blastoids and in a few well-preserved internal chert molds, a small medial canal has been observed that penetrates the center of the lancet plate and extends the entire length of the ambulacrum (Fay, 1960: 294). This canal has no observable connections to the exterior surface of the ambulacrum. On the peristome of these blastoids, these five medial canals from the lancet plates join a double ring of canals encircling the mouth (Text-fig. 9). Short branches from this double ring appear to lead to the external spiracles (as observed in *Globoblastus*, a spiraculate blastoid), and other branches pass internally through the base of the lancet at its extreme adoral end. This double-ring canal system around

A—anal area
CC—coelomic canal
CE—circum-esophageal ring
D—deltoid
DL—deltoid lip
DS—deltoid septum
ED—epideltoid
HC—hydrospire canal
HD—hypodeltoid
O—oral area
P—pore
R—radial
RC—radial canal
S—spiracle

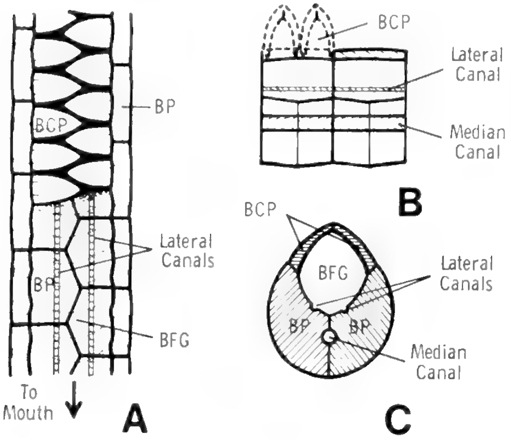


Text-figure 9. Internal system of canals in the blastoid *Globoblastus* (from Fay, 1960). Each median canal (RC) extending down through a lancet plate in an ambulacrum joins with the others at the summit to form a double circumoral ring (CE), sending off short branches to each spiracle (S). This complex system of canals could be water vascular, nervous, or perhaps both in function.

the mouth with its branches down each of the lancet plates has been interpreted as the circumoral ring and medial canals of the water vascular system by Fay (1956, 1960, 1961b) and by Nichols (1962), or alternatively as the "nervous system" (apparently the hyponeural nerve ring and canals) by Beaver et al. (1967) and Fay (1967b). At present, there is apparently no way to determine which of these conflicting interpretations is correct, although it is quite possible that both the water vascular and nervous systems are presented in this complex series of circumoral canals. A water vascular interpretation (in part) would be reasonable because the short branches to the externally opening spiracles could easily have served to regulate water pressure in this canal system in the same way as the stone canal–madreporite inlet does in most other echinoderms. If all or even part of this canal system with its radial extensions down each of the lancets can be shown to be water vascular in nature, then there is no question that blastoids (and probably rhombiferan cystoids and parablastoids) completely lacked tube feet in their ambulacra and on their brachioles, because there are no connections from these radial canals inside the lancets out to the exterior of the ambulacral areas or brachioles. This reasoning implies that the water vascular system in blastoids (and other advanced blastozoans) may have been considerably reduced in function, since externally projecting tube feet, podia, or papulae appear to have been completely lacking.

This complete absence of pores through the ambulacra of these blastozoan echinoderms can be interpreted in two ways. The possibility that I favor is that the water vascular system in these echinoderms was either internal and reduced or else completely absent. In either of these cases ambulacral tube feet would have been completely absent. This condition is unknown in living echinoderms and in most fossil ones except for homalozoans ("carpoids") where the water vascular system has not yet been satisfactorily identified. However, if epispires in early eocrinoids are interpreted as being part of the water vascular system, then this complete absence of ambulacral tube feet is a reasonable corollary, since epispires are nonambulacral and disappear without any major observable changes in the ambulacral system.

The other possibility (suggested by Albert Breimer and D. B. Macurda, Jr., 10 November 1969) is that the water vascular system with its radial canals and ambulacral tube feet may have been completely "external," lying in soft tissue beneath the



Text-figure 10. Brachiolar canals in the eocrinoid *Gogia longidactylus*. A, adoral view of a reconstructed brachiole showing large biserial brachiolar plates (BP) forming sides of food groove (BFG), biserial set of small domed cover plates (BCP) and traces of two small lateral canals. B, sutural side view of two brachiolar plates showing position of the cover plates, small lateral canal in food groove, and large median canal on the suture between two rows of brachiolar plates. C, cross section through a brachiole showing plating, food groove, and two sets of canals.

base of the ambulacral and brachiolar food grooves. The ring canal would probably have been external and a connection to the calyx interior would have had to enter the mouth into which the food grooves empty to reach the coelomic cavity. This arrangement is also completely unknown in all living echinoderms with a tight-sutured skeleton and to me seems less likely than the above alternate explanation. If an external water vascular system were present, then epispires in early eocrinoids probably could not have been part of this water vascular system, even though they seem to have housed external, soft, tube foot or papulae-like organs. Further problems also remain with this second explanation (see sections below), although it cannot be completely rejected on the basis of the presently available information.

Additional information comes from the study of blastozoan brachioles. If ambulacral tube feet were present in blastozoan echinoderms, then they should have been concentrated on the small, fingerlike, plated brachioles, since these are the primary food-collecting structures in all known blastozoans. This means that a branch from the radial canal should extend up each brachiole and give off tube feet, an arrangement similar to that in crinoid arms. Several lines of evidence, both direct and indirect, suggest that this was probably not true, and that brachioles did not have any tube feet.

Canals of any type on or in the brachiolar plates of blastozoan brachioles are very rare; none of the blastoid, rhombiferan cystoid, or parablastoid brachioles that I have examined show any traces of an internal canal system (see Text-fig. 5). Recently, however, I have observed a series of canals in the brachioles of several middle Cambrian eocrinoid species belonging to the genus *Gogia*. Well-preserved specimens of these eocrinoids show the presence of at least one and perhaps two sets of canals both in complete brachioles and in separate brachiolar plates. In these specimens, a relatively large canal runs down the center of the brachiole along the suture between the two sets of brachiolar plates (Text-fig. 10B-C). This canal is located about two-thirds of the way up the suture from its aboral side. There are no connections from this canal either to the nearby overlying brachiolar food groove or to the other exterior surfaces of the brachioles. In addition, several specimens show possible faint traces of two additional tiny canals lying laterally in the bottom of the brachiolar food groove on either side of the brachiolar plate sutures (Text-fig. 10A-C). These two tiny canals appear to have been located mostly in soft tissue lining the food groove, and are only slightly impressed into the brachiolar plate surface.

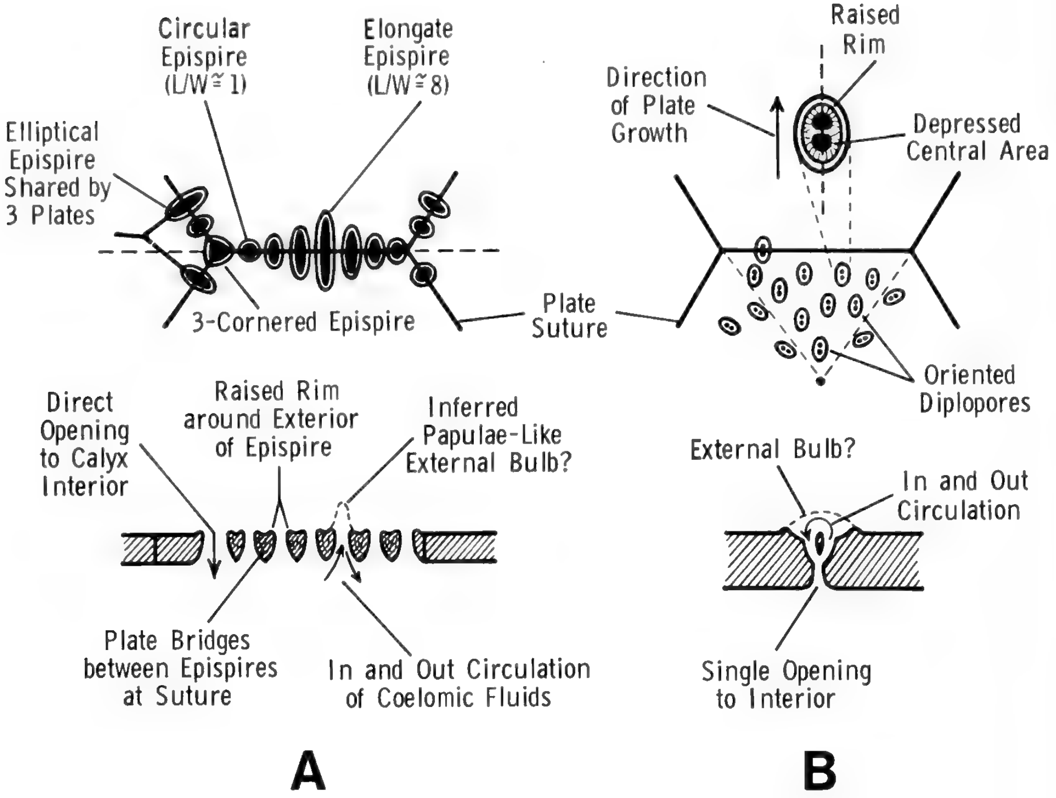
I have interpreted this observed system of brachiolar canals as follows. By comparison with the arms of modern crinoids, the larger canal through the center of the brachiole could be either a nerve canal or possibly a reduced water vascular canal.

In crinoids the entoneural nerve usually pierces the brachial ossicles, and it seems most likely that this canal piercing the brachiolar plates represents a nervous canal also, although probably not at the same level as in crinoids (see p. 19). A water vascular interpretation seems somewhat less likely, because in crinoid arms the radial water vessel lies in fleshy tissue well above the arm ossicles and just below the food groove. The two small canals at the bottom of the brachiolar food groove are most likely perihemal canals, although hyponeural (deeper oral) nerve canals are another less likely possibility. The biggest problem with these interpretations is the necessary comparison of eocrinoid brachioles with crinoid arms or pinnules. As shown elsewhere in this paper (p. 14), these appendages do not correspond closely in morphology, and may not be homologous. There is still no evidence of a water vascular canal in these eocrinoid brachioles unless it is represented by the central canal in the brachiolar plates; if this were true, then tube feet could not have been present in these brachioles because there are no connections between this enclosed canal and the overlying brachiolar food groove.

In *Gogia,* the brachiolar food groove is relatively large and usually covered by a series of high, domed, brachiolar cover plates (Text-fig. 10C), so it is conceivable that a water vascular canal and tube feet might fit into this food groove. This is apparently not true in more advanced blastozoans where the brachiolar food groove is much smaller (0.1 mm or less in width) and the cover plates are nearly flat and tightly sutured. This is several times smaller than the width of the food groove in most crinoid pinnules with tube feet (0.25–0.5 mm). Thus, there may have been a size problem in trying to fit a radial water vessel and tube feet into the food groove of most blastozoan brachioles, suggesting that tube feet may have been completely absent.

Several authors have commented on the prevalence of calyx respiratory structure in the various classes here included in the subphylum Blastozoa. A few early crinoids and paracrinoids with large globular calyces (*Porocrinus, Palaeocrinus, Sinclairocystis*) also have somewhat blastozoan-like, pleated respiratory structures through their calyx plates, but these structures are absent from nearly all crinozoans after the end of the Ordovician. Most crinozoans probably never needed to develop special calyx respiratory structures because the numerous soft tube feet on the arms fulfilled this respiratory function adequately (Regnell, 1945: 21). However, if ambulacral tube feet were absent in blastozoans as I have postulated, then this repeated and persistent development of specialized respiratory structures through the calyx plates would have been necessary in order to replace the respiratory function of these missing tube feet.

If all blastozoan echinoderms lacked ambulacral tube feet, then this is an especially strong argument for separating them off from crinozoans as a distinct subphylum. It also means that the presence of a well-developed water vascular system with ambulacral tube feet cannot strictly be used as a critical defining characteristic of all echinoderms, since at least one entire subphylum of echinoderms may have lost them. This implies that the development of a water vascular system concentrated on the ambulacral areas may have been a relatively late stage in echinoderm evolution (late Precambrian-middle Cambrian), and may not have occurred in some groups. The absence of tube feet may also give us a clue as to why blastozoan classes were somewhat less successful in competing against the relatively similar crinoids for the same general adaptive zone during most of the Paleozoic. Crinoids with well-developed, multipurpose, tube feet on their arms may have had a slight selective advantage over blastozoans without tube feet in such functions as feeding, respiration, and movement.



Text-figure 11. Pore-like respiratory structures in eocrinoids and diploporans. A, exterior view and cross section showing morphology of epispires (sutural pores) in an eocrinoid; note variations in ellipticity (measured by epispire L/W ratio), shape, and number of plate segments surrounding epispire. Raised rim around exterior of epispire suggests that these pore-like structures housed soft retractable papulae- or podia-like structures, perhaps similar to those found in modern starfish. B, morphology of diploporan diplopores; note Y-shaped cross section, orientation of long axis perpendicular to plate segment margin, and raised rim on exterior similar to that found in epispires. The two pores could have provided separate in and out circulation of coelomic fluids within an external, soft, papulae-like bulb.

Respiratory Structures

Highly developed pore- or foldlike structures, apparently respiratory in nature, are found crossing the calyx plates in most blastozoan echinoderms, and represent another of the major features characterizing this subphylum. Nearly all blastozoan echinoderms have structures of this type; only a small group of later eocrinoids (plus one or two rhombiferan cystoids and blastoids) lack them. Respiratory structures like these are not common in the calyces of other fossil and living echinoderms, probably because ambulacral tube feet are present for respiration. Two types of respiratory structures are now known in blastozoan echinoderms: the sutural pores or epispires found in many eocrinoids, and the different types of sutural folds found in the other three classes. The primary morphologic features of each of these types of respiratory structures is reviewed in the sections below, and this information is summarized in Table 1.

Eocrinoid epispires. Sutural pores or epispires found in many eocrinoids appear to be the most primitive type of respiratory system known in blastozoan echino-

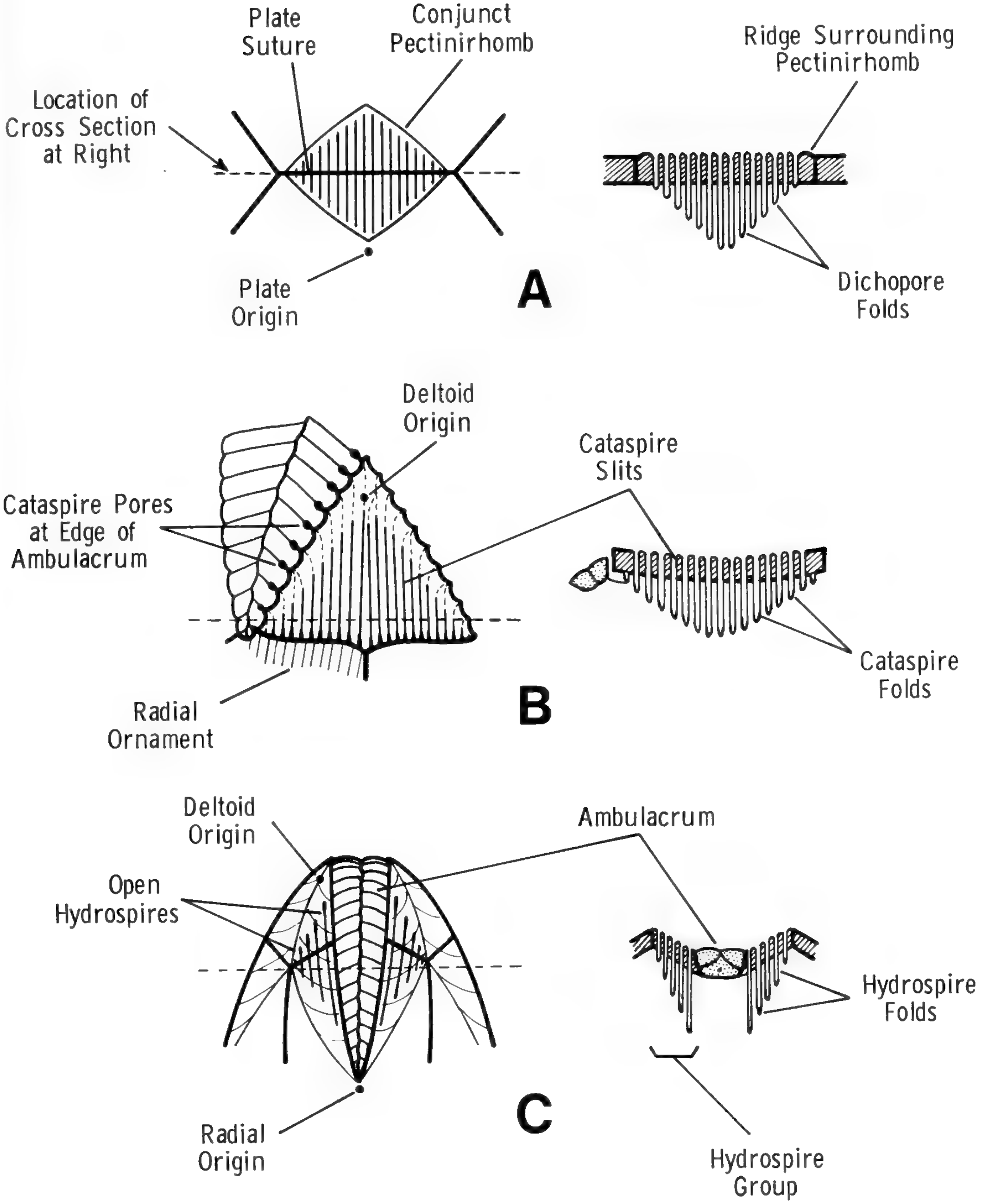
TABLE 1. COMPARISON OF RESPIRATORY STRUCTURES IN BLASTOZOAN ECHINODERMS (PLUS DIPLOPORANS)

Class	Respiratory structure	Type	Location	# Plates attached to	Longest opening	Incurrent opening	Excurrent opening
Eocrinoidea	Epispires (sutural pores)	open single pores	calyx plate sutures, random or adoral	2–3^{+}	central or all same size	only one opening (in & out together?)	
Rhombifera	Pectinirhombs	endospire folds	calyx plates, random or 3 fixed positions	2	central	both slits, or modified to grill vs. spout	
Parablastoidea	Cataspires	endospire folds	under deltoids, from radials to ambulacra	3	central?	short slits or multi-pore long slits	pores
Blastoidea	Hydrospires	endospire folds	alongside ambs., under radials and deltoids	2 (+ abut on lancets)	lateral on deltoids, central on radials	slits or pores	slit end or large pore (spiracle)
Diploporita	Diplopores	open double pores	through calyx plates, often random	1	all same size	2 pores together (in and out?)	

derms. Epispires consist of single, vertical, round to widely elliptical or triangular, porelike openings located on the suture(s) between two, three, or sometimes more adjacent calyx plates (Text-fig. 11A). These openings run vertically into the calyx interior with no calcite partition, except in *Rhopalocystis,* in which tiny covering plates are sometimes present on the exterior (Ubaghs, 1963: 35), and in *Acanthocystites,* in which an internal(?) partition blocks the center of each epispire (see p. 105). Epispires usually have a prominent raised rim surrounding them on the exterior of the plate and no markings on the interior. They are usually found either over the entire calyx surface or restricted to some degree to the adoral portions. In the family Lepidocystidae, the epispires are strongly restricted to the oral surface, probably because this is the only calyx region with exposed adjacent plating (see p. 61). Epispires are almost never found in close association with the ambulacral system; they usually die out as the food grooves or brachioles are approached. Eocrinoids with epispires range from the early Cambrian to the early Ordovician, with their maximum development in the middle Cambrian where at least four genera and 13 species have them. Some eocrinoids in the middle and late Cambrian and all eocrinoids after the early Ordovician lack epispires. Many eocrinoids elongated their epispires during calyx plate growth, but others with nearly circular or slightly elliptical epispires on the sutures of large calyx plates apparently filled in the trailing edges of the epispire as growth took place along the suture (Pl. 18, fig. 13). In a few cases, epispires were apparently "left behind" by calyx plate growth and show up inside the sutured boundaries of the plate; however, these still appear to have been normally developed and functional (see p. 72).

The most reasonable interpretation for epispires is that they were occupied in life by soft, papulae-like extensions to the exterior (Text-fig. 11A) that served for the circulation of coelomic fluids out into the surrounding seawater for the respiratory exchange of dissolved gases. Some modern starfish have sutural papulae that serve the same apparent function. These respiratory papulae or podia may have been connected internally with extensions of the water vascular system, and thus may have been homologous to ambulacral tube feet in other living and fossil echinoderms. Unfortunately, no trace of any radial or interradial water vascular canals has been observed on the calyx interior of eocrinoids with epispires.

Foldlike respiratory structures. Foldlike respiratory structures are found in all three of the later and more advanced blastozoan classes. They are called pectinirhombs in rhombiferan cystoids, cataspires in parablastoids, and hydrospires in blastoids; each of these is discussed in a separate section below. These foldlike respiratory structures differ strongly from eocrinoid epispires and moderately among themselves; however, they all show certain very similar features that may have resulted from certain respiratory preadaptations of their eocrinoid ancestors, or parallel evolution toward an "optimal solution" or "paradigm" (Rudwick, 1964: 36; Paul, 1968b: 708–709) for most efficient respiration. These foldlike respiratory structures have the following features in common: 1) They are internally located within the calyx with slit- or porelike openings to the exterior through the overlying plates; 2) all have thin, calcified, pleated, endospire folds for the closed circulation of oxygenated seawater into the coelom (and the counter circulation of CO_2-laden coelomic fluids between the folds (Paul, 1968b: 721–724)); 3) they are suturally centered (or modified from this) so that they are attached to two (or more) plates endwise and cross one (or more) plate sutures medially; 4) they are shared by only two plates along each suture (vs. *Porocrinus* and perhaps other early crinoids where



Text-figure 12. Fold-like respiratory structures in advanced blastozoans. A, rhombiferan pectinirhombs; note simple arrangement of slits and internal folds, equal development on only two plates, and longest slits (and folds) in center extending between plate origins. B, parablastoid cataspires; note interradial location, attachment to three sets of plates, and different incurrent (slit-like) and excurrent (pore-like) openings. C, fissiculate blastoid hydrospires; note open slits associated with ambulacral areas, longest slit lateral on deltoids, and lack of tubes at bottom of hydrospire folds (vs. spiraculate blastoids—see Text-fig. 6C).

similar foldlike respiratory structures are shared by three plates at a corner (Kesling and Paul, 1968: 7)); 5) they extend perpendicular (or nearly so) to the plate suture and growth fronts of the individual plates; and 6) they grow by lengthening at the suture(s) during the holoperipheral growth of the overlying plates, and increase in number by the addition of new folds and external openings laterally on the plate sutures; therefore, they often form a rhombic pattern with the oldest (and longest) respiratory structure usually located centrally and extending from one plate origin to the other. These common features are shown in Text-figure 12A–C. It seems most likely that evolution toward an "optimal solution" for respiration is primarily responsible for common features (1) and (2) above, while preadaptations of their eocrinoid ancestors with sutural epispires probably account for features (4)–(6) above. Major similarities and differences in these three types of foldlike respiratory structures are discussed in the following sections.

Rhombiferan cystoids have characteristic foldlike respiratory structures called pectinirhombs, which seem to be the earliest and most simply constructed of these foldlike respiratory organs. They cross the suture between only two calyx plates at right angles, are approximately equally shared by the two plates, and open to the exterior through slit- or porelike openings on the plate surfaces (Text-fig. 12A). Pectinirhombs are usually not associated with the ambulacral areas and in many early rhombiferan cystoids are widely distributed over the calyx in a nearly random manner; however, in a large group of later rhombiferans the number of pectinirhombs is reduced to three, and these occupy standard positions on the calyx. The internal folds (called dichopores) are straight-walled and apparently lack a tubelike enlargement at the bottom (as found in many blastoids). The longest and earliest formed fold extends between the centers of the two plates with shorter (and newer) folds lying on one or both sides (Text-fig. 12A). The slits to the exterior can extend the entire length of the pectinirhomb (conjunct pectinirhombs) or be developed only as short slits located at the two ends (disjunct pectinirhombs); other modifications, such as multiple slitlike openings (multidisjunct pectinirhombs) or single or multiple pores (cryptorhombs) also occur. This system of pectinirhombs may possibly have been connected by an internal plexus of canals from the water vascular system (see Paul, 1967b: 231, 243–247).

Pectinirhombs in early rhombiferan cystoids are very simple and probably had relatively inefficient flow control. In some later rhombiferans, the openings on one plate are partially modified to elongate and very thin slits for incurrent flow and particle restriction, while the openings on the other plate are modified into short wide slits sometimes enclosed by raised ridges or a spoutlike projection surrounding the slits for directing the excurrent waters away from the calyx (Paul, 1968b: 714–720). These later forms with modified openings probably had more efficient flow control through their pectinirhombs. At least one genus, the middle Ordovician bottom-living pleurocystid *Amecystis*, has completely lost these respiratory pectinirhombs (see p. 123), and several other rhombiferan genera have them partially or greatly reduced.

In parablastoids, internal foldlike structures called cataspires represent the primary respiratory organs. Two sets of disjunct openings allow seawater to circulate into the cataspire folds (Text-fig. 12B). The aboral openings (apparently incurrent) are located on the deltoid, and consist either of short slits on the aboral margin or long slits with multiple pores extending along much of the deltoid length. The adoral openings (apparently excurrent) are relatively large pores lying between the ambulacral plates at the adoral deltoid margin. The internal cataspire folds connecting these openings lie mainly under the deltoid but are attached to three sets of plates lengthwise and cross two sutures, a major difference from all other foldlike respiratory structures. Aborally they are attached to the radials or to the bibrachial and interbrachial plates (no openings); medially, to the deltoids where the main incurrent openings are located; and adorally, to the ambulacral plates where the excurrent openings are located (Text-fig. 12B). Like rhombiferan pectinirhombs, these cataspire folds apparently do not have a tubelike enlargement at the bottom (see Hudson, 1907: 105). During growth, the cataspires are increased in length and new slits are added laterally at the deltoid-radial or at the deltoid-bibrachial or -interbrachial suture; apparently relatively little growth takes place along the deltoid-ambulacrum suture. The aboral attachment either to the radials or to the bibrachials and interbrachials apparently is pushed adorally to maintain its position at the growing edge of these plates, an unusual feature (see p. 167). The contrast between the thin, slitlike, aboral openings and larger, porelike adoral openings implies a sea-water circulation in an adoral direction, according to the same sort of analysis that Paul (1968b: 714) applied to rhombiferan pectinirhombs. However, this is opposite to the direction deduced by Hudson (1907: 114). Parablastoid cataspires have well-developed pentameral symmetry and seem to be interradially centered and most strongly associated with the large deltoid plates in all three of the known parablastoid genera.

Blastoids have the most highly developed foldlike respiratory structures found in blastozoan echinoderms. These are known as hydrospires, and consist of two general types: open hydrospires (found in fissiculate blastoids), which are apparently the more primitive type and consist of one or more slits that open to the exterior along the hydrospire length (Text-fig. 12C), and closed hydrospires (found in spiraculate blastoids), which have multiple small porelike openings aborally and a single large opening (spiracle) adorally (see Text-fig. 6C). Both of these hydrospire types are closely associated with, and lie parallel to, the ambulacral areas, and are always found crossing the radiodeltoid suture. Usually there are ten groups, each lying parallel to one side of an ambulacrum, but in some fissiculates the number of groups may be reduced to nine or eight because of the absence of one or both hydrospire groups in the anal interradius. Hydrospires are always attached lengthwise to the same two sets of plates, the radials aborally and the deltoids adorally, and in spiraculate blastoids their adradial edge also abuts against the lancet plate underlying each ambulacrum. Single large adoral openings called spiracles are found in nearly all spiraculate and in some fissiculate blastoids, apparently for combined excurrent flow from all the hydrospires in one or two groups. Hydrospires, like the associated ambulacral areas, show a high degree of pentameral symmetry. In relation to the deltoid, the longest fold in a hydrospire group (and slit in fissiculates) is marginal, a major difference from rhombiferan pectinirhombs and parablastoid cataspires. Shorter folds lie towards the center of the deltoid along the radiodeltoid suture (Text-fig. 12C). The radial has the longest folds located centrally, the normal arrangement. Each deltoid has two sets of hydrospires along different radial sutures. Hydrospire folds in spiraculate blastoids (and perhaps some fissiculates) have well-developed tubes at the bottom of the folds (see Text-fig. 6C), apparently to channel the deoxygenated seawater up through the hydrospires to the excurrent spiracles. Some spiraculate blastoids have a further modification of the incurrent flow system in the thickening of the adradial edge of the hydrospires into an elongate plate with multiple inlet pores (as many as five per ambulacral side plate); this structure is called a hydrospire plate (Fay, 1961b: 14).

The standardized location of hydrospires across the radiodeltoid suture, their close association with the ambulacral areas and strong pentameral symmetry, and the presence of hydrospire tubes, spiracles, multiple pores, and a hydrospire plate, all indicate that hydrospires (especially in spiraculate blastoids) are probably the most highly developed and advanced respiratory structures found in blastozoan echinoderms. Blastoids probably had moderate to strong control over the flow of seawater through their hydrospires. Water apparently entered the slits or multiple small pores aborally, because these small or thin openings are well adapted for particle exclusion during incurrent flow. This incurrent water flowed down through the thin hydrospire folds where gaseous exchange took place, down into the hydrospire tubes (when present) at the bottom of the folds, and then adorally up the tubes to the spiracle (or the adoral end of the slits) where the excurrent flow was directed away from the calyx. Hydrospires are found in all blastoids, except for a few unusual fissiculates(?) from the Permian of Timor which appear to have lost many or all of the hydrospires.

Crinozoan respiratory structures. Some crinozoan genera also have pore- or foldlike structures between their calyx plates that serve as accessory respiratory structures. These structures are usually found in forms with more massive and globular calyces, and most of these genera are early Paleozoic in age. Crinozoans having a large globular calyx, short arms, and/or no pinnules may have needed some accessory respiratory structures to supplement the ambulacral tube feet on the arms. Some fossil crinoids have pores on the long anal tube or between the calyx plates, as in *Cleiocrinus.* However, in this genus, the differently shaped sutural pores on the exterior and interior are separated by a thin bridge of calcite about half way down the suture. At least two types of apparent respiratory folds are known in Ordovician globular crinoids. The crinoid *Palaeocrinus* has "ornamental ridges" crossing the plate sutures that represent thin folds from the interior extending out into the surrounding seawater for the apparently closed circulation of coelomic fluids (Sprinkle, unpublished; Brower and Veinus, in preparation). The genus *Porocrinus* has well-developed three-cornered respiratory folds called goniaspires extending into the calyx interior at junctions where three calyx plates meet (Kesling and Paul, 1968: 7). These are somewhat similar to conjunct pectinirhombs in rhombiferan cystoids, but no blastozoan form has three-cornered respiratory structures like these. Some paracrinoids also have pore- or foldlike structures similar (but again not identical) to those in blastozoans. Where pores are developed, they usually extend out from the interior but are covered by a thin external covering on the surface of the plate. Paracrinoids such as *Comarocystites* and *Amygdalocystites* have structures of this general type. Again, the relatively thin calcified partition between the coelomic fluids and the external seawater probably served for gaseous exchange.

Diploporan diplopores. Diploporan cystoids also have porelike structures through the calyx plates, but these structures are apparently different from the respiratory structures found in any other blastozoan or crinozoan class. Groupings of double pores, called diplopores, are present on the exterior surface of the plate (Text-fig. 11B), and these pores either connect to a single pore that opens into the calyx interior or continue through the plate and open internally as separate pores. Usually there is an elliptical raised rim which surrounds the two pores on the exterior. These diplopores are thus most similar to eocrinoid epispires and may possibly have been derived from them. Unlike epispires, diplopores are usually found within a plate and not on its sutured margin. Diplopores also seem to be oriented with their long axis (through the two pores) perpendicular to the plate margin in the segment where the diplopore is found (Text-fig. 11B). This implies that diplopores may be formed suturally and are then left behind inside the plate by later growth along the suture.

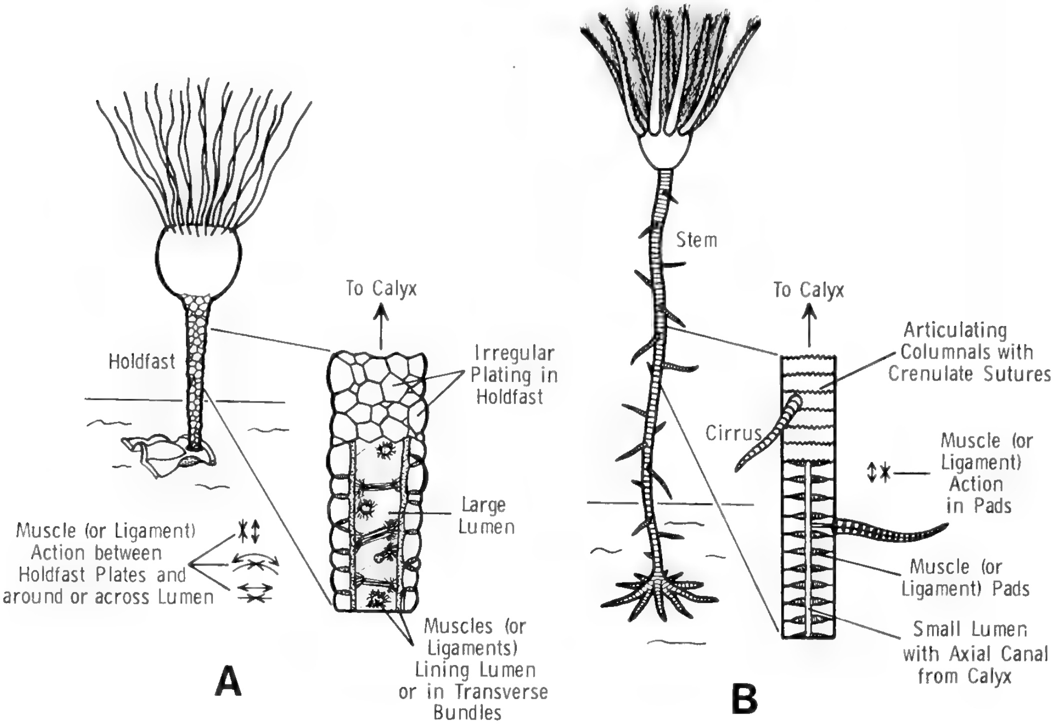
This observed morphology suggests that an elongate, bulb-shaped, papulae-like sac was present on the exterior surface to separate the outward-circulating coelomic fluids from the surrounding seawater (see Nichols, 1962: 134; Paul, 1971: 18–19). Two pores on the exterior would give separate incurrent and excurrent circulation directions into the sac where gaseous diffusion would take place. At present, since other supporting information is lacking, it is impossible to tell whether diplopores evolved from eocrinoid epispires or from some other unknown source.

These apparent respiratory structures in crinoids, paracrinoids, and diploporan cystoids all differ from those found in blastozoan echinoderms. Some features are very similar, such as the development of a thin calcified membrane for gaseous exchange, but the detailed arrangement is never identical.

History of blastozoan respiratory structures. The evolutionary history of blastozoan respiratory structures shows several important breaks; perhaps the most important of these occurs within the class Eocrinoidea itself. The earliest eocrinoids, ranging from the early to middle Cambrian, all have epispires on the sutures between their calyx plates, which are relatively thick. This early record apparently represents an ancient papulae- or podia-like, respiratory, water vascular system. Since epispire-like structures are also present in several other groups of primitive echinoderms, they may represent the earliest type of water vascular system that was evolved by Precambrian echinoderms. Possibly this early water vascular system was developed over much of the calyx as a respiratory system and was not confined to the ambulacral areas or involved with feeding. In eocrinoids the papulae- or podia-like organs extending through the epispires apparently never moved to the ambulacral areas when the epispires were subsequently lost because the brachioles and ambulacra do not show any important changes during this transition. Perhaps in other early echinoderm groups in the late Precambrian or early Cambrian, an epispire-like system of respiratory podia was successful in moving to the food-gathering areas to form ambulacral tube feet. Edrioasteroids may represent a class that successfully underwent a transition of this type in the early to middle Cambrian, since the earliest edrioasteriods have epispires (and no ambulacral tube feet?), whereas later ones have ambulacral tube feet and no epispires.

Eocrinoids lacking epispires between their calyx plates first appeared in the fossil record late in the middle Cambrian. These continued on to the last occurrence of eocrinoids in the middle Ordovician. Most of these later eocrinoids lacking epispires have relatively thin calyx plates (many are also strongly flattened), the implication being that respiration may have taken place across the entire thin, porous, plate surface, and that no separate sutural pores were needed. This loss of epispires seems to represent the most important transition in blastozoan respiratory structures. Both of these early respiratory systems in eocrinoids were apparently not completely successful, because eocrinoids having them were gradually replaced by more advanced blastozoans having more advanced respiratory structures.

In the early and middle Ordovician, three separate and independently derived eocrinoid offshoots having foldlike respiratory structures across the plate sutures appear in the record. These and other changes define the first appearance of the classes Rhombifera, Parablastoidea, and Blastoidea. Because epispires in ancestral eocrinoids had been located on the plate sutures, these sutural areas were probably preadapted for the development of the



Text-figure 13. Holdfast and stem morphology in attached echinoderms. A, multiplated holdfast in an early eocrinoid; note relatively short length, irregular arrangement of holdfast plates, distal attachment, and large central lumen containing coelomic systems and either a lining or transverse bands of muscles (or ligaments). B, columnal-bearing stem in a more advanced crinoid; note much greater length, regular plating, distal root system, small central lumen with thin canals from calyx, and simplified arrangement of muscles (or ligaments) between columnals.

three new foldlike respiratory structures. As in early eocrinoids, members of these three classes having foldlike respiratory structures have relatively thick calyx plates apparently for strength, because respiraiton had again been localized to protected sutural areas. It is possible that diploporan cystoids also evolved from an epispire-bearing eocrinoid ancestor and belong in this subphylum, but they cannot be assigned here with certainty at present.

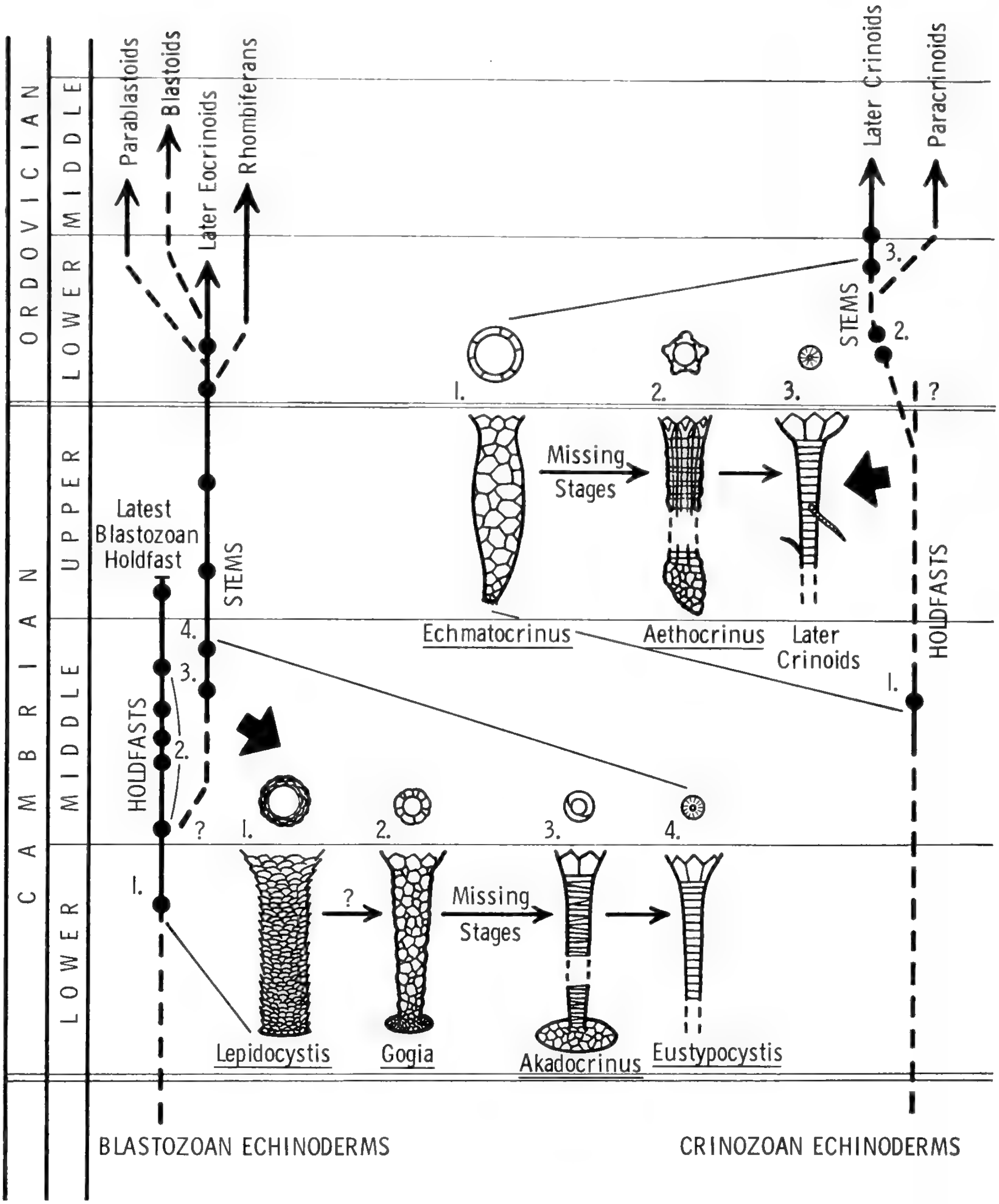
After the appearance of these three types of foldlike respiratory structures in the early and middle Ordovician, apparently very few major changes took place during the remainder of their history. These structures seem to have been relatively successful in solving the problem of respiration in later blastozoans. The only changes involved the development of improved flow control by modifications in the inlet and outlet openings, the enlargement of the bottom of the folds into tubes in some forms, and the gradual development of strong pentameral symmetry in the arrangement of these respiratory structures. In a few bottom-living or otherwise specialized genera, they were reduced or entirely lost.

Attachment Appendages

Two general types of attachment appendages, holdfasts and stems, are known in early "pelmatozoan" echinoderms. In addition, the base of the calyx itself may be attached to the bottom or to objects on the bottom, as is the case in such groups as edrioasteriods and some diploporan cystoids. The more primitive type of attachment appendages in these echinoderms I have termed a *holdfast* (Sprinkle, 1969: 287) (also called a hohlwurzel—"hollow-root" [Jaekel, 1904: 60; Robison, 1965: 359] or a stele [Caster and Pope, 1960: 1840]). The term holdfast has also been used in a similar sense by Moore and Jeffords (1968: 11) for the irregular attachment appendage found on the distal ends of some fossil and living crinoid stems. As used here, a holdfast (Text-fig. 13A) is a relatively short cylindrical, conical, or globular, irregularly multiplated, attachment appendage, probably representing a modified extension of the aboral end of the calyx. Holdfasts usually have a relatively large central cavity or lumen (1/3–4/5 of the holdfast diameter), and their plating (either adjacent or imbricate) is often gradational with that of the calyx to which they are attached. The bottom attachment surface of a holdfast usually has relatively small to very tiny adjacent or imbricate plates arranged in expandable "whorls," which the echinoderm apparently used to attach itself, probably by mucous secretion or cementation, to the bottom sediment or to objects on the bottom. Holdfasts are found in all early, most middle, and one late Cambrian eocrinoid (Text-fig. 14) and are also found in the only known middle Cambrian crinoid(?). True holdfasts are not found in any attached blastozoan or crinozoan echinoderm after the late Cambrian, and it appears that this primitive type of appendage evolved into a true stem in both eocrinoids and crinoids.

The second type of attachment appendage is a true stem, which is usually a moderate to very long, regularly plated appendage made up of one-piece, disklike columnals stacked on top of one another (Text-fig. 13B). Stems usually have a relatively small central lumen, and often have a distal root system or other structures for attachment to bottom sediments or to objects on the bottom. However, many early rhombiferan cystoids have stems that are strongly expanded proximally and have a very large lumen; these may not have been attached distally (Paul, 1967c: 115; 1968a: 596). At least two middle Cambrian eocrinoids have true stems (Text-fig. 14), and several late Cambrian and all Ordovician eocrinoids have this type of appendage, as well as all parablastoids, all rhombiferan cystoids (including several forms that may have been free-living), and nearly all attached blastoids. Most attached Paleozoic crinoids from the early Ordovician on, all paracrinoids, and many diploporan cystoids also have true stems. Several early Ordovician crinoids have a very primitive four- or five-part stem with a large central lumen and an irregularly plated area on the distal tip for attachment (Ubaghs, 1969: 7); this structure is apparently intermediate between a holdfast and a true stem, although it is relatively close to the latter (Text-fig. 14).

Holdfasts are best known in early and middle Cambrian eocrinoids. Some specimens of these eocrinoids have the tiny plates at the distal tip of the holdfast expanded into a doughnut or flattened arrangement (see especially Pl. 12, figs. 1–3), as if this were the usual attachment position. Although relatively few eocrinoids have been found definitely attached, scattered specimens in several different genera and species have now been found attached to small objects, usually fossil fragments, that apparently lay on the sea bottom. This may have been the usual mode of attachment for all early echinoderms with a holdfast. The types of fragments include: trilobite parts, usually larger flattened cephalons and pygidia (molts?); an inarticulate brachiopod; a possible hyolithid; a possible sponge; and a chitinous worm tube. These echinoderms apparently attached the expanded distal tip of their holdfasts to these objects by mucous secretion, cementation, or perhaps suction, in order to use them as bases of



Text-figure 14. Holdfast-to-stem evolution in blastozoan eocrinoids (left and bottom) and crinozoan crinoids (right and center). Note that both eocrinoids and crinoids go from very similar holdfast stages (*Gogia* vs. *Echmatocrinus*) to very similar stem stages (*Eustypocystis* vs. later crinoids such as *Hybocrinus, Palaeocrinus,* etc.), although they apparently did this through different intermediates (*Akadocrinus* vs. *Aethocrinus*), and eocrinoids accomplished it much earlier (middle Cambrian) than crinoids did (early Ordovician).

support to stand upright above the bottom sediment surface. This is similar to the way in which living gooseneck barnacles, chitons, and armored holothurians such as *Psolus* attach themselves to hard surfaces such as shells and rocks. In several cases (see Pl. 3, figs. 1–2; Pl. 12, figs. 4–5) the eocrinoid seems to be several times larger than the object to which it is attached; however, these objects may still have provided a relatively stable base, since most attached echinoderms were in near hydrostatic balance with seawater (Brower, in preparation). The earliest stems found in both eocrinoids and perhaps crinoids may have been attached in a similar manner, and later attachment methods may have evolved from this. In the many groups with stems, the most common type of attachment involves the development of a root system, requiring either columnal branching or cirri development. Other types of stem attachment include development of a "clasper" structure (Kesling, 1967a: S87), a "sinker" structure (Kesling, 1967a: S204), an "anchor" structure, as seen in the crinoid *Ancyrocrinus* (Ubaghs, 1953b: 727), a "float" structure, as seen in the crinoid *Scyphocrinites* (Hyman, 1955: 35), wrapping the cirri around other upright objects, as in the crinoid *Myelodactylus* (Ubaghs, 1953b: 730), or cementing the base of the stem to other objects (Hyman, 1955: 35).

Early members of both the blastozoan eocrinoids and crinozoan crinoids apparently made a similar but independent transition from a primitive and perhaps ancestral holdfast attachment appendage to a true and virtually identical columnal-bearing stem (Text-fig. 14). However, eocrinoids apparently made this transition in the late middle Cambrian, almost 40 million years before crinoids did in the latest Cambrian(?) to early Ordovician (Text-fig. 14). This holdfast-to-stem transition seems to represent a parallel but independent development of the optimal type of "high-rise" attachment structure available to these "pelmatozoan" echinoderms; this is apparently an example of parallel evolution towards "similar solutions" (Huxley, 1958).

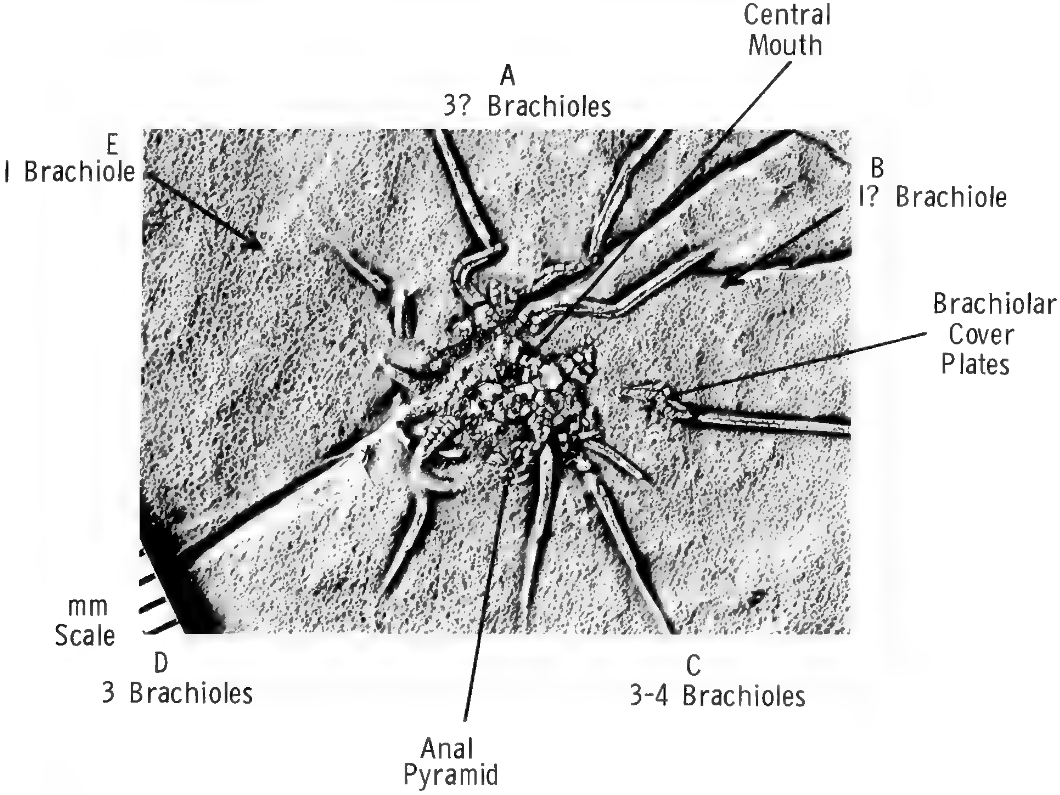
The apparent sequence of events in the change from a holdfast to a true stem in early eocrinoids and crinoids has been condensed into two evolutionary series in Text-figure 14. Some intermediate stages are missing from the fossil record, but it appears that eocrinoids and crinoids may have arrived at a similar columnal-bearing stem in somewhat different ways (compare *Aethocrinus* with *Akadocrinus* in Text-fig. 14). In eocrinoids the available evidence suggests that the small polygonal holdfast plates were modified by lateral growth into fusular rings that gradually became complete disklike columnals (Text-fig. 14, bottom center). In crinoids, however, to judge from the primitive stems found in some early Ordovician genera, the holdfast plates were first organized into repeating or alternating ringlike groups of five or more, which then fused together to form normal disklike columnals (Text-fig. 14, center). This change represents one of the most important advancements in morphology made within these two classes of primitive early echinoderms, and is probably one of the features responsible for the great success of attached, filter-feeding, blastozoan and crinozoan echinoderms during the middle and late Paleozoic.

Advantages of stems over holdfasts. There are several important advantages of a columnal-bearing stem over an irregularly multiplated holdfast. The major change in this transition involves a rearrangement of hard and soft structures from a large number of small irregular plates held together by ligaments or muscles and surrounding a large central cavity containing both viscera and muscles (Text-fig. 13A), to a smaller number of disklike columnals having muscles on their distal and proximal faces and a small central cavity or lumen containing only thin visceral canals to the calyx (Text-fig. 13B). This rearrangement involves a major change in the position of muscular structures, a reduction in the complexity of plating, and a reduction in the proportion of lumen, muscle, and viscera to plate volume. Because of these changes, stems appear to have a much greater relative strength than holdfasts. The rearrangement of muscles from operating around each small plate in the holdfast, and either transversely across the lumen or around its circumference to hold the sides together (Text-fig. 13A), to an arrangement where the muscles operate only longitudinally between each pair of columnals (Text-fig. 13B) greatly increases the efficiency, rigidity, and control in bending the attachment appendage or in holding the calyx directly upright. This rearrangement and the accompanying increase in strength mean that an echinoderm can make its stem very long without having to make it relatively wide, as in most holdfasts. In holdfasts the maximum observed L/W ratio is about 19–21, while in advanced blastoid and crinoid stems the L/W ratio can range up to 200 or higher. The visceral systems present in the large lumen of a holdfast can also be returned to the calyx and connected with the distal parts of the stem by using only thin canals. In addition, since a stem grows by the insertion of new columnals at the proximal end as well as lateral growth of the older ones as they are moved down the stem (Moore, Jeffords, and Miller, 1968: 19), it was probably easier for a stemmed echinoderm to lengthen its stem during growth than it was for one with a holdfast where growth takes place by the irregular insertion of new plates between older ones. Finally, the development of a root system is apparently possible only in columnal-bearing stems because of the difficulty of making holdfast plates small enough to produce very thin cylindrical branches from the base of the holdfast. No branching or root-bearing holdfasts are known from the fossil record.

There are practically no observable differences in terms of gross morphology, lumen development, and crenulated faces with areas for muscle "pads" between the columnal-bearing stems found in blastozoan echinoderms and those in crinozoan echinoderms (see Text-fig. 14). The one possible exception is that almost no blastozoan echinoderms, even those with long stems, have been observed with well-developed cirri, and these may possibly have been absent.

Pentameral Symmetry

Pentameral or five-sided radial symmetry is one of the most characteristic features of modern echinoderms. It is also present in many of the earlier members of this phylum as far back as the early Cambrian. Pentameral symmetry is usually observed in a five-fold arrangement of the calyx plates or ambulacral areas, as in many holothurians, echinoids, starfish, blastoids, and crinoids. Some echinoderms, such as holothurians and irregular echinoids, have adopted a mobile or burrowing way of life, but these groups preserve their earlier pentameral symmetry with a more recent bilateral symmetry superimposed on it. Several authors have tried to explain the origin of pentameral symmetry by using embryological evidence or the apparent evolution of this feature in various early fossil groups. Bather (1900: 11) proposed that it was a development of the ambulacral system from a more primitive bilateral or triradiate arrangement. Nichols (1962: 90–92; 1967: 221–223) has postulated that this pentameral arrangement has evolved as a strengthening feature for the first aboral plates secreted after metamorphosis in the young echinoderm. Some of the earliest blastozoan echinoderms studied for this project show a gradual development of pentameral symmetry in their various calyx systems. These observations are presented below for possible information about the origin of pentameral symmetry and the regions of the calyx in which it first appeared.



Text-figure 15. Imperfect pentameral symmetry in the ambulacral system of *Gogia kitchnerensis* n. sp. Specimen GSC 25935 showing nearly complete but somewhat weathered summit; note anal pyramid at bottom (defining the "CD" interradius), central mouth, food grooves on larger calyx plates (top and right), and 3–4 brachioles attached together in "A," "C," and "D" positions vs. only 1? brachiole in "B" and "E" positions.

In early and middle Cambrian eocrinoids, pentameral symmetry first appears in the ambulacral system with its erect brachioles. Lepidocystids from the late early Cambrian of Pennsylvania show that the ambulacral system already had an equally developed, five-sided, radial symmetry at this time (see Text-fig. 22). The plates on the oral surface and on the rest of the calyx are very numerous and have a completely random arrangement, along with the respiratory epispires between the oral surface plates. A similar arrangement of pentameral ambulacra on a calyx with irregularly arranged plates and respiratory structures is also known to occur in at least one middle Cambrian species of *Gogia* from the Rocky Mountains; however, this form (*G. kitchnerensis* n. sp.) has ambulacra that appear to be unequally developed (Text-fig. 15). Three of the ambulacra leading to groupings of brachioles on the edge of the oral surface (apparently "A," "C," and "D" based on the position of the anal pyramid) are developed approximately 120° apart and have many brachioles. The remaining two ambulacra, "B" and "E," appear to branch from "C" and "D," respectively, near the mouth, and these lead to areas where only one or two brachioles are attached. This arrangement suggests that ambulacra "B" and "E" with their brachioles are developed slightly later than the other three ambulacra during the ontogeny of this species of *Gogia,* and that they develop by branching from the two lateral ambulacra already present. It is not known for certain whether this feature is present in other species of *Gogia* or in other Cambrian eocrinoids.

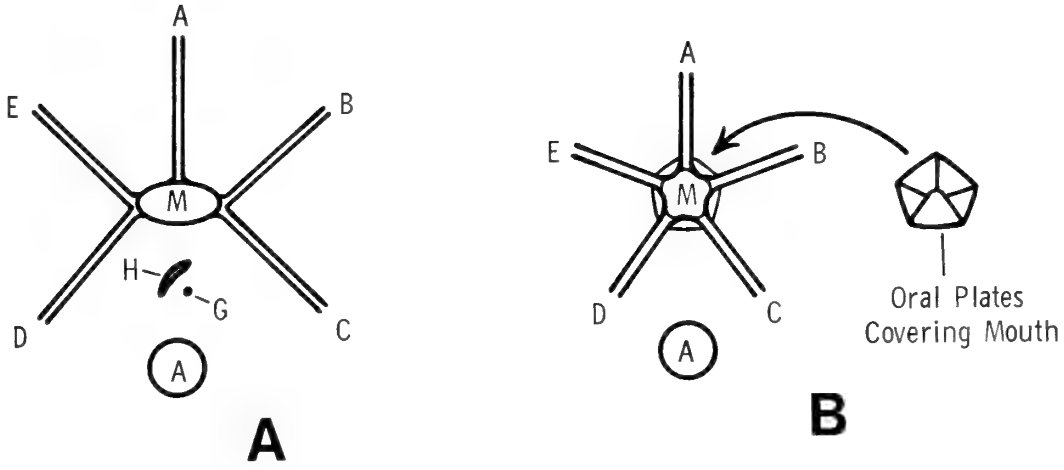
This unequal development of the five ambulacra in some of these early eocrinoids suggests that the observed pentameral symmetry may have been derived from an older triradiate arrangement of the ambulacra. This was also suggested by Bather (1900: 11), who used information derived from more advanced early and middle Ordovician cystoids; however, this is the first observation of possible triradiate symmetry found in Cambrian attached echinoderms.

The earliest blastozoan echinoderm having its calyx plates arranged in pentameral symmetry is the middle Cambrian eocrinoid *Lichenoides,* although this seems to be an isolated occurrence. Pentameral symmetry in the calyx plates first became common in early and middle Ordovician blastozoan echinoderms and was dominant after this. However, respiratory structures through the calyx plates were still randomly arranged until about the middle Ordovician when parablastoids, a few more advanced rhombiferan cystoids, and perhaps blastoids(?) appeared. As the calyx plates were reduced in number and arranged in a five-sided pattern, the respiratory structures through them gradually adopted this arrangement, and in blastoids, finally became very closely associated with the five ambulacral areas. The reduction in the number of calyx plates seems to have occurred at the same time that these plates were being arranged in pentameral symmetry; it was apparently easier to produce a high degree of symmetry in a calyx with relatively few plates (15–40) than in a calyx with several hundred plates.

From this brief review, it appears that pentameral symmetry appeared first in the ambulacral system of these blastozoan echinoderms and was already present here in several of the earliest eocrinoids in the early and middle Cambrian. During later evolution of these blastozoan echinoderms between the middle Cambrian and middle Ordovician, first the calyx plates and then the respiratory structures through them adopted this pentameral symmetry, a process that was aided by a gradual reduction in the number of plates.

It has been postulated on both embryological and fossil evidence that echinoderms had a Precambrian bilateral ancestor (see Ubaghs, 1967: S47) that was probably mobile and perhaps soft-bodied. Very early in their Precambrian history some echinoderms must have developed both a means of attaching to the substrate and plated appendages for capturing microscopic food around the mouth on the upper side of the calyx. As they thus became attached filter feeders, it seems likely that they would adopt some type of radial symmetry, since this is a common feature of metazoans with this life habitat. Since this symmetry change appears to have been a response to a new type of feeding, the ambulacral system would likely be the first system to adopt this new radial symmetry (and this change had apparently already occurred by the late early Cambrian), followed by the calyx plating, and finally the respiratory structures. From the arrangement seen in *Gogia kitchnerensis,* it appears that this radial symmetry may originally have been triradiate. This earlier arrangement was then modified to the standard five-sided symmetry by the addition of two more lateral ambulacra by means of branching. Apparently, no additional basic branching beyond five occurred in the ambulacral system, perhaps because of space limitations on the summit. However, a few later rhombiferan cystoids, such as the Devonian genus *Strobilocystites,* do have additional branches away from the summit.

This original triradiate symmetry has apparently persisted in most later blastozoan echinoderms as a slightly asymmetrical arrangement of ambulacra entering the



Text-figure 16. "2-1-2" arrangement of ambulacra entering mouth or oral plates covering mouth. A, arrangement of ambulacral food grooves around mouth in many early echinoderms; note ambulacra "D" and "E" enter together at left end, "A" enters alone at top, and "B" and "C" enter together at right end, forming a distinct plane of bilateral symmetry ("A"–"CD"). B, arrangement in some advanced parablastoids and blastoids where ambulacra show near perfect pentameral symmetry around mouth, but sutures between oral plates retain a slight "2-1-2" pattern (redrawn from a figure in Fay, 1961b).

mouth (or oral plates covering the mouth), here called a "2–1–2" pattern (Text-fig. 16A). Two of the ambulacra, "D" and "E," join and enter together at the left side of the mouth, ambulacrum "A" enters separately at the top, and ambulacra "B" and "C" join and enter together at the right side. More advanced blastozoan groups have adopted a completely symmetrical arrangement of ambulacra entering the mouth, but many still retain this "2–1–2" pattern in the arrangement of their oral plates (see Text-fig. 16B, and Fay, 1961b: 95, fig. 201).

During the Paleozoic history of blastozoan echinoderms, there apparently were repeated changes to a tertiary bilateral symmetry after the secondary pentameral symmetry had already become established. This change in symmetry was apparently a response to the adoption of a new mobile or bottom-living way of life. It occurred independently in several eocrinoids, several rhombiferan cystoids, and at least two blastoids. The eocrinoids *Cardiocystites*, *Lingulocystis, Rhipidocystis, Batherocystis,* and *Petalocystites* n. gen. all have a flattened calyx shape with two distinct sides. Most of these genera have reduced the number of ambulacra from five to two. The rhombiferan cystoids *Pleurocystites, Praepleurocystites, Amecystis,* and *Regulaecystis* have a similar flattened shape with only two brachioles branching off the summit. The blastoids *Eleutherocrinus* and *Astrocrinites* from the Devonian and Mississipian appear to have lost the stem and slightly modified the pentameral symmetry by the reduction of one of the ambulacra, thus achieving a somewhat flattened bilateral body shape.

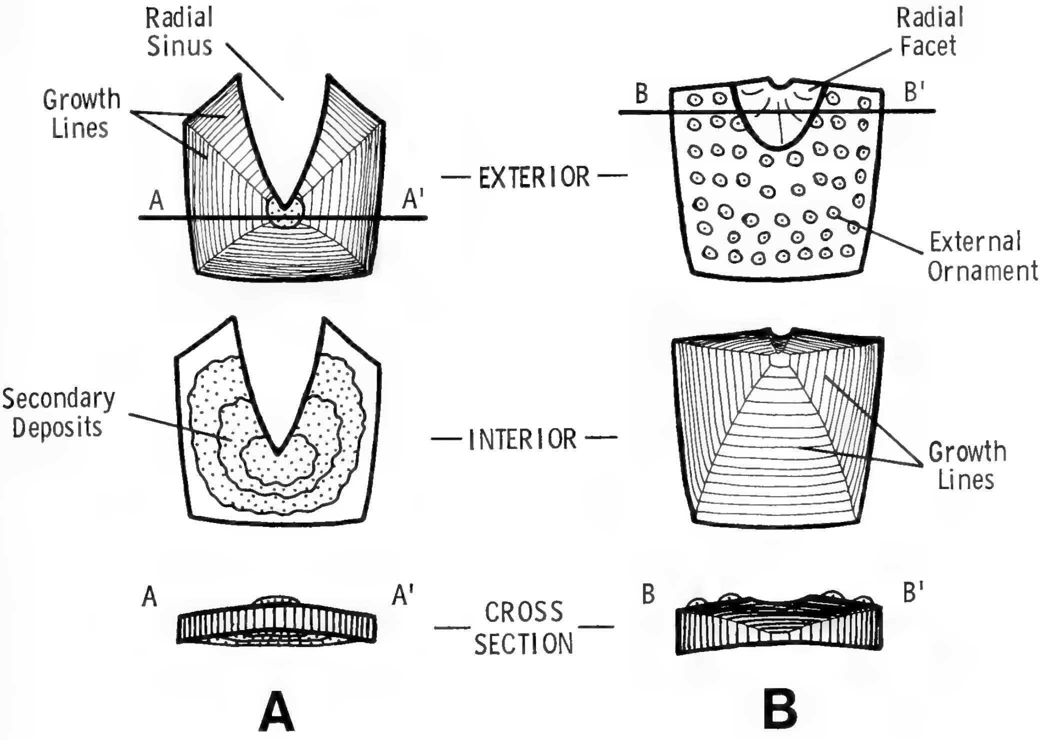
It appears that these blastozoan echinoderms have adopted a "flat-fish" or carpoidlike body shape and a bottom-living existence. In response to this change in environment, they have modified their symmetry, calyx shape and plating, ambulacral development, and location of respiratory structures. Many of them have strongly modified or completely lost the attachment stem. In several cases (*Lingulocystis, Pleurocystites,* etc.) there seems to be a convergence toward some "carpoids" with the development of a heavily plated rigid frame around the lateral margins of the flattened echinoderm, and the presence of one or two flexible surfaces with tiny plates covering either the bottom, or top and bottom surfaces of the animal. These flexible surfaces may have allowed pumping activity used either in respiration or movement.

Plate and Calyx Growth

Because echinoderms have an endothecal plated skeleton, there are two ways in which an echinoderm can increase its size. Either the plates themselves can grow as the animal increases in size or the echinoderm can add new plates to its skeleton as it grows. Other methods of skeletal growth, such as molting or ecdysis found in arthropods and other phyla, are not available to echinoderms because their skeleton is endodermal and covered on the exterior by living tissue. Most echinoderms combine these two available methods of calyx growth in differing proportions. Growth of the individual plates is found in all echinoderms, but is most important in forms with a relatively small (often constant) number of highly coordinated calyx plates, such as blastoids. Addition of new plates is most important in echinoderms with a large number of irregularly or regularly arranged calyx plates, such as most eocrinoids and echinoids. Individual systems, such as the ambulacra and brachioles, respiratory structures, and stem, also combine these two growth methods, usually with the addition of new elements predominating over the growth of older ones. Growth in each of these separate systems is discussed in the sections describing their morphology. The growth of the individual calyx plates and the way that new plates are added to the calyx are reviewed for blastozoan and crinozoan echinoderms in the following sections.

Types of plate growth. Two general types of growth, differentiated by a time factor, are found in individual echinoderm plates. Primary (calyx) plate growth is here used to include all of the original, relatively slow, and continuous growth of the plates. Primary plate growth appears as a series of tiny growth lines on one or more surfaces of the plate, and often in transverse and longitudinal sections through the plate. These tiny growth lines appear to represent minor interruptions in the more or less continuous secretion of new calcite during the slow primary growth of a plate. These growth lines have been observed in many living and fossil echinoderm groups representing at least four of the five subphyla. In blastozoan echinoderms, they have been found in nearly all blastoids, some parablastoids, several rhombiferan cystoids, and perhaps a few eocrinoids; in crinozoan echinoderms, they have been found in some fossil crinoids, and perhaps in some paracrinoids. Because two contrasting types of primary plate growth appear to be present in blastozoan and crinozoan echinoderms, this type of growth is considered in more detail in later sections.

In contrast to primary plate growth, which is responsible for the continuous formation of a major portion of the plate, another general type of growth, here termed secondary (calyx) plate growth (derived from the term secondary deposits as used by Macurda, 1966: 95), is also usually present. Secondary plate growth takes place after primary plate growth, and is usually developed as a surface layering, either on the exterior or interior of the plate. These secondary deposits usually lack fine growth lines and often have a much larger pore size in their microstructure than the calcite secreted during primary growth. Overlayering of secondary material often shows several concentric layers representing new calcite that has been added at several different times. These deposits are most often used to thicken a plate for greater strength, often at points of stress (see Macurda, 1966: 100), or to form pustular, knoblike, or ridgelike ornament (sometimes also for



Text-figure 17. Contrasting types of primary calyx plate growth in blastozoans and crinozoans. A, holoperipheral plate growth in a blastozoan showing growth lines on exterior extending through entire primary portion of plate (cross section), while secondary deposits (necessary to thicken plates during lateral growth) cover most of interior and scattered parts of exterior. B, overlayering calyx plate growth in a crinozoan showing growth lines on interior of plate, exterior covered with secondary ornament, and "nested" arrangement of growth lines in cross section with automatic thickening of plate.

strengthening) on the exterior. Secondary plate growth has been observed in many blastozoans and some crinozoans, and has also been seen in other groups of echinoderms, such as echinoids. However, it has been described in detail only in blastoids (Macurda, 1966: 95, 98, 100–102) and in one group of diploporan cystoids (Paul, 1971: 15–16).

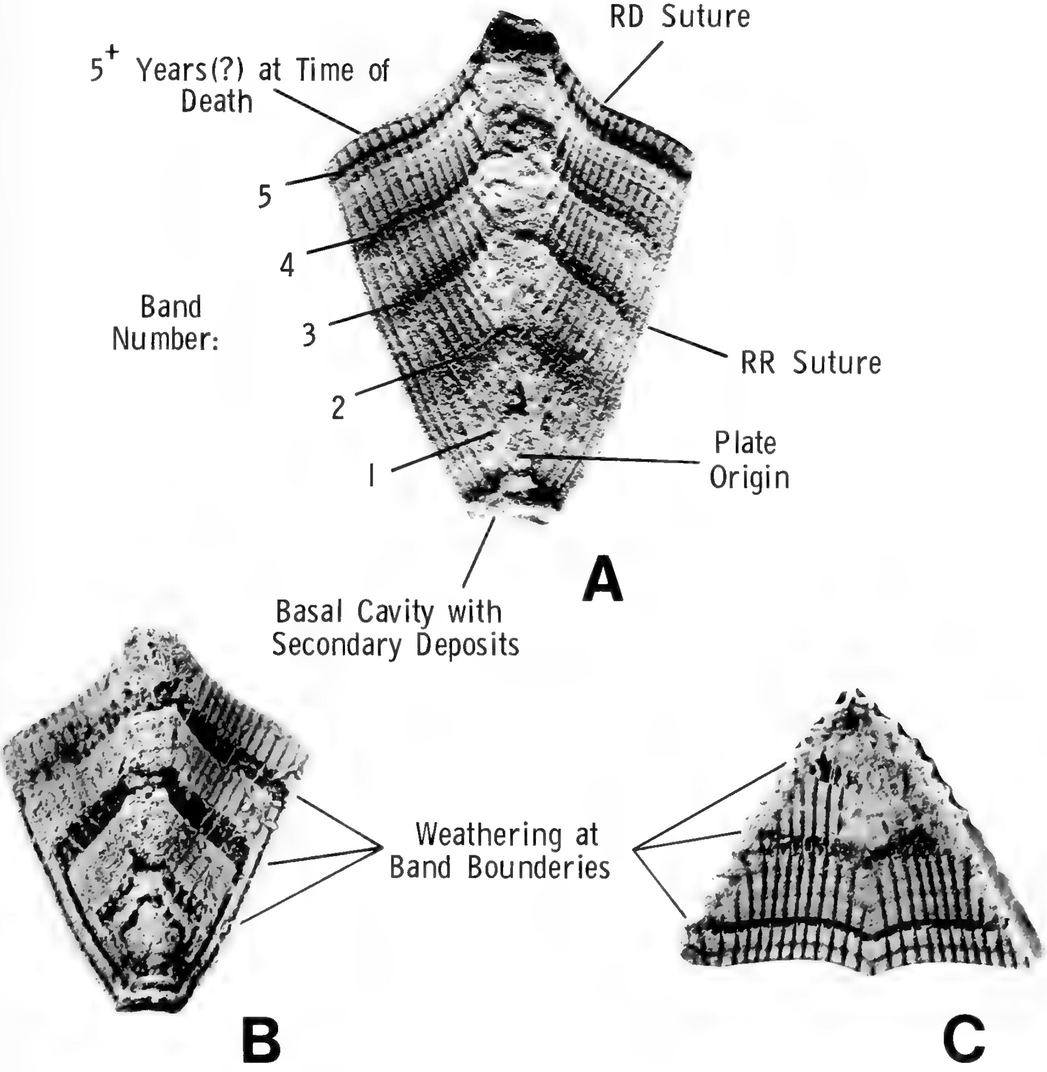
Holoperipheral versus overlayering primary plate growth. There appears to be a major difference between the types of primary plate growth found in blastozoan and in crinozoan echinoderms. With additional investigation, this difference may turn out to be an important feature which could be used to separate members of these two subphyla. Blastozoan echinoderms show holoperipheral primary plate growth (new term), whereby all of the lateral sutured margins of the plate show primary plate growth, but apparently none is present on the exterior or interior surfaces (Text-fig. 17A). Therefore, the growth lines for this type of growth extend through the entire primary portion of the plate and should show up both on the exterior and interior surfaces; in practice, however, growth lines are usually found only on the exterior of blastozoan plates, probably because the interior of these plates is often covered with extensive secondary deposits. These secondary deposits are necessary in order to thicken (and strengthen) the plates during growth, since thickening is not done automatically during holoperipheral primary plate growth. This type of plate growth is known to be present in most blastozoan echinoderms except possibly eocrinoids, whose growth features are poorly known.

Some fossil crinoids (and perhaps all crinoids and paracrinoids) show a different type of growth, here called overlayering primary plate growth (new term), whereby both the sutured lateral margins and the exterior of the plate show primary plate growth (Text-fig. 17B). Usually no calcite is added to the interior of the plate during primary or secondary growth, and this interior surface has prominent concentric growth lines showing the primary plate growth (Meyer, 1965: 1207; Macurda, 1968: 108–113). This location of growth lines on the interior of the plate is opposite to that found in blastozoan echinoderms, in which growth lines are usually present only on the exterior. In contrast to blastozoan echinoderms, crinoids with overlayering plate growth thicken the plate automatically during primary growth and need little secondary secretion on the interior or exterior. Growth lines should therefore be "stacked" on one another in a cross section through the plate (Text-fig. 17B).

Additional types of primary plate growth may be present in members of other subphyla of echinoderms. Echinoids show a somewhat different type of growth from either of those described above, probably because large spines and small pedicellaria for protection must be mounted on a secondarily secreted, thin exterior surface. Other living and fossil echinoderms need to be investigated for information on their primary plate growth. At present, the growth of the separate plates in fossil crinoids is better known than in living forms.

There may be a basic morphologic reason why these two different types of primary plate growth are present in blastozoan and crinozoan echinoderms. In crinoids, the hyponeural or aboral nerve canals extend upward on the interior surface of the calyx plates to the endothecal arms (Lane, 1963: 929; Brower, in preparation). Since there is no interior thickening of the plates during overlayering plate growth, these canals do not have to move vertically during growth, but only have to increase in length as the overlying plates increase in size. In addition, the arm facet on the exterior surface of the radial where the growing arm is attached to the calyx is also automatically enlarged by this overlayering type of growth found in crinoids (Meyer, 1965: 1208). In blastozoan echinoderms, however, there are no arms present to continue the calyx plating, and hyponeural canals do not appear to extend up from the base of the calyx on the interiors of the plates. Therefore, there are no restrictions to thickening the plates on the interior, and this is done with the secondary deposits accompanying holoperipheral plate growth. Also, brachioles apparently cease growing soon after being introduced, so that the brachiolar facets on the ambulacrum do not have to be continually increased in size. At present, these differences in morphology appear to be the best explanation for the observed differences in primary plate growth.

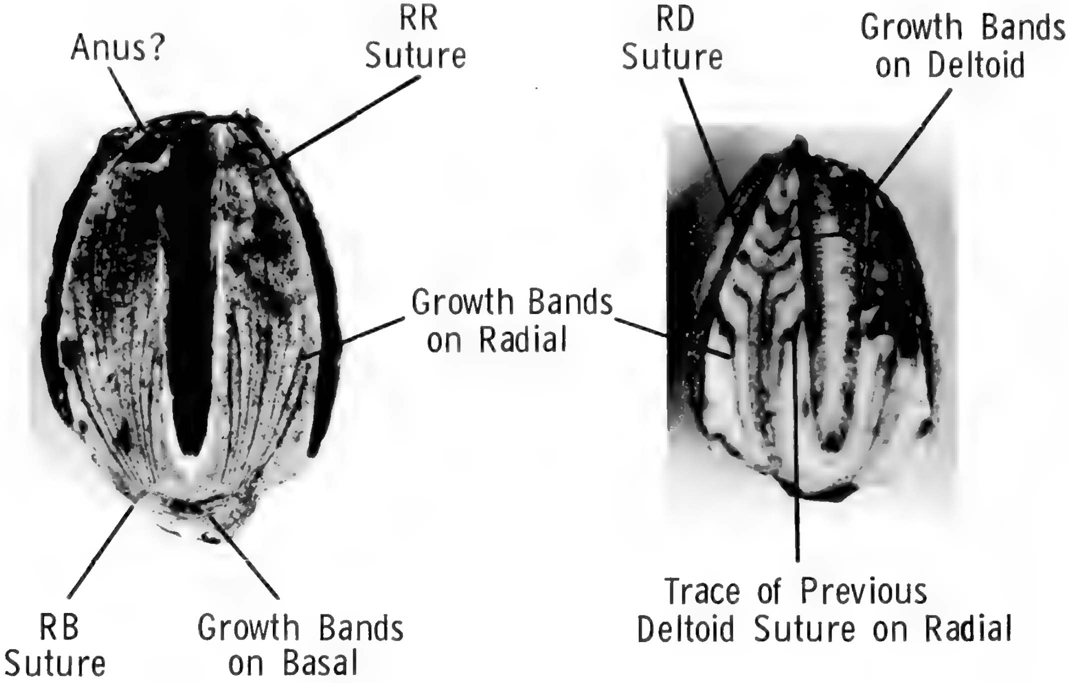
Plate addition versus plate growth. The second way by which echinoderms can increase the size of their skeletons is the addition of new calyx plates. In primitive forms with many irregularly arranged plates, this is apparently the more important method of growth. In these forms new plates are continually added between the older and larger ones at all stages during growth; many eocrinoids and some diploporan cystoids show this type of growth. Some later eocrinoids, most rhombiferan cystoids, and nearly all parablastoids and blastoids have greatly reduced the number of calyx plates and insert them at or soon after metamorphosis, so that few or no new calyx plates are added during later ontogeny. This results in a relatively small and nearly constant number of calyx plates that are often ar-



Text-figure 18. Banding of growth lines in the parablastoid *Meristoschisma hudsoni* n. gen., n. sp. A, well preserved large radial (illuminated from bottom) showing five prominent bands along the RD and RR sutures; note nearly constant band spacing, 9–15 tiny growth lines in each band, slight weathering just in front of #3 band boundary, and rapid growth from plate origin toward deltoids (RD suture) vs. slow growth toward radials (RR suture). B and C, band boundaries showing up as weathered "grabens" on a radial and a deltoid plate.

ranged in a symmetrical pattern, usually a five-fold radial symmetry (see p. 42). This reduction in the number of calyx plates appears to have facilitated the spread of pentameral symmetry from the ambulacral system to the calyx plates themselves and finally to the respiratory structures.

The change from a large number of irregularly arranged calyx plates to a much smaller number usually showing good pentameral symmetry appears to have occurred independently in several groups of blastozoan and crinozoan echinoderms. These two types of calyx plating arrange-



Text-figure 19. Color-marked blastoids showing growth bands. Specimens of *Hyperoblastus alveata* UMMP 37808 from the middle Devonian (left) and *Pentremites conoideus* UMMP M-58 from the middle Mississippian (right) having surface color markings forming bands of tiny growth lines. Note that color bands are present in corresponding positions on all plates, and that band spacing decreases away from plate origins. Both specimens photographed immersed in water.

ments apparently have different factors controlling their growth and arrangement. In forms having a large number of irregularly arranged calyx plates and addition of new plates throughout growth, the position and shape of each of these plates is apparently determined by its rate of growth, and by the "fit" with its neighbors with little genetic control over the latter factor. This corresponds rather closely with Raup's "fitting model" (1968: 63) based on the packing shown by soap bubbles. This type of plating gradually evolved into a more regular arrangement having considerably fewer calyx plates, and much greater overall genetic control over the position, shape, and rate of growth of these plates. This greater control made unusually shaped plates possible, such as the forked radial plate in blastoids and some rhombiferan cystoids. In more primitive forms, no two individuals in the same species have the same arrangement of calyx plates, and few even have the same number of plates. When the number of plates is reduced to 18–35 and arranged in a symmetrical pattern, nearly all individuals have the same number and arrangement of calyx plates with only minor variations. Fitting may still be important in maintaining tight sutures, but the shape and growth of these plates (and the resulting shape of the calyx) can be much more closely coordinated.

Possible yearly banding. In some blastozoan echinoderms, the tiny growth lines from primary holoperipheral plate growth appear to be interrupted and grouped into larger "bands" that include a variable number (usually between 7 and 20) of these smaller growth lines. Banding has previously been observed in blastoids (Reimann, 1961) and is reported here for the first time in a parablastoid (Text-fig. 18).

These bands are expressed in three ways; most commonly they show up as periodic ridgelike interruptions of the primary plate growth on well-preserved plate surfaces (Text-fig. 18A), but in some cases they are expressed as lines of color marking (Text-fig. 19) on the plate surface, or, in weathered specimens, as more deeply etched grabenlike depressions in the plate surface (Text-fig. 18B–C). All three of these banding features seem to be closely related; the surface pigmentation is localized right at, and the plate weathers most deeply just in front of, the position of these ridgelike interruptions. The multiple ridgelike areas producing this banding effect imply a periodic interruption in the primary growth of all the plates of the echinoderm; in complete specimens they are present in corresponding positions in most of the major plates in the skeleton (Text-fig. 19). The color marking implies a periodic secretion of pigmentation in the plate or on its surface during plate growth, while the weathered-out depressions seem to imply that in some way the actual structure or composition of the calcite secreted during growth of the plate changes periodically. This variation could possibly represent a change in the pore size of the echinoderm microstructure or a change in the chemical composition of the secreted calcite (perhaps magnesium [Mg] content) or could be the result of some other unknown factor (Heinz Lowenstam, personal communication, 23 March 1970).

These observed banding features seem to imply a periodic interruption of primary plate growth accompanied by possible physiological changes in the echinoderm and possible changes in the physical or chemical composition of the plate material. I suspect that these "periodic interruptions" are seasonal (yearly) in nature. They are very similar to the bands found in living and fossil echinoid plates, which have been interpreted as being yearly but have not yet been conclusively proved so (Deutler, 1926: pl. 3; Durham, 1955: 86). In medium to large-sized blastozoan specimens in which these bands have been observed, there are usually between three and seven of these bands present, and three to seven years would seem to be a reasonable estimate for the life span of these relatively small echinoderms. Thus, the *Meristoschisma* radial figured in Text-figure 18A and showing five bands would have come from a complete specimen that was about five and a half years old when it died, or more exactly, from a specimen that had deposited more than five yearly increments of calcite on this radial during its growth after metamorphosis.

If these observed bands are in fact yearly, then there is probably some seasonal climatic or physiological factor that is responsible for this (yearly) interruption of plate growth. The climatic factor most likely to cause an interruption of growth in these echinoderms is a decrease in the sea-water temperature during a winter period; however, an increase in temperature during the summer over the optimum for plate growth might also have the same effect. Some physiological cause, such as possible yearly breeding, might also be responsible for these observed interruptions in calyx growth, perhaps in association with a climatic factor. Many living echinoderms, including crinoids, breed only once a year during a short time interval (see for example Boolootian, 1966: 562); during this breeding period nearly all growth stops and most of the activity of the echinoderm is diverted into gamete production. If this yearly breeding also occurred in blastozoan echinoderms, then this might be the factor responsible for the observed interruptions in calyx plate growth with or without an accompanying climatic factor.

PALEOECOLOGY OF EARLY BLASTOZOAN ECHINODERMS

Early eocrinoids, such as the lepidocystids from Pennsylvania and the many species of *Gogia* from the Rocky Mountains, show several distinctive features in their morphology, preservation, and occurrence from which information about their paleoecology and environment can be inferred. Since these early eocrinoids seem to be similar in morphology to later blastoids, rhombiferan cystoids, and parablastoids, much of the paleoecologic information based on these later and more advanced classes can also be applied to these earlier forms with only minor modifications. For example, most early ecocrinoids have a globular calyx with the mouth, ambulacral areas, and food-gathering appendages concentrated at one end (the summit or oral surface) and a long attachment appendage (holdfast) at the opposite end, similar to the arrangement found in later blastozoans. This implies that they almost certainly lived in a similar upright position with the food-gathering appendages held well above the sea floor and facing upward. Both this orientation and the size of the food grooves in the food-gathering brachioles and ambulacra (0.2–1.0 mm) indicate that most of these echinoderms were microphagous filter feeders, capturing planktonic food as it settled from the overlying water column or was swept past them by currents. Also, to judge from their occurrence in limy or sandy thin-bedded shales and from the associated fauna, these early blastozoan echinoderms, like their more advanced relatives, probably lived in a marine environment with slight to moderate turbidity, relatively soft and fine-grained bottom sediments, shallow to moderate water depth, and often near carbonate banklike areas. From my collecting experience, I would infer that these early blastozoan echinoderms were gregarious and apparently lived in large colonies or "gardens," like many other echinoderms both living and fossil. This development of gardens may have occurred at especially favorable localities for feeding or attachment, or it may have been necessary for efficient external reproduction in these early echinoderms (Brower, in preparation; Lane, 1969: 891).

Some factors were probably different between these early blastozoans and their later relatives. Since these early eocrinoids had an irregularly multiplated holdfast instead of the columnal-bearing stem found in later attached echinoderms, their method of attachment was probably different, perhaps limiting their range of possible environments. Most of these holdfast-bearing echinoderms are found unattached (a point considered later), but a few specimens have now been found with the holdfast attached to fossil fragments or to other objects apparently lying on the sea floor. This type of attachment, by the use of mucous secretion, suction, or cementation, was probably necessary because holdfasts were not able to develop root systems for anchorage directly in soft sediment. Large flat trilobite cephalons or pygidia seem to have been especially favorable sites of attachment, probably because of their stability and ease of attachment. All early echinoderms with holdfasts may have been attached in this manner, but some may possibly have lived with the holdfast buried in the sediment or attached to it in some other way. Some early lepidocystids from Pennsylvania may have been able to change the length of their imbricately plated holdfasts to raise themselves further off the bottom for feeding or other functions (see p. 67).

One of the more interesting problems in the paleoecology of these early blastozoan echinoderms is the cause of death and method of preservation. Several factors in the mode of preservation, completeness, and distribution of many of these echinoderms suggest that they were killed and then buried by periodic sediment slumps from more shallow water, a type of preservation not commonly considered for most later echinoderm occurrences. These factors are reviewed in the sections below.

At most localities where these early eocrinoids have been found, specimens seem to be relatively to extremely abundant in some of the beds, and in many cases range unevenly through an appreciable thickness of sediments. Complete specimens are almost always more common than broken-up plate debris, and these specimens usually have even the long and delicate brachioles well preserved. This preservation of delicate appendages implies that these specimens were buried very rapidly, perhaps almost instantaneously, at the time of death. Otherwise, the calyx, with its porelike epispires, as well as the holdfast and delicate brachioles would have become disarticulated and then disaggregated relatively soon after death, even with only very slight current activity. Usually there is a wide range in the size of the specimens present, from very small to large (see, for example, Pl. 18, fig. 8). This implies that these eocrinoids probably have an autochthonous origin, and have not been transported any appreciable distance after death. Most complete specimens have the calyx crushed almost flat and slightly disarticulated, but this has almost certainly been caused by later diagenetic compaction of the soft surrounding sediments (see Sprinkle and Gutschick, 1967: 388–390). The delicate brachioles and the stoutly plated holdfast usually survive this later compaction with little distortion or change. A few specimens show possible slight disruption after burial by burrowing organisms (perhaps worms).

At many of the localities, groups of *Gogias* (and sometimes lepidocystids) on the same slab show a strong preferred orientation (Pl. 18, figs. 1–2; Pl. 21, fig. 1), as if all the specimens were "facing" or had been "knocked over" in the same direction. In some cases this orientation for three to eight specimens on the same slab is within ± 30° of the mean direction; in other cases the orientation is much less exact and sometimes it is almost random. When several specimens are attached to the same fossil fragment lying on the bottom, they are usually strongly aligned with each other (Pl. 7, fig. 4). In a relatively large thick block with several *Gogia*-bearing layers quarried out intact from the small shale pit at locality EC-1. in southeastern Idaho, the *Gogias* in each layer or surface are relatively well aligned in one direction, but the alignment for each of the layers in this block is very different. This suggests that, at least at this locality, whatever factor was responsible for the orientation on a single slab face varied considerably in direction with time.

At several localities, these eocrinoids seem to be localized to, or most abundant in, thin shale layers separating much thicker limestone beds, in thin shaly layers separating thicker sandier beds, or in distinctly more sandy beds separating barren shale layers. At other occurrences there is no observable variation in the surrounding matrix, although the *Gogias* and lepidocystids still occur most commonly in distinct layers or patches. These eocrinoids are known to occur sporadically in the intervening beds between these layers, but they seem to be much less common, and sometimes are represented only by completely disarticulated plate material. These observations suggest that the environment conditions responsible for the preservation as complete, oriented specimens may have been associated in many cases with a sudden change in sedimentation.

All of the above features suggest that many of these early eocrinoid occurrences having thin shaly or sandy interbeds bearing numerous complete and well-aligned specimens originated as sudden sediment slumps (either mud slides or turbidity currents) that resulted in "mass kills" of large local populations of attached *Gogias* or lepidocystids living on the sea bottom. This method of entombment would produce very rapid burial of a large number of unattached specimens, strong alignment, and a wide range in size. Since almost all the specimens are still complete, these sediment slides could not have been very violent, and may not have directly killed the specimens by knocking them down and tearing them from their attachment positions. Instead, these slides may either have knocked the specimens over and then quickly buried them under an inch or two of mud or silt (resulting in a 1/8–1/2 in. interbed) so that the specimens could not uncover and right themselves, or else killed them indirectly by roiling the water and clogging either the tiny respiratory papulae extending through the epispires or perhaps the delicate food-gathering brachioles for a long enough time to cause these eocrinoids to die and then be covered by the settling sediment. Some specimens (probably the larger ones) would survive these sediment slides and live on to start new colonies, but many were apparently killed. This seems to be the only reasonable explanation to account for all of the observed features found at many of these early eocrinoid occurrences. Some other occurrences (such as in the Chisholm Shale at Pioche, Nevada) may have been produced by more usual "death and slow burial" conditions, but have produced proportionally fewer complete and well-preserved specimens.

EVOLUTIONARY HISTORY OF BLASTOZOAN ECHINODERMS

Earliest Fossil Record

The first appearance of blastozoan echinoderms consists of possible eocrinoid plates in the upper Poleta Formation in the Waucoban Series of earliest Cambrian age (*Holmia-Nevadella* zone) at several localities in eastern California. These plates have epispires, and many are similar to, but not identical with, *Gogia* plates found in the middle Cambrian. Unfortunately, even after extensive search, no complete specimens of this possible eocrinoid have been found, and relatively little is known about its calyx morphology (see pp. 107–108). Recently, a few complete eocrinoid-like calyces with brachioles have been found in this same stratigraphic interval and are now being studied (J. W. Durham, personal communication, 6 July 1971).

The first completely preserved eocrinoids are the two genera of lepidocystid eocrinoids found in the Kinzers Formation, of late early Cambrian age (*Olenellus* zone), in southeastern Pennsylvania. These genera apparently differ from the Poleta form and other eocrinoids in having imbricate plates over much of their calyx and holdfast. Both genera have a conical calyx, a moderate to long cylindrical holdfast, numerous true brachioles mounted alternately along five radially arranged ambulacral areas leading to the central mouth on the oral surface, well-developed epispires present between the oral surface plates, and a lateral anal pyramid with a possible hydropore-gonopore combination. Thus, they are similar in many respects to slightly later middle Cambrian genera, while differing primarily in the unusual imbricate calyx and holdfast plating.

Eocrinoids show a moderate expansion during the middle Cambrian with approximately six to seven genera and 18–20 species present. This moderate record makes eocrinoids the most diverse and dominant class of echinoderms known in the middle Cambrian. Most of this expansion at the species level results from the single middle Cambrian genus *Gogia,* which has ten species in various zones of the middle Cambrian in western North America. This genus is probably the best known Cambrian eocrinoid, having an irregularly plated globular calyx with epispires between the calyx plates over much or part of the calyx, a cylindrical to globular holdfast, adjacent plates in the calyx and holdfast, a flattened summit area ringed with numerous brachioles branching off in groups, and three to five ambulacra leading from the brachiole groups to the central mouth. Thus, both early and middle Cambrian eocrinoids already have many of the characteristic features of the subphylum although some of these features, such as calyx plating and symmetry, respiratory structures, arrangement of ambulacra, and attachment appendage, are very primitive in their development.

The earliest crinozoan now known from the fossil record is a probable crinoid(?), *Echmatocrinus brachiatus* n. gen., n. sp., from the middle Cambrian Burgess Shale (*Bathyuriscus-Elrathina* zone) of western Canada. Unlike later crinozoans, this genus has an irregular calyx with adjacent plates, a holdfast with irregular adjacent plates (instead of a stem), but well-developed uniserial arms, perhaps bearing tube feet in at least one specimen. Again many of the morphologic features of this genus are very primitive, but it appears to be a true crinozoan, and very likely a true crinoid. There is no fossil record of other crinozoans until the early Ordovician when more advanced crinoids and paracrinoids first appear in the fossil record.

These earliest blastozoan and crinozoan echinoderms in the early and middle Cambrian were already very distinct and had many of the characteristic features shown by later members of their subphyla. The strong contrast in food-gathering appendages is probably the most important feature separating these two groups, and is present even in the earliest record. This implies that the divergence between these two groups of attached echinoderms probably took place sometime in the late Precambrian before the beginning of the known fossil record of echinoderms.

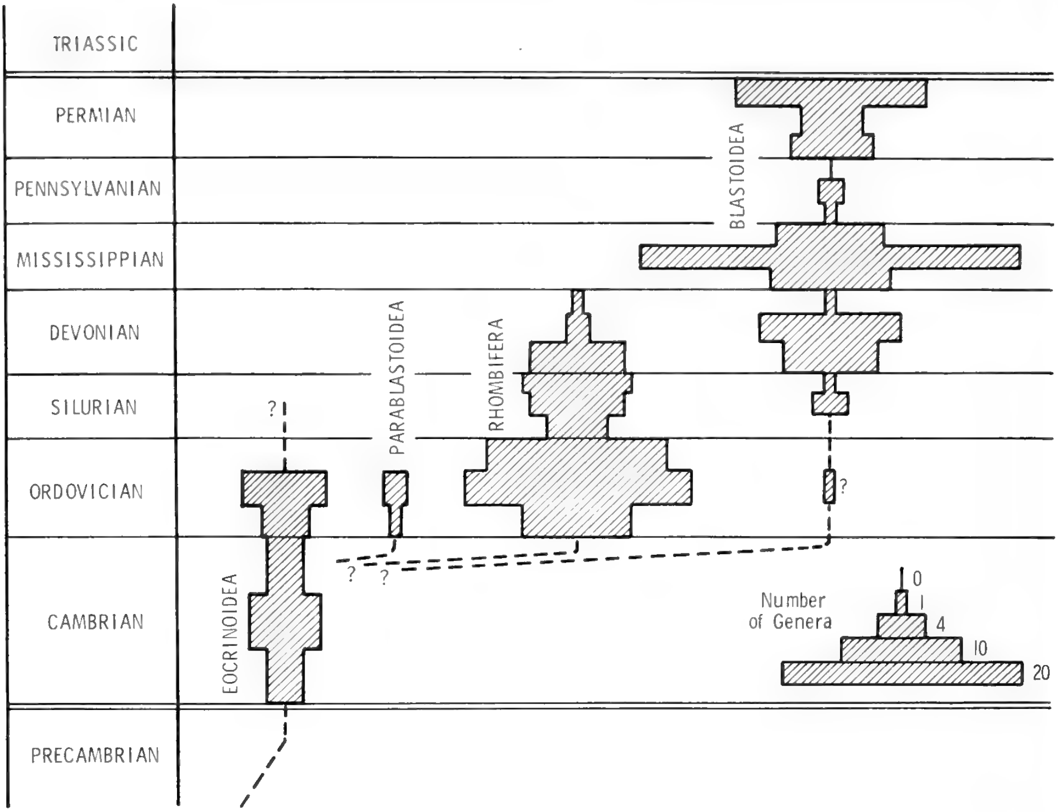
Later Evolution of Blastozoan Echinoderms

The record of eocrinoids is marked by a major middle Cambrian expansion and then a contraction in the late Cambrian. This apparent taxonomic contraction may partially result from facies problems in the sediments that have been examined for echinoderm remains, or changes in the respiratory system in these eocrinoids (especially the adoption of very thin calyx plates) that may have resulted in few complete specimens having been preserved. Eocrinoids show a moderate re-expansion in the early to middle Ordovician before apparently becoming extinct at this time. They may have been adversely affected by the appearance of several apparently more advanced groups of attached crinizoan and blastozoan echinoderms. Rhombiferan cystoids, parablastoids, and blastoids(?) first appear in the fossil record in the early and middle Ordovician and probably represent three independent developments from different eocrinoid ancestors.

The three larger blastozoan classes show a sequential replacement of each other within the subphylum during the Paleozoic (Text-fig. 20). Rhombiferan cystoids (along with other pelmatozoan groups) apparently replaced eocrinoids in the early to middle Ordovician and probably were partially responsible for the extinction of this group. Blastoids apparently replaced rhombiferan cystoids between the middle Silurian and middle Devonian, as has been noted by Newell (1952: 379). This sequential replacement apparently took place because of the development of more advanced and better adapted morphologic features in these newly evolving classes.

Morphologic Improvements in Blastozoan Echinoderms

The four classes of blastozoan echinoderms ranging from the early Cambrian to late Permian show several gradual or abrupt morphological improvements in their calyx and appendage structures. The first of these was the change from a holdfast to a true stem, which apparently occurred independently in blastozoan eocrinoids (late Middle Cambrian) and crinozoan crinoids (earliest Ordovician) (see Text-fig. 14). Both groups apparently evolved the most efficient attachment structure possible, and the resulting columnal-bearing stems are very similar in both of these groups and their descendants.



Text-figure 20. Geologic distribution and diversity of the four known blastozoan classes; horizontal scale measures diversity in terms of number of genera (½ inch = eight genera). Note total range of subphylum and possible replacement of eocrinoids by rhombiferans in the Ordovician and replacement of rhombiferans by blastoids in the Silurian and Devonian.

Respiratory structures also show several gradual and abrupt improvements in structure and function. The epispires of early eocrinoids were replaced in this class sometime in the middle to late Cambrian by an arrangement that eliminated the epispires and apparently replaced them with very thin calyx plates, allowing respiration over the entire plate surface. This apparently was not a successful design for these blastozoan echinoderms, and in the early and middle Ordovician three similar but independent types of internal fold respiratory structures suddenly appeared, thereby defining the three new classes Rhombifera, Parablastoidea and Blastoidea. These internal fold respiratory structures gradually acquired better flow control by modifications in the external openings and folds, and a more symmetrical arrangement; they showed few additional changes during their later history in the Paleozoic. This system of internal sutural folds apparently represented the optimal type of respiratory structure that blastozoan echinoderms evolved during their long history.

The ambulacral areas with their brachioles also show a gradual modification and improvement in design. Cambrian eocrinoids have the brachioles mounted on slightly modified calyx plates on the summit. This is improved in Ordovician eocrinoids and in the three other blastozoan classes by the development of specialized ambulacral plates for the support of the brachioles. This development allowed for better organized ambulacra, better symmetry in the ambulacral area, and a longer extension of the ambulacra with many more brachioles. There were also several experimental attempts to modify the recumbent ambulacra to erect arms similar to those found in crinoids, but this apparently was never completely successful in blastozoan echinoderms since it never became a dominant feature. Brachioles, on the other hand, showed very little change during their history, and appear to have been extremely conservative appendages. This usually (but not always) makes them a relatively reliable feature to use in identifying blastozoan echinoderms.

The calyx plating and symmetry in blastozoan echinoderms also shows a gradual improvement. There was a general reduction in the number of calyx plates in eocrinoids and early members of the other three classes as well as an accompanying gradual rearrangement of these plates into well-developed pentameral symmetry. These changes probably increased the strength of the calyx and allowed the echinoderm more genetic control over the shape of its calyx and the separate plates. Other systems, including the respiratory structures through the calyx plates, followed this rearrangement and also adopted pentameral symmetry in more advanced groups, such as blastoids and some of the rhombiferan cystoids. The better growth coordination using a reduced number of larger calyx plates enabled the development of such features as the forked radial plates in blastoids and some rhombiferan cystoids.

Paleoecology and Competition with Crinozoans

The combined Paleozoic record of the four classes of blastozoan echinoderms is relatively similar in its expansions and contractions to that found in crinozoan crinoids from the early Ordovician on (see Text-fig. 1). These blastozoan and crinozoan echinoderms were probably occupying the same general "crinoid-blastoid adaptive zone" during most of the Paleozoic. This zone included echinoderms (and perhaps other marine invertebrates) which were attached, "high rise," filter feeders having a globular, radially symmetrical calyx enclosing most of the soft parts of the animal, well-developed appendages for filter feeding, and a long attachment appendage. Only about five to ten percent of these blastozoan and crinozoan echinoderms modified this attached filter-feeding pattern and changed to benthonic mobile swimmers or resters, living directly on the sea bottom.

Blastozoan echinoderms were apparently somewhat less successful in competing to fill this adaptive zone than crinoids; the record in terms of genera and species for all blastozoan echinoderms combined is only about one-third to one-half the record of crinoids during most of the Paleozoic (see Text-fig. 1). The most reasonable explanation for this record seems to involve a comparison of their food-gathering appendages. Crinoids have arms with tube feet that serve as the major food-gathering appendages in this group. All blastozoans have brachioles apparently without tube feet. The combination of multipurpose tube feet on movable arms may have been a decisive advantage for crinoids throughout the entire Paleozoic in functions such as feeding, respiration, sensory perception, and movement, and may explain why they were much more successful in occupying this adaptive zone than blastozoan echinoderms.

The End–Permian Extinction of Blastoids

The record of blastozoan echinoderms extends from the early Cambrian to the late Permian when they apparently became extinct. Blastoids are the only blastozoan echinoderms to survive to the Permian, and they show a very characteristic pattern in this period. Blastoids had a major expansion in the Mississippian followed by a very meager record in the Pennsylvanian. In the Permian they show another moderate expansion, but this is strongly restricted geographically and perhaps ecologically during the later portion of the period. Although moderately widely distributed in the early Permian, blastoids are restricted to the East Indian-Australian region in the late Permian and occur most commonly in an unusual facies which may have been strongly restricted to warm water banks and reefs, especially in the region just north of the present site of Timor. Some Permian blastoids also show unusual modifications in their ambulacra and respiratory systems, which may possibly have contributed to their extinction at the end of the Permian. Apparently, the general crisis in marine life at the Permo-Triassic boundary, no matter what its cause, most severely affected groups that were "relicts" (in terms of diversity) or "restricted" either geographically or ecologically (Sprinkle, unpublished; Rhodes, 1967: 63). Blastoids fit at least two and perhaps all three of these conditions, and were apparently reduced to extinction at this boundary. Considering these factors there is probably no need to appeal to unknown outside or "extraterrestrial" environmental changes to explain this final extinction of blastoids as Fay (1967b: 283–284) has done.

SYSTEMATIC PALEONTOLOGY[1]

Phylum **ECHINODERMATA**
Bruguière, 1789
Subphylum **BLASTOZOA**
new subphylum

Diagnosis. Extinct Paleozoic "pelmatozoan" echinoderms having a globular multiplated calyx bearing erect food-gathering appendages called brachioles and attached to the sea bottom by a stem or holdfast attachment appendage. The characteristic brachioles are relatively small but long, erect, biserially plated, nonpinnulate, food-gathering appendages usually attached to specialized recumbent ambulacral areas for support. Brachioles (and ambulacra) in all blastozoans may have completely lacked tube feet, and the water vascular system may have been considerably reduced. The calyx is usually more or less globular (sometimes flattened), has numerous adjacent tightly sutured plates (except for a few early eocrinoids with imbricate plates), and often shows well-developed pentameral symmetry in the ambulacral system, calyx plating, and other structures. Calyx respiratory structures are present in most forms and consist either of sutural pores (epispires) connecting to the interior, or thin internal calcified folds located suturally and opening to the exterior through the overlying plates. The calyx plates grow by primary holoperipheral growth on the sutured margins, with secondary deposits covering the interior and scattered parts of the exterior where primary growth lines are located. Attachment appendage usually consists of a columnal-bearing stem nearly identical to that in crinoids, but many early eocrinoids have a more primitive, irregularly multiplated, cylindrical or globular holdfast for attachment. In a few mobile, bottom-living blastozoans, the stem has been modified, reduced, or completely lost and the calyx has a flattened shape and bilateral symmetry. The subphylum contains at least

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[1] Abbreviations used for repositories include: MCZ = Museum of Comparative Zoology, Harvard University; GSC = Geological Survey of Canada; USNM = U. S. National Museum; USGS = U. S. Geological Survey; UU = Department of Geological and Geophysical Sciences, University of Utah; UC = Department of Geology, University of Cincinnati; AMNH = American Museum of Natural History; UMMP = Museum of Paleontology, University of Michigan; NYSM = New York State Museum; GCM = Grand Canyon Museum; ISU = Idaho State University; and PE = North Museum, Franklin and Marshall College.

4 classes—Eocrinoidea (+ Lepidocystoidea), Rhombifera, Parablastoidea, and Blastoidea—with a total of approximately 160 genera; a fifth class (Diploporita) may possibly belong here also. Blastozoans range from the early Cambrian to the late Permian, have a nearly world-wide distribution, and were common, attached, filter-feeders in a wide variety of shallow water marine environments. There are no known living blastozoan echinoderms.

Discussion. The new subphylum Blastozoa proposed here contains four classes of "pelmatozoan" echinoderms removed from the subphylum Crinozoa of Matsumoto (1929: 27), Fell (1965: 13), and Ubaghs (1967a: S51–52), leaving the revised Crinozoa with two (perhaps three) classes (see p. 174). In addition to the Homalozoa ("carpoids"), the subphylum Blastozoa is the only other echinoderm subphylum that has no living representatives. Although at least four classes are assigned to the Blastozoa, this extinct subphylum contained relatively few genera and was only moderately important during most of the Paleozoic. The most characteristic morphologic features include the presence of brachioles usually mounted on recumbent ambulacral areas, the development of calyx pore- or foldlike respiratory structures, holoperipheral primary calyx plate growth, a holdfast or columnal-bearing stem as an attachment appendage, and the possible absence of ambulacral tube feet. Biserial brachioles are probably the single most important defining feature for blastozoan echinoderms, but cannot be used alone because not all blastozoans have normal brachioles, and a few other crinozoans have developed very similar food-gathering structures. Indeed, none of these characteristic morphologic features are known to be present in all blastozoan echinoderms, nor are they confined to this subphylum. However, no other group of echinoderms commonly has more than one or two of these characteristic features, and it is this combination of features that defines this new subphylum.

Several authors in the past have stressed the differences between brachiole-bearing and arm-bearing attached echinoderms, but this is the first time that this important difference has been recognized and defined taxonomically. As pointed out by Carpenter in his report on the stalked crinoids from the Challenger Expedition (1884: 191), Burmeister, as far back as 1856, divided pelmatozoan echinoderms into "Crinoidea brachiata" or true crinoids and "Crinoidea anthodiate," including cystoids and blastoids. This proposed division ". . . clearly brought out the difference between true Crinoids with segmented arms attached to the radials and . . . Blastoids and Cystoids, in which there are either no arms at all or structures of an entirely different nature from those of true Crinoids." (Carpenter, 1884: 191). Other authors, such as Bather (1900: 3, 95) and Jaekel (1899: 90–91), have also pointed out this basic difference between arm- and brachiole-bearing echinoderms, but neither of them incorporated Burmeister's suggested division into their classifications. More recently, Hyman (1955: 43, 698) also cited this same difference in attempting to work out the evolution of these early echinoderm classes, and Ubaghs (1953a: 20; 1967a: S55, 1967b: S476; personal communication, 24 June 1969) has emphasized this difference for many years. Beerbower (1968: 393) has recently asked ". . . is the difference between brachioles (cystoids and eocrinoids) and arms (crinoids) significant in phylogeny?" I feel that this difference is indeed significant, and have used it here as a basis for a new subphylum classification of attached Paleozoic echinoderms. The most probable reason why this major morphologic difference has not received acceptable taxonomic status previously is that information on the morphology and evolution of brachiole- and arm-bearing echinoderms in the Cambrian has been very scarce. Recent work summarized both here and in the Treatise volumes has added strong support for a major taxonomic division at the subphylum level.

In establishing this new subphylum, the name Blastozoa, derived from the class Blastoidea, was chosen over other possibilities (such as "Cystozoa") for several reasons. First and probably foremost, I began my paleontological work in blastoids, so there is a personal bias in this choice of a name. Blastoids were also the most successful, diverse, longest-lived, and morphologically advanced of the known blastozoan classes. In addition, they represent the earliest established taxonomic grouping of blastozoan echinoderms, dating back to Say (1825). Finally, the possible name "Cystozoa" seemed inappropriate, since the class Cystoidea (von Buch, 1845) has now been split into two separate classes, Rhombifera and Diploporita (Paul, 1968a: 594; 1968b: 727), one of which may not belong in this subphylum. Therefore, I chose the taxonomic name Blastozoa for this proposed new subphylum in mid-1968, and until now have used it only informally as a descriptive adjective ("blastozoan echinoderms"—see Sprinkle, 1969: 287–288). However, Brower (1969: 846–847) has informally used the identical term "Blastozoa" (quotation marks his) plus the term "blastoid-spectrum" (quotation marks his) for a possible grouping of three classes of blastoid-like echinoderms, Blastoidea, Parablastoidea, and Edrioblastoidea. Recent work has shown that these three included classes are apparently not all phylogenetically related (see p. 188), but are only convergent on a single design. The new subphylum Blastozoa here contains only two of the three classes in Brower's grouping "Blastozoa" as well as parts of three of the four classes in his grouping "Cystozoa"; the other classes either belong to other subphyla or are at present unassignable.

Class *EOCRINOIDEA* Jaekel, 1918

Diagnosis. Early blastozoan echinoderms having an irregular adjacently or imbricately plated calyx with or without epispires (sutural pores), an irregularly multiplated holdfast or a true stem as an attachment appendage, a primitive ambulacral system bearing normal or modified brachioles, and usually little pentameral symmetry. The calyx is more or less globular or else flattened, and usually plated with numerous irregularly arranged adjacent plates (imbricate in 2 early genera). Many early eocrinoids have characteristic epispires or sutural pores on the sutures between the calyx plates, but these are lost in some middle Cambrian and most later genera. The calyx in early eocrinoids is attached aborally by a cylindrical or globular irregularly multiplated holdfast with a large central lumen. During the middle Cambrian, however, this primitive appendage evolved into a true columnal-bearing stem. The ambulacral system is usually confined to the adoral end of the calyx (oral surface) and consists of 2–5 (or more) ambulacral grooves located on slightly modified calyx plates and leading to groups of erect brachioles. Most eocrinoids have normal straight brachioles with biserial plating and tiny adjacent or imbricate cover plates, but a few forms have spiralled brachioles, modified brachioles with apparent uniserial plating, or the entire ambulacral system developed as erect "arms" with "pinnule-like" brachioles. In most genera the numerous calyx plates are usually irregularly arranged and only the ambulacral system shows any evidence of pentameral symmetry. The mouth is usually central on the oral surface with the anal opening lateral; a hydropore and gonopore may also be present between these. Plate growth unknown in most forms but probably holoperipheral. Twenty-five ± genera. Early Cambrian to middle Ordovician (perhaps later). Nearly world-wide range (but many localities known only from plates).

Discussion. Eocrinoids are the most primitive class of blastozoan echinoderms now known. They appear to represent the basic stock from which all three later and more advanced blastozoan classes radiated near the beginning of the Ordovician. Eocrinoids also appear to be the dominant class of echinoderms in terms of abundance, diversity, and distribution in the middle Cambrian; this may also be true for the early and late Cambrian, but the record is more obscure here. Eocrinoids already possessed at their first appearance many of the important morphologic features of blastozoans: brachioles, plated ambulacra, a distal attachment structure (holdfast), and perhaps pentameral symmetry and holoperipheral plate growth. Later eocrinoids also developed a true stem and strong pentameral symmetry in their calyx plating. In a sense, the only "problem" not adequately "solved" by eocrinoids was that of calyx respiration after the loss of the more primitive calyx water vascular system with epispires (see p. 35). However, this is only apparent since the transition to each of the three later blastozoan classes is presently defined as the point where an eocrinoid ancestor successfully developed one of the three later internal foldlike respiratory systems. Later eocrinoids, by elimination, are restricted to genera that did not undergo one of these three transitions to the other blastozoan classes.

Eocrinoids were first set up as a separate grouping by Jaekel (1918: 24), who proposed the subclass Eocrinoidea in the class Crinoidea for several primitive genera that did not fit well in any of the later "pelmatozoan" classes. Regnell (1945: 35–37) raised this group to class rank because of their many morphologic features intermediate between cystoids and crinoids; however, he apparently did not know of the existence of epispires (sutural pores) in many of these forms, even though they had been figured and briefly mentioned by Walcott (1886) and Pack (1906). These were incorporated into the definition of eocrinoids by Ubaghs (1953a: 14) in his revision of *Lichenoides,* and further discussed by Ubaghs (1963: 34) and by Robison (1965: 357). Several authors have proposed that Cambrian eocrinoids were ancestral to several later classes, such as the "cystoids" and crinoids (Moore, 1954: 131; Regnell, 1960: 71, 76). I have tried to show that the three later classes of blastozoan echinoderms (rhombiferans, parablastoids, blastoids) all evolved from different(?) Cambrian or early Ordovician eocrinoid ancestors, but that crinozoan forms cannot be derived from eocrinoids, and in fact were already present as a separate evolutionary line in the middle Cambrian (see p. 53). Apparently, blastozoan eocrinoids and crinozoan crinoids represent two very early, independent attempts to exploit an attached filter-feeding way of life.

Early Cambrian eocrinoids are among the first echinoderms to appear in the fossil record. The class is marked by a major expansion in the middle Cambrian, greatly reduced apparent diversity in the late Cambrian, and a moderate expansion again in the early and middle Ordovician before apparently becoming extinct at this time. Competition with more advanced and successful blastozoan and crinozoan classes probably was at least partially responsible for this extinction of eocrinoids in the middle Ordovician. The relatively incomplete record of eocrinoids in the Cambrian and the wide gaps between many eocrinoid genera indicate that the true fossil record of eocrinoids, especially in the Cambrian, is probably much larger than is presently known.

Because of this incomplete record, the classification of eocrinoids at the order level is now in a confused state, as pointed out by Ubaghs (1967b: S477–478). Jaekel's ordinal classification (1918: 24) is inappropriate because it was based on only a few morphologic features, included many genera now put in the paracrinoids and other classes, and did not consider the many eocrinoid genera described since 1918. I have proposed one new order, and have indicated (but not formalized) several other possible ordinal groupings. In total, the eocrinoids comprise a class with approximately five orders, 10–11 families, 24–26 genera, and 37± species. At present, most of the genera are monotypic (probably because many are based on material from only a single locality), but one genus, the middle Cambrian eocrinoid *Gogia,* now has at least ten species, ranges through the entire middle Cambrian, and is known from 18 or more widely scattered localities in the Cordilleran Geosyncline of western North America. I suspect that many other eocrinoids probably had a diversity and distribution pattern similar to that of *Gogia,* but the complete record has not been found yet.

Approximately seven genera which have been assigned to the eocrinoids in the past are removed or provisionally removed from this class (see pp. 136–142). I have also suggested (p. 122) that the genus *Macrocystella,* which has recently been transferred from the eocrinoids to the rhombiferan cystoids (Paul, 1968a: 580), be returned to the eocrinoids; otherwise, I agree with Paul in his interpretation that this genus is truly transitional between these two classes.

Order **IMBRICATA** new order (= Class *LEPIDOCYSTOIDEA* Durham, 1967)

Diagnosis. Early eocrinoids having a strongly differentiated calyx with both imbricate and adjacent calyx plates. Aboral portion of conical calyx and cylindrical holdfast composed of adorally imbricate plates lacking epispires. Oral surface composed of adjacent plates having numerous epispires and bearing the ambulacral system with 5 symmetrical food grooves and numerous true brachioles. Early Cambrian.

Discussion. The recently established class Lepidocystoidea Durham, 1967b (p. S361), based on the single genus *Lepidocystis,* is here rejected, and this genus is transferred back to the eocrinoids to which it had originally been assigned by Foerste (1938: 212–213) and Bassler and Moodey (1943: 172). A second lepidocystid genus, *Kinzercystis* n. gen., is described below and also assigned together with *Lepidocystis* to Durham's family Lepidocystidae in the new order Imbricata. Both of these genera occur together in the Kinzers Formation of late early Cambrian age in southeastern Pennsylvania.

Durham (1967b: S631–634) gave a short redescription of *Lepidocystis* based primarily on the six type specimens (USNM 90773) and at least one other specimen, and concluded that this taxon was sufficiently different from all other echinoderms to warrant both a new family and the new class Lepidocystoidea. He differentiated lepidocystids from eocrinoids (p. S633) on the following features (order my own): 1) the presence of "circlets of arms" on the oral surface, 2) the mode of attachment of these arms, 3) the presence of imbricate plates on the aboral surface, and 4) the restriction of the epispire-bearing area to the oral surface. In addition, he postulated that lepidocystids were either free living or imbedded in the sediment (Durham, 1967b: S631, and fig. 399), unlike most eocrinoids, which are attached by either a holdfast or stem.

Many of these apparent differences have now disappeared and the similarities to other eocrinoids have been accentuated by the discovery of new, more complete, and better preserved lepidocystid specimens in the Kinzers Formation. All lepidocystids are now known to have true brachioles, and not "arms," for appendages. Both Foerste and Durham correctly described the morphologic features of these brachiolar appendages, but inadvertently obscured the close relationship to other blastozoans by calling them "arms." These brachioles are each mounted on three or four modified oral surface plates and attached alternately along *both* sides of each ambulacral food groove (see Text-fig. 23). This arrangement produces a heterotomous branching pattern (Ubaghs, 1967b: S470) for each ambulacrum instead of the radially arranged, uniserial, "circlet" pattern described by Durham. However, he correctly inferred (p. S631) that a five-fold radial arrangement of these appendages (= five brachiole-bearing ambulacra) was present around the central mouth.

Apparently none of Durham's studied specimens showed much of the distinctive cylindrical holdfast attached to the aboral end of the calyx. This attachment appendage is similar in morphology to holdfasts found in other early eocrinoids. In addition, the epispires or sutural pores between the oral disk plates in lepidocystids are very similar to the epispires between the calyx plates of many other eocrinoids. Indeed, it is difficult to distinguish between epispire-bearing portions of the oral surface of *Kinzercystis* n. gen., and the calyx of an eocrinoid such as *Gogia longidactylus*. The similarity between *Lepidocystis* and other eocrinoids is less striking only because the oral surface plates are very much smaller and have fewer epispires. The restriction of epispires to the oral surface in lepidocystids results from the restriction of exposed, vertically sutured adjacent plates to this surface and their absence elsewhere in the calyx. Epispires apparently cannot develop on any portion of the calyx that has strongly imbricate plating.

Therefore, the only important remaining difference that could be used to separate lepidocystids from eocrinoids is the marked differentiation between the adjacent oral surface plating and the strongly imbricate calyx and holdfast plating. I do not feel that this contrast in plating types is a sufficient difference to warrant the establishment of a separate class for lepidocystids. Several other echinoderm classes, including the edrioasteroids, echinoids, and stylophoran carpoids, have members in good standing with partial imbricate plating combined with the more usual adjacent plating. Therefore, because of the many similarities to eocrinoids and the presence of only one major difference (imbricate vs. adjacent calyx plating), I have rejected Durham's class Lepidocystoidea and have returned his family Lepidocystidae with its two genera (one new) to the eocrinoids as the new order Imbricata.

Family LEPIDOCYSTIDAE Durham, 1967

Diagnosis. Early eocrinoids with strongly differentiated oral and aboral plated surfaces. Aboral portion made up of a large conical calyx and a smaller, long or short, cylindrical, attachment holdfast, both having numerous adorally imbricating plates. Oral surface covers large adoral end of conical calyx and consists of large or small adjacent plates bearing numerous epispires (sutural pores). Ambulacral system confined to oral surface, consisting of a central covered mouth, 5 radially arranged ambulacral grooves depressed into the oral surface, and numerous biserial brachioles alternately arranged alongside each ambulacrum. Anal pyramid located at edge of oral surface in "CD" interradius; possible hydropore-gonopore combination located between it and mouth. Two genera; early Cambrian.

Genus *Lepidocystis* Foerste, 1938

Type species, Lepidocystis wanneri Foerste, 1938

Generic diagnosis. Calyx conical, expanding adorally; covered by large, wide, imbricate calyx plates without pores, plates both overlapping and gradually increasing in size adorally, with exposed portion ornamented with vertical ridges; holdfast cylindrical, relatively long and thin, attached to base of calyx; covered by many very small imbricate plates overlapping adorally, each plate longer than wide and slightly ornamented; oral surface nearly circular and somewhat domed, covering adoral end of conical calyx from which it is sharply differentiated; composed of many very small adjacent plates bearing epispires (sutural pores) on their margins, about 3–4 per plate; ambulacral system confined to oral surface, consisting of a centrally located domed oral pyramid covering the mouth; plus 5 simple ambulacra extending radially from the oral pyramid to the edge of the oral surface, each made up of a depressed food groove lying on larger wedge-shaped plates without epispires and covered by very small cover plates; and 3–8 biserial brachioles mounted alternately on opposite sides of an ambulacrum on circular bases of modified nonpore plates; number of brachioles apparently increasing during ontogeny and brachioles greatly increasing in size aborally, with the largest (and oldest?) brachiole at the end of each ambulacrum; brachiolar food groove covered by 1 or 2 sets of biserial overlapping cover plates; large anal pyramid at edge of oral surface in "CD" interradius; hydropore and gonopore unknown; Kinzers Formation, Lower Cambrian (*Olenellus* zone), southeastern Pennsylvania.

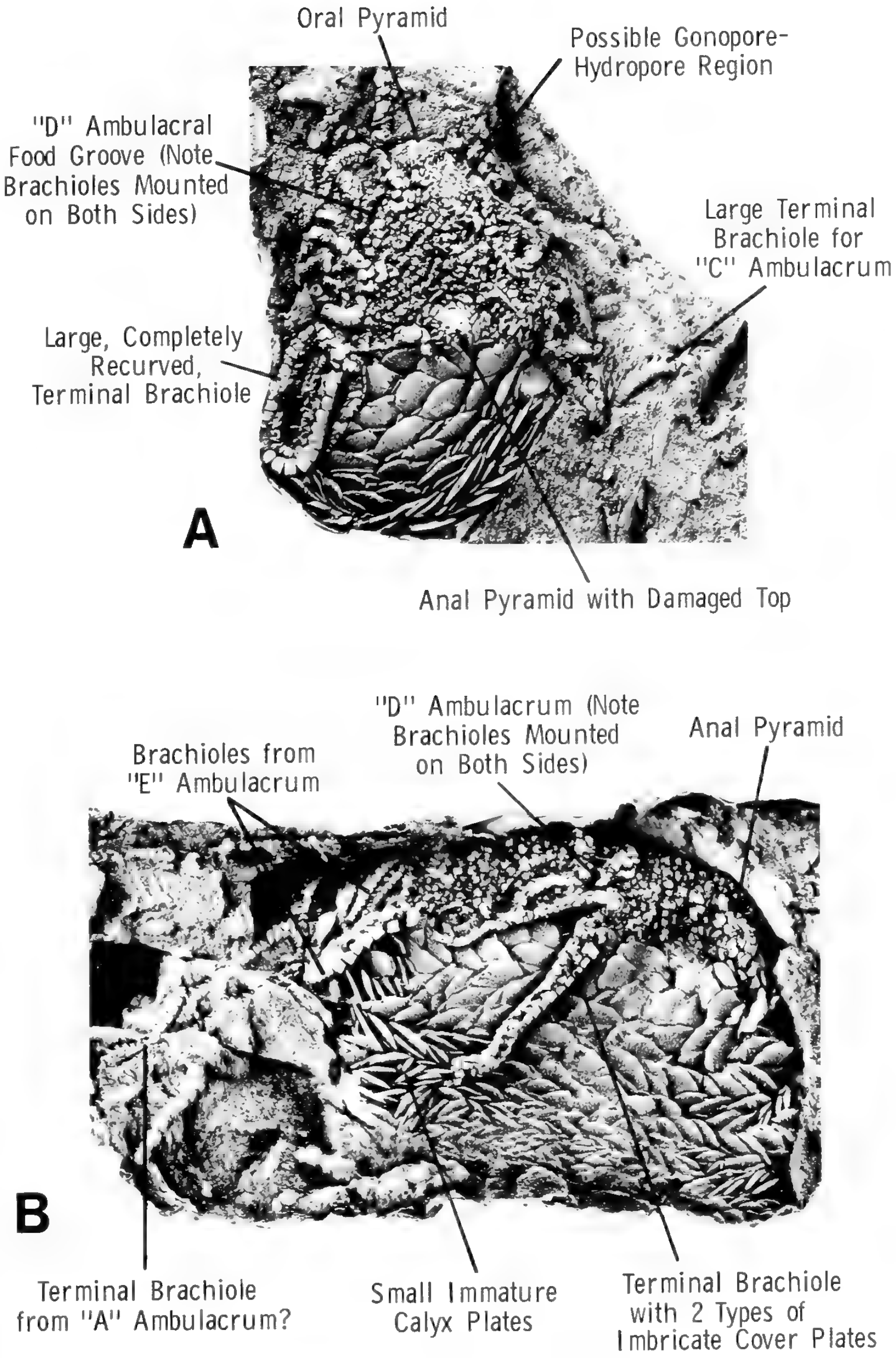
Lepidocystis wanneri Foerste
Plates 1–2; Text-figure 21

Lepidocystis wanneri, Foerste, 1938: 212–213, pl. 2, figs. 5–9; Bassler and Moodey, 1943: 172; Durham, 1967b: S631–S634, figs. 398, 1a–c and 399.

Nearly all of the known specimens of *Lepidocystis wanneri* were restudied for this project. The type suite of specimens (USNM 90773, –A, –B, –C1–3) was borrowed and new latex casts were prepared of these molds; these are illustrated on Plate 1, figures 1–8. Six of the seven type specimens represent *Lepidocystis;* one (unfigured) is apparently a specimen of *Camptostroma.* Many additional specimens were collected from the Kinzers Formation in southeastern Pennsylvania between 1967–69; most of these came from localities SH-1. and EM-1. Several specimens from these localities collected by Martin Anné of Wrightsville, Pennsylvania, and Kraig Derstler of Columbia, Pennsylvania, were borrowed and cast. Approximately 25 additional specimens were studied in detail (but see p. 66).

Foerste's original description of *Lepidocystis wanneri* (1938: 212–213) was relatively short and partially incomplete because he apparently did not prepare casts of the natural molds. He did correctly describe the calyx plating and shape, the plating and five-fold nature of the brachiole appendages, which he called "arms," and provisionally assigned this genus and species to the Eocrinoidea. He also described a "vesticular mass" (representing the oral surface with its epispires and ambulacral system), but did not realize its significance. Durham (1967b: S631–634), using latex casts, restudied these type specimens and at least one additional specimen. He described the oral surface plating, anal pyramid, and other previously unknown features, and presented an excellently drawn and mostly correct reconstruction (p. S633). However, certain features of the lower portion of the calyx and the arrangement of the ambulacral system were not well shown on any of the specimens that Durham studied, and his reconstruction must be modified. Durham also continued Foerste's incorrect designation of the brachiole appendages as "arms"; this is perhaps one of the reasons that he removed this genus and species from the eocrinoids and established the separate class Lepidocystoidea for it. I disagree with this phylogenetic interpretation (see p. 60), and I have here returned *Lepidocystis wanneri* to the eocrinoids.

Specific description. The plated skeleton of *Lepidocystis wanneri* consists of a large conical calyx with imbricate plating, a cylindrical holdfast attached to the smaller aboral end, and a differently plated, epispire-bearing, oral surface covering the larger end of the calyx and bearing the



Text-figure 21. Calyx and brachiole morphology of *Lepidocystis wanneri*. A, plesiotype MCZ 588A showing calyx plating and portion of oral surface; note oral pyramid, nearly complete "D" ambulacrum at left with brachioles mounted on both sides, slightly damaged anal pyramid at bottom, and very large recurved terminal brachioles. B, paratype USNM 90773B showing large portion of calyx and "D" and "E" ambulacra; note anal pyramid, imbricate cover plates on brachioles, small oral surface plates with epispires, and small immature plates scattered around calyx.

ambulacral system with its fingerlike food-gathering brachioles and other structures. The calyx is conical in shape, and probably somewhat higher than wide. It expands in size adorally from the edge of the holdfast to the edge of the large oral surface. The calyx is covered by relatively large, adorally imbricate, arc-shaped, calyx plates (Text-fig. 21A and B). These plates gradually increase in size adorally by a factor of 3–4. Near the top of a large specimen, each calyx plate is as much as 4.0 mm wide, slightly wider than high, and has about 40–50 percent of the plate surface exposed. The remainder is strongly overlapped on the aboral margins by 2 or 3 plates lower in the calyx. The exposed portions of these calyx plates are usually ornamented with inverted V-shaped vertical ridges of pustules.

The holdfast in *L. wanneri* is relatively long and narrow, and apparently nearly cylindrical in shape. It is best preserved on specimen MCZ 589 (Pl. 2, figs. 4–5), where it has a flattened cylindrical shape approximately 14–15 mm long and 7.5 mm wide distally versus 5.5 mm wide proximally. The original uncrushed diameter would have been approximately 5.0–5.5 mm distally and 4.0–4.5 mm proximally. The sides of the holdfast in *L. wanneri* are covered by very small, adorally imbricate, tongue-shaped plates about 0.5 mm wide. These holdfast plates are somewhat longer than wide, unlike the larger calyx plates just above them (see Pl. 1, fig. 3). The distal attachment base of the holdfast is poorly preserved only in specimen MCZ 589 (Pl. 2, fig. 4) and is apparently composed of very tiny elongate plates approximately 0.2–0.3 mm long that are somewhat similar to those on the side of the holdfast. The presence of a cylindrical holdfast in *L. wanneri* implies that this echinoderm probably attached itself either to the bottom sediment or to objects lying on the bottom (see p. 67 and Pl. 3, fig. 4), and did not bury the aboral end of the body as shown in Durham's recent reconstruction (1967b: S633).

The oral surface covers the larger adoral end of the conical calyx. It is a nearly circular domed area containing the ambulacral system with its brachioles, the anal pyramid, and many small epispires (sutural pores) leading to the interior of the calyx. Most of the oral surface between the ambulacral areas is made up of numerous, very small, adjacent, oral surface plates bearing epispires on their margins. These oral surface plates are much smaller than the imbricate calyx plates (the reverse is true in *Kinzercystis*), and are usually 3–5 sided and average about 0.5–0.8 mm in size. In some of the larger specimens of *L. wanneri*, each of these plates bears a strongly domed or knoblike central projection. Epispires are present on the margins of most of these oral surface plates, usually 3–5 per plate. Many of these epispires seem to be shared by 3 plates at plate corners. They are circular to slightly elliptical in shape (L/W ranges between 1.0–2.0), and are surrounded by prominent raised rims on the exterior. These epispires pass vertically down the suture and open directly into the calyx interior. Epispires are probably confined to the oral surface in *Lepidocystis* (and *Kinzercystis*) because the entire rest of the calyx is covered with strongly imbricate plates.

The ambulacral system is confined to the oral surface and consists of a central oral pyramid, 5 ambulacral food grooves extending radially from it to the edge of the oral surface, and numerous biserial brachioles mounted alternately alongside each ambulacrum. The oral pyramid is well exposed only on 1 specimen of *L. wanneri*, plesiotype MCZ 588 (Text-fig. 21A), where it is located near the center of the oral surface. It is an elongate domed structure made up of many tiny, elongate, wedge-shaped plates oriented vertically. In this specimen the oral pyramid is 3.0–3.5 mm long in the "E"–"B" direction (long axis), at least 1.5 mm wide in the "A"–"CD" direction (short axis), and about 1.0–1.5 mm high. The ambulacra seem to enter in a standard "2–1–2" pattern (see Text-fig. 16A). The covered mouth may have been considerably smaller than the covering pyramid, but probably had a similar shape (see Pl. 2, fig. 6).

The 5 food grooves extend radially from the oral pyramid to the edge of the oral surface. They were apparently covered in life by small covering plates but these are usually not preserved intact. On plesiotype MCZ 588, the well-preserved "D" ambulacrum is about 12.0–12.5 mm long and 0.5–0.8 mm wide. The bottom of each ambulacrum appears to be depressed into the oral surface and made up of large, wedge-shaped, oral surface plates lacking epispires. These plates are partially shown by one of the newly collected specimens (Pl. 2, figs. 6–7).

The brachioles in *Lepidocystis wanneri* are attached in an apparently alternate arrangement to modified oral surface plates alongside each ambulacrum. There are from 3 to 8 brachioles per ambulacrum in the studied specimens, a somewhat smaller number than in *Kinzercystis*. Also, in *L. wanneri* the brachioles gradually increase both in size and length aborally along each ambulacrum; the terminal brachiole at the edge of the oral surface is especially large. In MCZ 588 (Text-fig. 21A), the brachiole closest to the mouth on the "D" ambulacrum has a total length of about 9.5 mm, while the aboralmost brachiole has a length of about 25.5 mm, almost 2½ times as great. This increase in brachiole size is much greater than in *Kinzercystis*.

The brachioles in *L. wanneri* are made up of larger alternating biserial brachiolar plates (BP) covering the aboral and lateral sides of the brachiole, and bearing the wide, deep food groove on their adoral surface. This brachiolar food groove is covered over by 1 (and perhaps 2) set of smaller, alternating biserial, brachiolar cover plates (BCP), overlapping in an aboral direction (Text-fig. 21B), and having jagged distal edges, as figured by Durham (1967b: fig. 399). There is 1 cover plate (or 1 group of 2) per brachiolar plate along the entire length of the brachiole. I have observed 2 sets of brachiolar cover plates only on the large, well-exposed brachiole at the end of the "D" ambulacrum in paratype USNM 90773B (Pl. 1, fig. 4; Text-fig. 21B); here a smaller accessory set of biserial cover plates is present at the thick proximal end of the brachiole beneath the overlapping portions of the larger, normally present set. Only 1 set of brachiolar cover plates was observed in all other *L. wanneri* brachioles examined, the implication being that this second set may only develop on the proximal portions of the large aboralmost brachiole and perhaps only as a late growth feature.

Each of these brachioles is attached to a circular ring of modified oral surface plates alongside the ambulacrum. There are usually 3–4 arc-shaped plates in this ring, with the basal brachiolar plates mounted on their inner edge. These mounting plates are considerably larger than the other oral surface plates and appear to lack epispires on their outer margins. The brachioles face adorally and are mounted at an angle of about 45° to the direction of the food groove; a very short side food groove leads from each brachiole down into the depressed main food groove. The large aboralmost brachiole in each ambulacrum is located right at the edge of the oral surface where it joins the imbricately plated calyx; the calyx plates just beneath its mounting ring are smaller than usual and depressed, probably to allow this brachiole a full range of flexible movements.

The anal pyramid in *L. wanneri* is shown only by 2 specimens, paratype USNM 90773B, and plesiotype MCZ 588. It is located at the extreme lateral edge of the oral surface in the "CD" interradius. In both specimens the anal pyramid is approximately 3.0 mm in diameter and about 1.0–1.5 mm high, and is composed of small, wedge-shaped, vertically oriented plates similar to the oral surface plates but lacking epispires (Text-fig. 21A and B). As above, the imbricate calyx plates bordering the anal pyramid on the aboral side are smaller than usual and slightly depressed, apparently to allow the pyramid to flex and open during elimination of fecal material.

At present, no hydropore-gonopore region is known in *Lepidocystis wanneri.* However, plesiotoype specimen MCZ 588 shows an area of small oral surface plates apparently lacking epispires near the "C" ambulacrum and just below the mouth (Text-fig. 21A); this is similar to the position of these openings in *Kinzercystis* (see p. 74). Unfortunately, this area is too poorly preserved to show any other morphologic features, and the presence of these structures cannot be confirmed.

Little is known about the growth of *Lepidocystis wanneri.* None of the observed calyx plates show any growth lines, so it is not known if holoperipheral growth was present as in other blastozoans. Durham (1967b: S633), in his reconstruction, suggested that the small plates in the lower part of the calyx might be immature; however, these plates have now been shown to belong to the holdfast. The presence of several tiny calyx plates high in the calyx of paratype 90773B (Text-fig. 21B) suggests that new plates were continually added to all parts of the calyx of *Lepidocystis* as it increased in size. By comparison with *Kinzercystis* (p. 72), this may also have been true for the oral surface plates. The marked change in brachiole size along an ambulacrum may imply that the large terminal brachioles were the first to form. The more adoral brachioles along the ambulacrum would then have been inserted (perhaps sequentially) during later growth of the lepidocystid. If this assumption is correct, this would be directly opposite to most later blastozoan echinoderms having separate calyx and ambulacral plates, in which new brachiole formation takes place at the aboral end of the ambulacrum (see p. 19). However, this growth pattern in *Lepidocystis* is very similar to that found in the Ordovician eocrinoid *Ascocystites* (see p. 118), which also shows a gradation in brachiole size.

Stratigraphic and geographic range. All specimens are from the Kinzers Formation, upper Lower Cambrian (*Olenellus* zone), near York, southeastern Pennsylvania. The type specimens are from Walcott's locality 8q, listed as "Kinzers Formation, Lightners Hill near the contact with the Triassic, 2.0 mi. NW of York, Pa." This locality has not been satisfactorily pinpointed, but may have been covered by a large shopping center on route 238 built about five years ago (Martin Anné, personal communication). I have collected specimens of *Lepidocystis wanneri* from the Kinzers Formation at localities SH-1., SH-2., and EM-1.

Studied specimens. Holotype USNM 90773 (two counterparts), paratype USNM 90773A (two counterparts), B, C1–3 (specimen C4 is apparently a portion of *Camptostroma roddyi*), all from Walcott's locality 8q; plesiotypes MCZ 588–590 from localities SH-1. and 2.; as well as MCZ 591 (ten additional specimens from SH-1.), MCZ 592 (three additional specimens from EM-1.), and MCZ 593 (many new unstudied specimens from SH-2.).

Lepidocystis, cf. *L. wanneri* Foerste
Plate 3

After the previous section had been written, two local collectors in southeastern Pennsylvania, Martin L. Anné of Wrightsville, and Kraig Derstler, a high school student in Columbia, turned up a large number of additional specimens of *Lepidocystis* from the Kinzers Formation. At least two of these new specimens, figured in Plate 3, figures 1–6, are sufficiently different from all previous material that they may possibly represent a new species. These two specimens have the longest holdfasts ever observed in *Lepidocystis,* at least twice the length of the calyx. In previous specimens the partially or completely preserved holdfast, although longer than in *Kinzercystis,* has usually been somewhat shorter than the length of the calyx. It seems possible that all of the previously collected specimens of *Lepidocystis* had incomplete holdfasts or holdfasts that were preserved in a contracted position. There is also some difference in the observed shape of the upper part of the calyx in these new specimens, but this may also be related to the extension of the holdfast. Since these specimens of *Lepidocystis* with long holdfasts occur with others that appear to be normal specimens of *L. wanneri* (but without the holdfasts preserved), they could easily represent the same species only better (or differently) preserved. I have therefore decided to describe these two new specimens as *Lepidocystis,* cf. *L. wanneri.* Additional collecting and study will probably be necessary to determine whether they actually represent *L. wanneri* or a new species.

In many of their morphologic features these new specimens are very similar to *Lepidocystis wanneri.* The general calyx shape, calyx, holdfast, and oral surface plating, arrangement of ambulacra and brachioles, and location and shape of the oral and anal pyramids are all nearly identical to that found in specimens of *L. wanneri.* Also the brachioles show the characteristic marked increase in size aborally along the ambulacra, and the holdfast has about the same diameter as the specimen of *L. wanneri* figured on Plate 2, figures 4–5. However, the holdfasts in these two new specimens are extremely long, between two and three times the greatest length previously observed. In the slightly larger specimen (Derstler Collection; Pl. 3, figs. 5–6), the holdfast is at least 50 mm long (incomplete) and lies beside a calyx more than 27 mm long (also incomplete) and about 26 mm wide. The smaller specimen (Anné Collection; Pl. 3, figs. 1–4) is nearly complete and very well preserved, with a holdfast about 52 mm long attached to a calyx 26.5 mm long. In both cases the holdfast is crushed flat and has a diameter between 5.0–6.5 mm, thus giving a rough holdfast L/W ratio of 8–10+. There are about 110–120 rows of tiny overlapping plates in the complete holdfast of the latter specimen, and in both specimens the plates seem to be extended to their furthest overlapping positions. Perhaps the shorter holdfasts observed in other specimens could also be extended to the lengths observed here.

The second major difference between these two new specimens and other specimens of *L. wanneri* involves the shape of the upper part of the calyx and the size of the oral surface. In most specimens of *L. wanneri* collected previously, the calyx has its maximum diameter at the top near the wide oral surface. In both of these new specimens the calyx has its maximum diameter well below the top, and the oral surface is constricted to a width of only about one-half to two-thirds this maximum diameter (see Pl. 3, figs. 2 and especially 6). Although this observed difference might be caused by preservation, it seems more likely that it represents a real difference. Perhaps the lepidocystid bulged the middle portion of its calyx or constricted the oral surface when it extended its holdfast, as these two specimens have apparently done, and therefore the difference might be physiological, and not taxonomic. This possible ability to change the holdfast length and calyx shape may explain why imbricate plates were so well developed and extensive in these lepidocystid eocrinoids.

In addition to the features noted above, the smaller specimen has its holdfast attached to the cephalon of a small olenellid trilobite (Pl. 3, fig. 4). The tip of the holdfast is attached to the dorsal convex surface of this cephalon, which may have been a molted exoskeleton fragment lying on the bottom. The "top" direction of this attachment agrees with the "top" direction indicated by the orientation of the oral surface. Several *Kinzercystis* holdfasts have also been found similarly attached to arthropod fragments (see Pl. 5, fig. 7), and perhaps many or all of the lepidocystids in the Kinzers Formation lived attached in this manner.

Besides being attached in its apparent life position, this smaller specimen also shows a portion of the inside surface of the oral surface near the mouth through a large "hole" in the opposite calyx wall (Pl. 3, figs. 1, 3). This view shows a ring of large plates surrounding the mouth and sending off branches which "floor" the five ambulacra. One T-shaped plate from each ambulacrum, as well as a small additional plate on the anal side, surrounds the mouth. The esophagus was probably attached to the inner surface of this ring of plates. Some of the larger plates flooring the ambulacra have been observed in other specimens of *Lepidocystis*, but until now it was not known how these plates were connected near the central mouth.

Derstler's specimen comes from locality SH-1., where I have collected most of my lepidocystid material, while Anné's specimen comes from a new locality SH-2. in a field about 500 feet to the northeast. Anné and Derstler discovered this new locality in November, 1969, and I visited it with them early in December. In one month of collecting, this prolific new locality has yielded more than 200 specimens of *Lepidocystis,* most of which are still unstudied. Two small slabs with half-inch layers completely packed with well-preserved, partially oriented, and overlapping lepidocystids have been found at this new locality; they have each yielded between 12–16 specimens. This type of preservation suggests a mass kill of gregarious specimens living in a lepidocystid "garden," perhaps by a turbidity current or sediment slump from the carbonate bank that apparently lay just to the west of this locality (Lyle Cambell, personal communication, 2 April 1969). This interpretation may also apply to many of the occurrences of the middle Cambrian eocrinoid *Gogia* in the Rockies.

Martin Anné has kindly donated his figured specimen (MCZ 628A, B) to the Museum of Comparative Zoology. Kraig Derstler's figured specimen is now in his private collection, but will be deposited as specimen PE-199 and 199-A in the paleontological collections of the North Museum, Franklin and Marshall College, Lancaster, Pennsylvania, within the next year. Latex castings of this latter specimen are on file at the Museum of Comparative Zoology (MCZ 629A and B).

Genus *Kinzercystis* new genus

Type species, Kinzercystis durhami new species

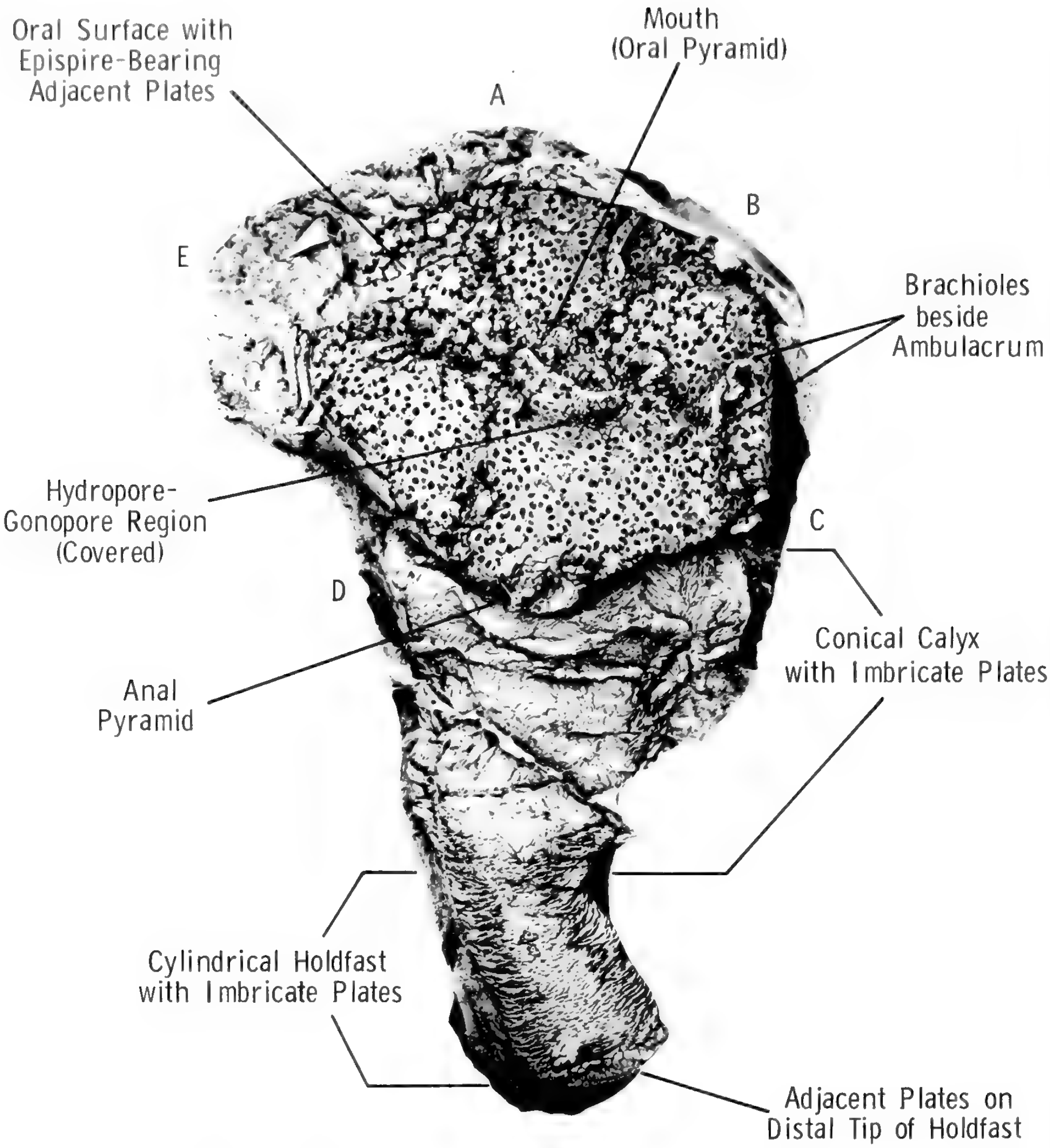
Diagnosis. Calyx conical, expanding adorally, covered by relatively small, imbricate calyx plates without pores, plates both overlapping and slightly increasing in size adorally, each plate wider than high and slightly ornamented; holdfast cylindrical, attached to base of calyx, length about 1/3 of calyx length, diameter 1/2–2/3 of its length, covered by many small imbricate plates overlapping adorally and similar in size, shape, and ornament to aboral calyx plates; attachment base of holdfast plated with small, adjacent, rhomboid-shaped plates; oral surface nearly circular, slightly domed, covering adoral end of calyx in tegmenlike manner, composed of numerous, large, adjacent plates, each having 5–11 circular to slightly elliptical epispires on its sutured margins; ambulacral system confined to oral surface, consisting of a centrally located, elongate, slightly domed oral pyramid covering mouth, as well as 5 unbranched covered ambulacra extending radially from oral pyramid nearly to edge of oral surface, lying on depressed oral surface plates lacking epispires; and 8–12, long, biserial brachioles mounted alternately alongside each ambulacrum, number increasing during ontogeny, brachioles increasing only slightly in size toward edge of oral surface, and 1 set of distally overlapping biserial cover plates covering brachiolar food groove; large domed anal pyramid covering anus at edge of oral surface in "CD" interradius; and small spoutlike gonopore(?) and pyramidlike hydropore(?) located in region of tiny plates in same interradius just below oral pyramid and near "C" ambulacrum; Kinzers Formation, upper Lower Cambrian (*Olenellus* zone), southeastern Pennsylvania.

Etymology. The generic name is derived from the Kinzers Formation in southeastern Pennsylvania, the only place where lepidocystid eocrinoids have been found.

Discussion. Kinzercystis is apparently closely related to *Lepidocystis* Foerste, but seems to differ from it in several important respects. Unlike *Lepidocystis,* which has large calyx plates and very small oral surface plates, *Kinzercystis* has relatively small calyx plates and very large oral surface plates with many more epispires. Also, the calyx plates do not decrease markedly in size aborally as they do in *Lepidocystis.* The holdfast in *Kinzercystis* is probably somewhat shorter than in *Lepidocystis* (much shorter than in *Lepidocystis,* cf. *L. wanneri*), and has plates similar in size and shape to those in the lower portion of the calyx instead of having smaller and differently shaped plates. The oral surface has a similar arrangement in both genera, but seems to be somewhat wider in *Kinzercystis,* having longer ambulacra and more brachioles. Also, the brachioles all seem to be relatively similar in size along an ambulacrum, instead of greatly increasing in size and length aborally as found in *Lepidocystis.* No major change in the size of the oral surface plates is found beneath the ambulacra in *Kinzercystis.* Finally, no gonopore-hydropore area(?) similar to that found in *Kinzercystis* has been observed in *Lepidocystis* although similar openings may have been present.

Complete specimens of *Kinzercystis* have only been found at one locality in the Kinzers Formation, a small overgrown roadcut on state route 74, about 2.0 miles west-northwest of York, Pennsylvania (locality designated SH-1.). This outcrop is just southeast of the contact with the Triassic and has been mapped as upper Kinzers Formation by Stose and Jonas (1939: plate 1). However, the lithology and fauna seem to indicate that this outcrop belongs to the lower Kinzers (Lyle D. Cambell, personal communication, 2 April 1969), and was probably just east (seaward?) of a major carbonate bank that occupies the Kinzers stratigraphic interval in the Thomsville, Pennsylvania, area.

Several different lithologies seem to be present at this locality, the most prominent of which is a relatively massive, dark blue, silty limestone with abundant *Scolithus* burrows and hyolithids. However, the echinoderms (and most of the other fossils) come from loose blocks of dark yellow-brown, porous, sandy siltstone, which may occur just above the limestone beds or may possibly have been derived from the limestone beds themselves by extensive leaching during weathering. *Kinzercystis* occurs here with *Lepidocystis* and the strange echinoderm *Camptostroma* (both sometimes found on the same slab surface with *Kinzercystis*), plus olenellid trilobites, hyolithids, and *Scolithus* burrows. Most of these echinoderms have been found in 6–12-inch thick, jumbled blocks of this weathered material collected from all parts of the vegetation-covered bank and split along bedding surfaces. Since the matrix here is more silty than most other Kinzers localities, the echinoderm-bearing beds have not been so badly affected by regional deformation and metamorphism, and therefore tend to split directly across the flattened leached-out echinoderms lying in the bedding planes, yielding excellent matched counterpart molds.



Text-figure 22. Morphology of *Kinzercystis durhami* n. gen., n. sp. Holotype specimen MCZ 581A showing oral surface covering collapsed calyx and short cylindrical holdfast; note five equally developed ambulacra leading to central oral pyramid, brachioles draped over summit, anal pyramid at edge of "CD" interradius, and contrast in plating types.

Kinzercystis durhami new species
Plates 4–6; Text-figures 2, 5A, 22–23

The excellent holotype specimen of this new taxon is probably one of the most complete and best preserved lepidocystid specimens that has ever been found in the Kinzers Formation. This specimen is approximately 90 percent complete and almost perfectly laid out, showing a nearly complete and still articulated oral surface on one of the two matched counterparts (Text-fig. 22). At least five other partially complete specimens, as well as several apparent *Kinzercystis* holdfasts attached to arthropod fragments, have now been collected (Pls. 4–5), but most of these are less complete and not so well preserved. Most of the information for the following description was derived from the holotype (MCZ 581) and the best paratype (MCZ 582).

Specific description. The calyx is large, conical, and slightly higher than wide. As reconstructed from holotype MCZ 581 (Text-fig. 22), the calyx is approximately 32 mm high, gradually increasing from a diameter of about 6.5 mm near the base where it is attached to the holdfast, to about 27 mm at the edge of the oral surface. It is composed of relatively small imbricate calyx plates, both overlapping and slightly increasing in size adorally. Each plate is rounded pentagonal, somewhat wider than high, and averages about 1.0–1.5 mm wide by 0.8–1.0 mm high, with an adoral exposed portion about 0.3–0.5 mm high. Slightly more than half of the total plate area is overlapped by the 2 plates diagonally below it in the next lower row, and by the plate directly below it in the second lower row. The adoralmost calyx plates are only about 1.5 times as large as the aboralmost plates, in contrast to *Lepidocystis* in which they are about 4 times as large. The exposed adoral portion of each calyx plate is slightly ornamented with tiny granules as well as 3–4 small nodes lying along the margin. It is not known how the conical calyx grew in size, but I suspect that new plates were probably added randomly to all parts of the calyx wherever needed.

The holdfast is relatively small in *Kinzercystis* compared to the size of the calyx (Text-fig. 22). In holotype MCZ 581, the holdfast is a crushed cylinder, slightly expanded aborally. As now preserved, it is 9.7 mm long, 7.8 mm wide adorally where attached to the calyx, and 8.8 mm wide at its base. Recalculation of the original uncrushed diameter gives a figure of approximately 6.5 mm adorally and 7.0 mm aborally. The sides of the cylindrical holdfast are covered by small imbricate plates overlapping adorally and very similar in size, shape, and ornamentation to the adoralmost calyx plates. This contrasts with *Lepidocystis* in which the plating size and shape change relatively abruptly between the calyx and holdfast.

The attachment base of the holdfast in *Kinzercystis* is best known in the holotype specimen where it appears on both of the flattened counterparts (Pl. 6, figs. 4–5). This attachment surface appears to have been almost round, flat, and plated with small, radially arranged, wedge-shaped, adjacent plates about 0.7 mm long and 0.4 mm wide. There is a sharp contact between the imbricately plated sides of the holdfast and the adjacently plated base. This basal portion of the holdfast was probably used to attach the animal to objects lying on the bottom (see pp. 50 and 67), in a manner similar to the inferred holdfast usage in the middle Cambrian eocrinoid *Gogia.* The use of adjacent plates on the base of the holdfast may have been necessary to produce an almost flat, tightly sutured attachment surface for this type of semipermanent fixation. The similar holdfast in *Lepidocystis* was probably used in the same way, and not partially buried in the sediment as inferred by Durham (1967b: S633).

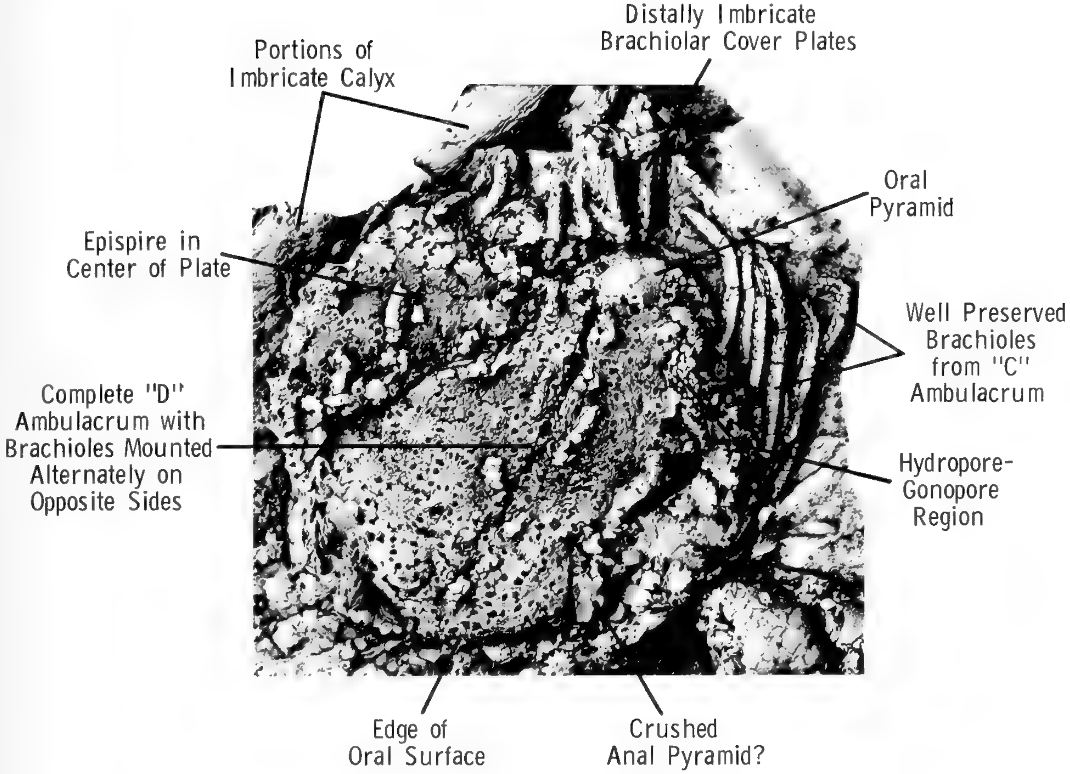
The oral surface caps the larger adoral end of the conical calyx and contains the ambulacral system, mouth, anus, hydropore-gonopore complex, and numerous other small openings (epispires) into the interior of the calyx. The oral surface is subcircular to rounded pentagonal in outline and slightly domed. In the holotype where it is about 90 percent complete, the diameter of the oral surface is approximately 27.5 mm. It is made up of numerous, relatively large, adjacent oral surface plates bearing numerous epispires on their margins. These oral surface plates are somewhat larger near the centers of the interambulacral (interradial) areas, and smaller near the ambulacra, oral pyramid, and anal pyramid. Smaller plates are occasionally interspersed between the larger ones over the entire area. In holotype MCZ 581, the larger plates range from 1.5 to 2.0 mm in diameter and are about 0.25–0.33 mm thick, while in the slightly larger paratype MCZ 582, they range up to 2.5 mm in diameter with about the same thickness. Most of these plates are polygonal in shape, having between 4–8 nonequal sides where they abut on adjacent plates. They have a subdued granular ornamentation and low rims around the epispires.

Epispires (sutural pores) are present over the entire oral surface area except beneath the ambulacra and associated brachiole attachment facets, and adjacent to oral and anal pyramids and the hydropore-gonopore region. The larger oral surface plates have as many as 9–13 epispires on their sutured margins, while the smallest observed plates have only 3–5. Each epispire is about 0.3 mm in diameter, usually subcircular but sometimes slightly elliptical (epispire L/W varies from 1.0–2.0). They occur most often on the suture between two plates, but are also found at corners where three or sometimes four plates meet. Each epispire passes vertically down the suture between the adjacent plates and opens directly into the calyx interior (see Pl. 5, fig. 3). The epispires appear to have remained relatively constant in size as the oral surface plates around them grew. If the oral surface plates increased in size by holoperipheral growth, then the epispires would have to be infilled where they are indented into the plate and extended out radially along the suture. Several instances have been noted where an epispire lies inside a plate and not on its sutured margin; these epispires still appear to have been normally developed and functional. Perhaps an epispire was sometimes "left behind" by the advancing suture during growth of the plate and ended up within the plate and not in its normal sutural position.

These oral surface plates with their well-developed epispires represent one of the most eocrinoid-like features of *Kinzercystis*. The closely related genus *Lepidocystis* has much smaller oral surface plates with fewer epispires per plate, and therefore the oral surface is somewhat less eocrinoid-like than *Kinzercystis*. Nevertheless, the construction and arrangement of the epispire-bearing oral surface plates in these 2 genera is virtually identical. Unfortunately, there is no evidence from the present specimens to indicate whether the structures extending through these epispires were connected by internal extensions of the water vascular system.

The ambulacral system of *Kinzercystis* is confined to the oral surface and consists of the oral pyramid covering the mouth, 5 simple ambulacra made up of long covered food grooves, and numerous brachioles mounted on facets alongside each ambulacrum. In holotype MCZ 581, the mouth is located approximately in the center of the oral surface, and is covered by an elongate pyramid of very small, tightly sutured cover plates. This oral pyramid is approximately 5 mm long by 2 mm wide by 1 mm high. If the position of the anal pyramid is used to orient this specimen, the ambulacra are found to enter the oral pyramid in a standard "2–1–2" pattern (see p. 43 and Text-fig. 22). The mouth is hidden by the oral pyramid on both specimens that show its position, but probably has a similar elongate shape.

The 5 ambulacra in *Kinzercystis* are relatively long, and unbranched, and extend radially from the oral pyramid almost to the edge of the oral surface. In holotype MCZ 581, the essentially complete "C" ambulacrum is 14.4 mm long by 0.7–0.9 mm wide, while in the slightly larger paratype MCZ 582, the complete "D" ambulacrum is 16.9 mm long by 0.6–0.8 mm wide. Each ambulacrum con-



Text-figure 23. Oral surface features of *Kinzercystis durhami* n. gen., n. sp. Paratype MCZ 582A showing oral surface plates with epispires, complete "D" ambulacrum with brachiole "stubs" on both sides, oral pyramid at top, and well preserved brachioles of equal size with distally imbricate cover plates on other ambulacra.

sists of a long, nearly straight, depressed food groove lying on modified and depressed oral surface plates lacking epispires and covered by tiny cover plates. Brachiolar facets, connected by very short side food grooves, lie alternately alongside each ambulacrum (see Text-fig. 23) in a heterotomous pattern (Ubaghs, 1967b: S470) for most of its length. There is a ridge on the interior of the oral surface beneath each depressed ambulacral food groove, as shown by paratype MCZ 582B where an internal mold of a portion of the oral surface is preserved (Text-fig. 2; Pl. 6, fig. 6). This unusual view also shows that the oral surface plates are continuous below the ambulacrum, that epispires are lacking in the plates underlying the ambulacrum, and that there are no other openings connecting the calyx interior to either the ambulacrum or its brachioles lying alongside.

The well-developed brachioles in *Kinzercystis* are another major feature indicating a close relationship to other Cambrian eocrinoids (Text-fig. 5A). Each brachiole is a long fingerlike appendage attached to a brachiolar facet lying alongside an ambulacrum. On large paratype MCZ 582, the largest brachioles appear to have a total length of at least 17.5 mm on a specimen having an oral disk diameter of between 32–35 mm. They have an elliptical cross section, averaging about 0.8 mm high by 0.6 mm wide, and are composed of 1 set of biserial brachiolar plates (BP) and a single set of distally overlapping, biserial, brachiolar cover plates (BCP), 1 per brachiolar plate, forming a domed interlocking canopy over the adoral food groove. Each brachiolar plate is about 0.5 mm long by 0.6 mm high by 0.3 mm wide and occupies 1 side of the brachiole. Each cover plate is roughly rectangular in shape and slightly curved, about 0.20 mm long by 0.15 mm wide, and has a jagged distal edge with 2 small projections that overlap into the next cover plate (Text-fig. 5A). In life, these cover plates could probably have been opened along much of the brachiole length to expose the food groove for ciliary feeding.

A large pyramid covering the apparent anal opening is best shown in holotype MCZ 581 at the extreme edge of the oral surface in the "CD" interradius. As now preserved, it is slightly damaged and incomplete at the top, and appears to be located slightly closer to the "D" ambulacrum on the left than to the "C" ambulacrum on the right (Text-fig. 22). This domed anal pyramid is composed of small wedge-shaped plates lacking epispires, and is nearly 5.0 mm in diameter and about 2.0 mm high. These anal pyramid plates appear to grade laterally and adorally into normal oral surface plates. The position, size, and shape of this anal pyramid in *Kinzercystis* is very similar to that found in *Lepidocystis*.

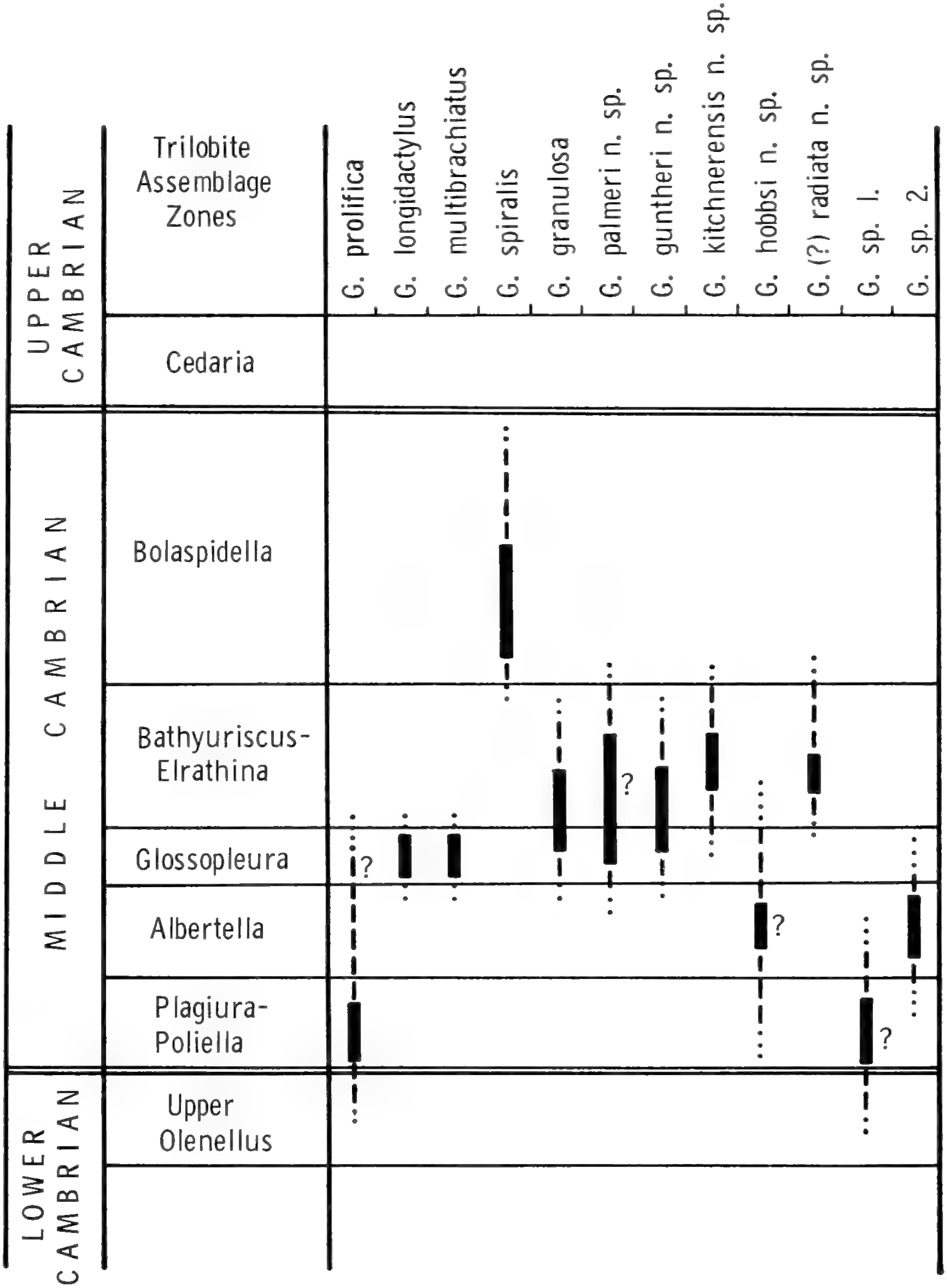
A region of small plates, apparently containing both the hydropore and gonopore openings, is also located in the "CD" interradius just below the mouth and near the "C" ambulacrum. It is best shown by the first latex cast of holotype MCZ 581A; in later latex casts of this same specimen, these structures are partially obscured by a brachiole draped across the oral surface (compare Pl. 6, figs. 1 and 2). This region is also partially preserved in paratype MCZ 582A (Text-fig. 23). In the holotype, this area is about 3.0 mm long and 2.0 mm wide and consists of a small sievelike pyramid of plates and a conical "spout," both surrounded by many tiny plates lacking epispires (Pl. 6, fig. 3). The pyramid is on the adoral side of the small-plated area, has a diameter of about 1.0 mm, and is not raised above the surrounding area; 11–12 wedge-shaped plates in 2 overlapping series make up this pyramid. The conical spout is draped over the oral surface alongside the pyramid and is about 2.0 mm long and 0.5 mm in diameter at the smaller open end. It originates just aboral to the pyramid in a region of tiny plates, which is partially obscured by a slight warping of the oral surface (Pl. 6, fig. 3).

A comparison with later eocrinoids, cystoids, and paracrinoids indicates that these pyramid and spoutlike openings in *Kinzercystis* may correspond to openings that have been called the hydropore and gonopore, respectively, in these later forms. The hydropore is usually either a long slitlike opening on the suture between 2 plates or a sievelike madreporite plate lying just adoral to the gonopore, which is usually a single small porelike opening. In *Kinzercystis*, the adoral "pyramid" may represent a sievelike madreporite or hydropore, while the spoutlike projection may be an elevated gonopore. This identification appears to be most reasonable even though the hydropore-gonopore morphology is somewhat different from that found in most later forms.

Etymology. This species is named after J. Wyatt Durham of the University of California, Berkeley, who restudied the known lepidocystid material for Treatise Volume S (1967b) and gave the best description of these early echinoderms up to that time. Although we disagree somewhat on the exact taxonomic assignment of lepidocystids, I have greatly profited from discussions with him on the nature of these and other primitive echinoderms.

Stratigraphic and geographic range. Kinzercystis durhami is known only from the lower part of the Kinzers Formation, upper Lower Cambrian (*Olenellus* zone), locality SH-1., southeastern Pennsylvania.

Studied specimens. Holotype MCZ 581



Text-figure 24. Stratigraphic occurrence of the known *Gogia* species in the middle Cambrian of the Rocky Mountains. Wide line = known occurrence; dashed line = possible occurrence; dotted line = possible extension of range; several occurrences questioned because of poor stratigraphic information or uncertain *Gogia* identification. Partially based on Robison (1965: text-fig. 2).

(two counterparts), figured paratypes MCZ 582–587, and unfigured paratypes MCZ 729, all from locality SH-1.

UNNAMED ORDER #1

Diagnosis. Eocrinoids with numerous irregular to relatively regular adjacent calyx plates bearing epispires over much of the calyx. Attachment appendage, if present, consists of a holdfast or true stem. Brachioles normal, relatively numerous, attached in groups to relatively primitive ambulacra on the oral surface or adoral part of the calyx. Early Cambrian(?)–early Ordovician.

Discussion. This provisional order contains eocrinoids having epispires, adjacent calyx plates, and normal brachioles. Provisionally assigned genera include: *Gogia, Acanthocystites, Akadocrinus, Lichenoides, Rhopalocystis*(?), and a possible eocrinoid(?) from the Lower Cambrian Poleta Formation. The order has been left unnamed at present because I am not certain that the above genera form a natural phylogenetic grouping.

Family EOCRINIDAE Jaekel, 1918

Diagnosis. Calyx plates numerous, irregularly arranged, bearing epispires. Attachment appendage consists of irregularly multiplated holdfast or primitive stem. Ambulacral system confined to oral surface, consisting of 3–5 simple ambulacral grooves leading to groups of normal brachioles. Four genera. Early Cambrian(?)–middle Cambrian.

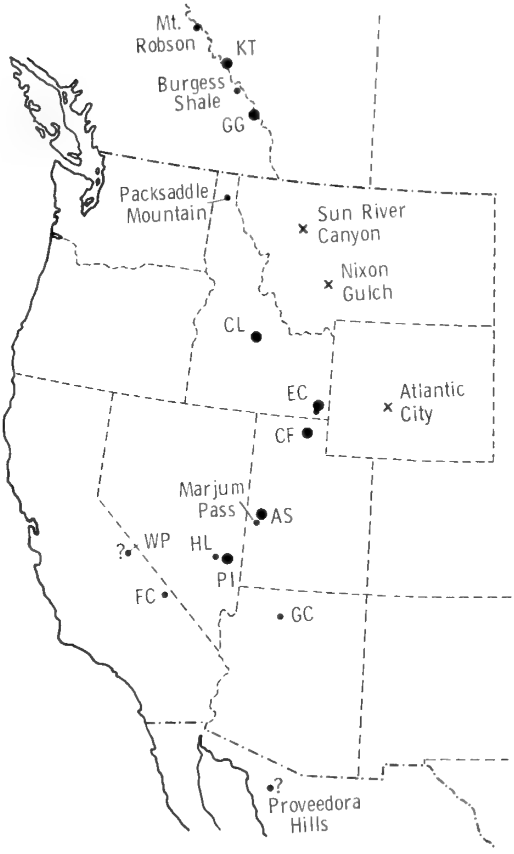
Genus *Gogia* Walcott, 1917

Type species, Gogia prolifica Walcott, 1917

Diagnosis. Eocrinoids with an irregular multiplated calyx bearing numerous epispires, an irregularly plated holdfast used for attachment, and numerous biserial brachioles attached to the calyx summit. The conical, globular, or barrel-shaped calyx is composed of 40–400 irregularly arranged adjacent plates. Epispires (sutural pores) are present either over the entire calyx surface or confined to the adoral portions. A cylindrical or inflated-globular holdfast is used to attach the animal to the substrate. This appendage has numerous, small, irregularly arranged plates surrounding a large central cavity. Between 3 to 45+ food-gathering brachioles are mounted separately or in groups of 2–6, usually on spoutlike projections of modified calyx plates, on the edge of the calyx summit. The brachioles are long, biserially plated, and either straight or spiralled (left-handed). One or sometimes two sets of adjacent, domed, biserially arranged cover plates protect the brachiolar food groove. The mouth is central on the calyx summit with 3–5 short covered food grooves leading to the projections where the brachioles are mounted. The anal pyramid is lateral, either on the edge of the summit or on the upper part of the calyx. No hydropore or gonopore is known at present. Middle Cambrian (ranges through all zones), western North America.

Discussion. Gogia is now the most abundant, diverse, widest ranging, and longest-lived of the known Cambrian eocrinoids. In his 1965 paper, Robison described six species of *Gogia,* two of which were new; I have now raised this total to 12 species (see Table 2) with the description of five new species in the following sections. *Gogia* extends stratigraphically through all of the zones in the middle Cambrian (Text-fig. 24) and perhaps even down to the late early Cambrian. Geographically it ranges throughout much of the Cordilleran Geosyncline from Mt. Robson in British Columbia to the Sonora region in northern Mexico (Text-fig. 25). At some localities, it is the most abundant metazoan fossil, surpassing even the ubiquitous trilobites. During the summers of 1967 and especially 1968, I made large collections of *Gogias* at seven widely scattered localities during field work in the Rockies; one of these *Gogia* collections, from a single small shale pit in southeastern Idaho (EC-1.), now includes over 400 complete specimens. When preserved as natural molds, or in a matrix suitable for making artificial molds by acid etching (see p. 10), these eocrinoids often yield superb latex casts. Because of the excellent preservation and large collections, a great deal of information is available about the morphology and range of intraspecific variation in the many species of *Gogia*. The apparent local nature of the known species and the wide range of morphologic variation both suggest that additional species of *Gogia* are probably present in the Cordilleran region and remain to be discovered.

Gogia is characterized by many irregularly arranged adjacent calyx plates, epispires opening to the interior without obstructions over the entire calyx or confined to the adoral portion, a cylindrical or inflated attachment holdfast, and numerous brachioles attached in groups to the edge of the oral surface with three to five ambulacra leading to the central mouth. *Gogia* differs from *Akadocrinus, Eustypocystis, Lichenoides,* and other eocrinoids by having a holdfast instead of a stem (or no attachment appendage). It differs from *Lepidocystis* and *Kinzercystis* by having adjacent and not imbricate calyx and holdfast plates. *Gogia* seems most closely related to the European middle Cambrian eocrinoid *Acanthocystites* (see p. 105), and differs from this genus in having unobstructed epispires instead of ones partially closed off by an internal(?) plate. Also the attachment appendage in *Acanthocystites* is still unknown and may not have been a holdfast. *Gogia* could have evolved into other middle and late Cambrian eocrinoid genera by the gradual loss of epispires and the modification of the multiplated holdfast into a primitive stem. At present, its immediate ancestor is still unknown.



Text-figure 25. Geographic occurrence of *Gogia* species in the Cordilleran area of western North America. Large dot = *Gogia* locality personally collected during field work; small dot = known *Gogia* locality not visited, or where no specimens were found during field work; questioned small dot; locality based on possible *Gogia* plates only; X = studied locality where no *Gogias* found. Two-letter locality designations from Appendix 1. Expanded from Robison (1965: text-fig. 1).

Most of the known species of *Gogia* seem to show a definite distribution pattern in the Cordilleran area. They seem to be confined to the more shaly units, either limy or sandy, in the portions of the Cambrian miogeosyncline termed the "outer detrital zone" by Palmer (1960: 53) and Robison (1960: 43). Except in one or possibly two cases, *Gogias* were not found in similar suitable sediments of middle Cambrian age in the "inner detrital zone" (same authors as above) further east in the Cordilleran area, such as the lower Meagher Formation at Nixon's Gulch,

TABLE 2. MORPHOLOGY OF THE NAMED *GOGIA* SPECIES FROM WESTERN NORTH AMERICA

Species	Stratigraphic occurrence	Usual calyx size	Calyx shape	# Plates per side	Plate ornament	Epispire location	# Epispires per plate	Epispire L/W ratio	Holdfast shape
G. prolifica	*Plagiura-Poliella* zone	medium to large	conical to subglobular	20–75$^+$	none to very slight	all over + HF top	3–18	2–7	long tapering conical to cylindrical
G. longidactylus	*Glossopleura* zone	medium to v. large	rounded conical to globular	40–200	none to slight knobs	top ⅙–⅔ of calyx	4–33$^+$	1–7	very long cylindrical
G. multibrachiatus	*Glossopleura* zone	large to v. large	barrel-shaped to subglobular	80$^-$–120	scattered pustules	all over	6–24$^+$	3–12	very large inflated globular
G. spiralis	*Bolaspidella* zone	medium to large	rounded conical to ellipsoidal	15–48	none	all over	7–17	2–6	medium-long cylindrical to slightly inflated
G. granulosa	*Glossopleura* to *Bathyuriscus-Elrathina* zones	medium to large	globular to ellipsoidal	14–72	moderate radiating granules	all over	5–20	1.5–7	medium cylindrical
G. hobbsi n. sp.	*Albertella*? zone	small to medium	rounded conical to club-shaped	12–28	none to very slight	all over	5–14	2–8	short cylindrical
G. kitchnerensis n. sp.	*Bathyuriscus-Elrathina* zone	medium to v. large	rounded conical to subglobular	40–85	none to slight knobs	top ¼–½ of calyx	5–15	1–4	long cylindrical
G. palmeri n. sp.	*Glossopleura* to *Bathyuriscus-Elrathina* zones	medium to v. large	barrel-shaped to subglobular	20–105	varies over calyx from lge. pustules to none	all over	3–20$^+$	1.5–10	medium cylindrical
G. guntheri n. sp.	*Glossopleura* to *Bathyuriscus-Elrathina* zones	medium to v. large	ellipsoidal to globular	25–90$^+$	none to slight pustules	all over + HF top	5–13	1.5–8	large inflated globular to conical
G. (?) *radiata* n. sp.	*Bathyuriscus-Elrathina* zone	small (?) to large	bowl-shaped to globular	60–100?	large ridges radiating to sides	all over	3–9	1.5–5	very long cylindrical

TABLE 2. MORPHOLOGY OF THE NAMED *GOGIA* SPECIES FROM WESTERN NORTH AMERICA (continued)

Species	Holdfast L/W ratio	HF/C length ratio	# Holdtast plates per ½ circumference	Holdfast-to-calyx transition	Number and type of brachioles	Brachiole size and length	BR/C length ratio	BCP/BP	Brachiole attachment to calyx
G. prolifica	5.5–9	0.8–1.3	2.5–4	very gradational	3–8 straight	medium and relatively long	2.0–2.8	1.6–1.8	1–3 together, no spouts
G. longidactylus	9–24	1.2–2.0^{+}	4–8	relatively gradational	8–22^{+} straight	large and long	1.5^{+}	1.7–2.0	1–2 alone or together, no spouts
G. multibrachiatus	1.2–1.3	0.6–0.7?	12^{+}?	relatively abrupt	9–48^{+} straight	large and long	1.6–1.8^{+}	2.0–2.4	6–10 together, no spouts
G. spiralis	1.6–7	0.6–1.5	4–7	abrupt	4–15^{+} spiralled	medium and long	2.4–4.0	?	2–5 together, small spouts
G. granulosa	2–6.5	0.3–0.8	5–7	relatively abrupt	2–13^{+} spiralled	medium and very long	2.8–4.2	2.0–2.3	2–5 together, moderate spouts
G. hobbsi n. sp.	2–3	0.3–0.4	3–6	gradational	4–8 straight?	small and relatively short	1.2–1.5	1.6	1–2 alone or together, small spouts
G. kitchnerensis n. sp.	8–12	0.6–1.3	3–4	relatively abrupt	3–14^{+} straight	relatively large and relatively long	1.8–2.7^{+}	1.8–2.1	1–5 together, no spouts
G. palmeri n. sp.	2.3–7	0.4–0.7	4–7	relatively abrupt	4–18 straight	relatively small and long	2.4^{+}–4.0	1.1–1.3 (large)	2–5 together, relatively large spouts
G. guntheri n. sp.	1.1–1.4	0.4–0.6	7–16^{+}	relatively gradational	4–15 spiralled	relatively large and medium length	2.0–2.6	2.2–2.5	1–4 together, relatively large spouts
G. (?) *radiata* n. sp.	20–25^{+}	~4??	5–8	abrupt	4^{+}? straight?	unknown	unknown	unknown	unknown

southwestern Montana, the Pentagon Shale in Sun River Canyon, northwestern Montana, or the Gros Ventre Formation in western Wyoming (see Text-fig. 25). Perhaps this distribution was influenced by such ecologic factors as water depth, turbidity, or temperature. It is also possible that many of these middle Cambrian *Gogias* had not yet acquired the ability to traverse or colonize the very shallow-water "middle carbonate bank" separating these two detrital zones.

The many different species of *Gogias* apparently lived in large, gregarious, local populations. Some of these eocrinoids (and perhaps most or all of them) are known to have lived with the holdfast attached, probably by mucus secretion or cementation, to fossil fragments lying on the sea bottom (see p. 50); however, some specimens may have lived directly attached to or imbedded in the bottom sediments with no supporting base. Many of these *Gogia* occurrences seem to have been produced by catastrophic sediment slumps (see p. 51) that killed and buried large "gardens" or colonies of these gregarious eocrinoids. Specimens preserved in this way are complete with still-articulated brachioles, are current oriented, show a wide size range, and occur in distinct bands or partings having a different matrix from the over- and underlying sediment. A few other occurrences, however, such as the localities at Pioche, Nevada, show evidence that the specimens died naturally and lay on the bottom for a time before being buried by the sediment. Here the specimens with their brachioles are often partially disaggregated, randomly oriented, occur primarily with specimens of their own size, and are found in a matrix showing little vertical variation or interruption.

More extensive collecting will be necessary to modify the present "one-species-to-one-locality" distribution pattern now shown by most of the *Gogia* species. Each of these species probably had an appreciable geographic range, and perhaps a moderate stratigraphic one also. It is interesting that no two *Gogia* species are known to occur together; when two species are found at a single locality, they seem to occur in different stratigraphic intervals. Perhaps this results from the apparent gregarious nature of the individuals in each species, excluding other species from a single "garden" or colony. *Gogia* seems to have been one of the most successful eocrinoids that ever lived, and much more still remains to be learned about its taxonomy, distribution, and paleoecology.

Gogia prolifica Walcott
Plates 7 and 8

Gogia prolifica Walcott, 1917b: 68–69, pl. 8, figs. 1, 1a–b; Robison, 1965: 360, pl. 51, figs. 1–2, 4–5; Ubaghs, 1967b: S473, figs. 306, 1–3.

Walcott (1917b: 68) first described this species and made it the type for his new genus *Gogia*, apparently named after Gog Lake in Mount Assiniboine Provincial Park, British Columbia, where this species is found. Walcott apparently did not try to clean or cast his eight to ten studied specimens, of which only two were figured. Robison (1965: 360) gave a short redescription of this species and designated one of Walcott's figured specimens as lectotype. A. R. Palmer, then of the U. S. Geological Survey, Washington, apparently had prepared this lectotype specimen USNM 64350 (compare Pl. 7, figs. 1–2) by dissolving away the rest of the weathered or buried calcite plates with acid and then casting the resulting mold in latex rubber (see Robison, 1965: 359). In July, 1968, I collected 70 complete specimens of *Gogia prolifica* in one and a half days on the talus slopes at Naiset Point, above Gog Lake, British Columbia. These specimens were prepared by acid etching, soaking, and latex casting; 34 of them were well enough preserved to form the basis for the following redescription.

Specific description. The specimens range in size from relatively small (4–6 mm calyx length) to large (the lectotype is 22 mm and my largest specimen is 25.5 mm in calyx length). The calyx has a conical, rounded conical, or subglobular shape with a domed summit. The calyx L/W ratio ranges from 1.3 to 2.1, usually averaging about 1.8 in the larger specimens. The observed number of calyx plates per side ranges from 20 to 75+; the average number in a medium-sized specimen is about 50. The largest plates are located in the upper middle portion of the calyx with a gradual change to smaller plates toward the holdfast and to many small plates around the summit. Most of the calyx plates are flat to slightly convex with almost no ornamentation, but near the holdfast the calyx plates become strongly convex and some have a slightly rugose surface texture (Pl. 7, figs. 4–6).

Epispires are strongly developed over the entire calyx and even extend down onto the upper part of the holdfast (Pl. 7, fig. 5). They seem to be somewhat more numerous, better developed, and much more elliptical near the summit, although the epispires lower on the calyx seem to be slightly larger in size. There are between 3–18 epispires per calyx plate, the average usually being about 11 for a large plate in the upper part of the calyx. These epispires range from slightly to moderately elliptical in shape (epispire L/W ratio = 2–7), and the exterior opening seems to be somewhat longer than the interior opening below, a feature also described in *Lichenoides* by Ubaghs (1953a: 16). Epispires are present both on the sutures between 2 plates and at corners between 3 or more plates.

The holdfast in *G. prolifica* is long and thin, with a tapering-conical to cylindrical shape. It ranges in length from 8 to 9 mm in the smallest specimens up to 28 mm in the largest one. The HF/C length ratio ranges from 0.8 to 1.3, averaging about 1.05. There is a gradual taper from the large proximal end where the holdfast is attached to the calyx down to the small distal tip; usually the holdfast diameter decreases by a factor of 2–3 over this distance. Using an average diameter (width) for these tapering holdfasts, the holdfast L/W ratio ranges from 5.5 to 9.0, averaging around 6.8 for the nine specimens measured. The holdfast plates are relatively large (up to 1.5 mm in size), polygonal to nearly circular in shape, and moderately to strongly convex or "bulged." There are only about 2.5–4 plates in ½ circumference of an average holdfast. In a few specimens (Pl. 8, fig. 4, left), the adjacent and "bulged" holdfast plates may grade distally into plates near the attachment tip that appear to be partially imbricate, a feature somewhat similar to the holdfasts found in the early Cambrian eocrinoids *Lepidocystis* and *Kinzercystis*. Except for the largest specimens, there is little evidence for any alternate "whorls" of larger and smaller holdfast plates, and there is little or no ornamentation on any of these plates. The contact between the holdfast and the calyx is very gradational (Pl. 7, fig. 5). The calyx shows a gradual expansion in size at this point and the plating becomes somewhat larger and less convex. Epispires first appear on the upper part of the holdfast and gradually increase in number in the lower part of the calyx. At the distal tip, the holdfast is first constricted and then expanded to form a round flattened base for attachment. This expanded portion is composed of numerous, very tiny, rhombic plates arranged in diagonal whorls. Some of the collected specimens have the tip of the holdfast turned 90° from the orientation of the rest of the specimen (Pl. 8, figs. 1, 3, and 4), as if the holdfast had been attached to the bottom sediment where the specimen is now preserved. In addition, 4 specimens in 2 groups of 2 were found attached to fossil fragments (arthropod carapaces?) lying on the bottom. The relative rarity of other fossil fragments in these eocrinoid beds and the grouping of specimens attached to the few fragments that were found indicate that these rare fossil fragments were probably "choice" attachment sites.

The brachioles in *G. prolifica* are few in number, relatively long and of medium size, and completely straight (nonspiralled). None of the collected or type specimens from Gog Lake have more than eight brachioles and the observed range is from 3 to 8. These brachioles are moderately long, with the BR/C length ratio ranging from 2.0 to 2.8 and averaging about 2.3. Away from the calyx the brachioles are about 0.5 mm high and 0.5 mm wide, with the single biserial set of relatively small brachiolar cover plates (BCP) covering the food groove on the brachiolar plates (BP). In three specimens with long, well-preserved brachioles, the BCP/BP ratio falls in a narrow range from 1.6 to 1.8. These brachioles are attached to the edge of the calyx summit without projecting spouts in groupings of 1–3. Several specimens (see especially Pl. 8, fig. 5), having the oral surface obliquely exposed, show three groups of brachioles ringing the summit; each of these seems to have an ambulacral groove leading to the central mouth. Two of these ambulacra have three brachioles apiece, and the third has two brachioles (Pl. 8, fig. 5).

The mouth is central on the oral surface and apparently covered with a low pyramid of tiny cover plates. The shallow ambulacral food grooves leading to the brachiole groups are located on medium-sized modified calyx plates. The anal pyramid (Pl. 8, fig. 5) is located on the side of the calyx below and between two groups of brachioles (possibly "C" and "D"). It is not well preserved in either of the specimens showing its position, but appears to have been about 2.5 mm in diameter, 1–2 mm high, and composed of many small tooth-shaped plates. No hydropore, gonopore, or other oral surface features are known at present.

Discussion. Gogia prolifica is quite distinct from all of the other species of *Gogia* having a medium or long holdfast. Compared to the three long holdfast species (*G. longidactylus*, *G. kitchnerensis*, n. sp., and *G.*(?) *radiata* n. sp.) it is the only form having an appreciably tapering holdfast with relatively few large plates, a rounded conical calyx with epispires down to the base, and relatively few, medium-sized brachioles. Compared to the two species with medium length holdfasts (*G. granulosa* and *G. palmeri*), *G. prolifica* differs in its calyx shape, holdfast shape, number of brachioles and BCP/BP ratio. *G. prolifica* is one of the earliest species of *Gogia* now known, and it appears to be relatively primitive because of the gradation between the calyx and holdfast, the epispires covering the entire calyx, and the simple arrangement of ambulacra and brachioles.

Stratigraphic and geographic range. Mt. Whyte Formation, lower Middle Cambrian (*Plagiura-Poliella* zone), Naiset Point above Gog Lake (Walcott locality 62x), and talus slopes below these exposures (my locality GG–1.), Assiniboine Provincial Park, southeastern British Columbia. Several additional specimens (NYSM) apparently belonging to this species come from a locality listed as "Titkana Fm., N side, Mt. Mumm, elev. 6500 ft. on creek flowing into Lake Adolphus, British Columbia"; this horizon, if correct, is at least two zones above the Gog Lake horizon. Finally, one additional slab of specimens in the USNM possibly belonging to *G. prolifica* comes from a locality listed as "Chetang Fm. (Middle Cambrian), SW base of Robson Peak, British Columbia."

Studied specimens. Lectotype USNM 64350 (studied from two USNM latex casts after preparation, and one University of Cincinnati cast before preparation); syntype USNM 6431 (studied from a University of Cincinnati latex cast); six to eight additional unnumbered specimens in the USNM collection; plesiotypes MCZ 656–665 (ten specimens), plus MCZ 668 (24 additional specimens); plesiotypes NYSM 12758–9, two (out of four) small specimens from Mount Mumm; and an unnumbered slab of three large specimens from Mount Robson in the USNM collection.

Gogia longidactylus (Walcott)

Plates 9 and 10; Text-figure 10

Eocystites?? *longidactylus* Walcott, 1886: 820–821, pl. 5, fig. 3, pl. 6, figs. 1, 1a–c; Pack, 1906: 292–294, pl. 1, figs. 1, 1a–b; Shimer and Shrock, 1944: 125, pl. 47, figs. 7–8, 27.

Eocystis longidactylus, –Bather, 1900: 49, fig. 10, 1–2.

Eocrinus longidactylus, –Jaekel, 1918: 24; Bassler and Moodey, 1943: 157.

Gogia longidactylus, –Robison, 1965: 360, pl. 50, figs. 2, 4–5.

Gogia sp. cf. *G. longidactylus,* –Robison, 1965: 360, 362, pl. 50, fig. 3.

This species was originally described by Walcott (1886: 820) and represents the first eocrinoid known from western North America. Several additional specimens, including one with a partially complete holdfast, were described by Pack (1906: 292–294). Other additional material was found in the USNM collections and borrowed from various people for study. In 1967 and 1968 I collected 111 additional specimens from Chisholm Shale talus piles in the Ely Mountains near Pioche, eastern Nevada, plus a few poorly preserved specimens from the Highland Range about ten miles further northwest. Small and medium-sized specimens appear to be relatively gregarious and are often found with trilobite fragments and an unusual edrioasteroid-like echinoderm which is now being studied. This occurrence was probably not formed in the same way as most other *Gogia* occurrences (see p. 51), because slabs of plate material are approximately three times more common than slabs with complete *Gogia* specimens, many of which are partially disarticulated and disaggregated. It may also represent an occurrence in the "inner detrital zone" where *Gogias* are usually absent (see p. 77). Approximately 40 of these specimens were used for the following redescription.

Specific description. The calyx in *Gogia longidactylus* ranges from very small to very large. The largest specimen observed, which is Walcott's incomplete syntype, is at least 33–35 mm long and approximately 35 mm wide. The calyx shape ranges from elongate globular (sometimes almost spherical) to rounded conical in the smaller specimens. The number of calyx plates per side is very high, ranging from 42 in a small specimen up to approximately 200 plates in some of the largest ones. These plates range in size from relatively large in the upper middle portion of the calyx to medium or small around the summit and to relatively small around the holdfast attachment area; some small plates are also interspersed between the largest ones. Most of the calyx plates are smooth and nearly flat, but a few of the larger plates near the summit have slightly domed or convex granular plate centers. However, a single specimen from locality PI-6. (Pl. 9, fig. 7) has moderate radiating granules on all the calyx plates, but no other specimens are known with this type of ornamentation.

Epispires in this species are more or less restricted to the upper portion of the calyx. Smaller specimens show a very strong restriction of epispires, whereas larger ones have less of a restriction with sparse and poorly developed epispires sometimes present almost to the base of the calyx In one of the better preserved large specimens from my own collecting (Pl. 9, fig. 10), the lower half of the calyx shows no epispires at all, the lower 2/3 of the upper half of the calyx shows scattered small round epispires, while the top 1/3 of this upper portion around the summit has well-developed elliptical epispires. In smaller specimens no epispires are present until the top 1/4 to 1/6 of the calyx (see Pl. 10, fig. 6). The larger calyx plates near the summit have extremely numerous epispires, the total number ranging from 4 to 33+ epispires per plate, and averaging approximately 18 for a medium-large plate. This upper limit (see Pl. 10, figs. 7–8) represents the highest number of epispires per plate that I have observed in any species of *Gogia.* These epispires usually range from nearly round to moderately elliptical with an epispire L/W ratio between 1.0–7. The epispires seem to be slanted so that the exterior surface is more elongate than the interior surface; this has also been noted in a few other species of *Gogia* and in other eocrinoids. Epispires may be completely absent in the smallest observed specimen, which has a calyx only 5 mm long (Pl. 9, fig. 11).

The holdfast in *Gogia longidactylus* is very long and cylindrical; unfortunately, because of this, it is rarely found complete. In the few specimens with relatively complete holdfasts, the holdfast L/W ratio ranges from 9 to 25, and averages around 18, while the HF/C length ratio ranges from 1.2 to 2.0+, averaging around 1.6. The holdfast plates are mostly small, although in larger specimens they may range up to medium size. These plates are polygonal to slightly rounded, have a slightly convex profile, are relatively thick, and show little evidence of alternation in size or whorling. There are between 4–8 holdfast plates per half circumference. The distal tip is preserved only on a few specimens and has tiny whorled imbricate plates like other species (see Pl. 9, figs. 5–6). The contact between the holdfast and the calyx is relatively gradational, with holdfast-sized plates continuing up into the lower portion of the calyx (Pl. 9, fig. 10) and the calyx width expanding gradually. Epispires are absent until well up on the calyx.

The brachioles in this species are numerous, long, relatively large, and straight. The observed number of brachioles ranges from 6 to 14, although the probable total number may have been as high as 22, since brachioles from only half the calyx have been observed in most of these specimens. The longest observed brachioles range between 66 to 70 mm long on an incomplete calyx perhaps as much as 40–45 mm long, giving a BR/C length ratio of about 1.5±. The brachioles are relatively large with a height, including the brachiolar cover plates, of approximately 0.8 mm and a width of approximately 0.6 mm. They have a rounded bowl-shaped cross section with high and prominent brachiolar cover plates (BCP) equal in height to the brachiolar plates (BP) (see Pl. 9, fig. 3). There is only one biserial set of brachiolar cover plates present, and the BCP/BP ratio ranges from 1.7 to 2.0, averaging approximately 1.9. These brachioles are usually attached to the calyx in groups of 1 or 2, and in some of the larger specimens are apparently attached separately all the way around the rim of the calyx summit (Pl. 10, fig. 9). Spouts are either absent or very low and poorly developed. One specimen shows 2 distinctly smaller brachioles with curled tips (Pl. 9, fig. 3) that are approximately half of the size of the larger ones and only 5–8 mm long. These may be newly formed immature brachioles that have not yet grown to normal size.

Three or more wide and relatively shallow ambulacra are present leading from the apparently central mouth to the brachioles attached around the rim of the summit. Only one specimen, preserving the top surface, shows this ambulacral system in any detail (Pl. 10, fig. 10). Another specimen has the anal pyramid very well exposed and located high on the side of the calyx just below the edge of the summit (Pl. 10, figs. 3 and 5). It is approximately 2.5 mm by 2.0 mm, and was probably between 1.0–1.5 mm high originally. This anal pyramid is composed of approximately 12 tooth- or blade-shaped plates with smaller rectangular plates located outside of these, apparently forming a periproctal area. The total size of this area is approximately 3.5 mm.

Discussion. Gogia longidactylus is a relatively distinctive species of *Gogia* most closely related to *G. kitchnerensis* n. sp., from the Stephen Formation of Alberta. It differs from this and other species in having a marked restriction of the epispires to the upper part of the calyx, very many unornamented calyx plates, a very large number of epispires per plate in the upper part of the calyx, a very long cylindrical holdfast with many small plates, and long straight brachioles with relatively large cover plates. The number of calyx plates, number of epispires per plate, and the length of the holdfast are probably the most characteristic features that can be used to separate this species from *G. kitchnerensis*.

Stratigraphic and geographic range. Chisholm Shale, Middle Cambrian age (*Glossopleura* zone), talus piles from mining in Half Moon Gulch and nearby areas, PI–1. to 7., Ely Range, just west of Pioche, eastern Nevada. Also found in the Highland Range, approximately ten miles further northwest from Pioche. A single specimen apparently belonging to this species (GCM 2641; Pl. 10, fig. 11) has also been found at a locality in the Bright Angel Shale, Tonto Trail, ½ mile northeast of Indian Gardens, Grand Canyon National Park, northern Arizona.

Studied specimens. Lectotype USNM 15315, syntypes USNM 15315; pleisotypes AMNH 20001–20003 (Pack's 1906 specimens), MCZ 691–705, GCM 2641, and a single specimen loaned from B. L. Stinchcomb (E-3340; cast MCZ 669); unfigured specimens MCZ 670.

Gogia multibrachiatus (Kirk)
Plate 11

Eocrinus multibrachiatus Kirk, 1945: 185–187, pl. 16.

Gogia multibrachiatus, –Robison, 1965: 362–363, pl. 1, fig. 1.

This species was originally described by Kirk in 1945 from two large matched-counterpart specimens (USNM 108556a and b) apparently collected by N. J. Cameron and Charles D. Walcott in 1915 from the Bright Angel Shale at a locality just north of Indian Gardens (Walcott locality 74e) in Grand Canyon National Park, northern Arizona. Kirk apparently made castings (now missing) of the two described specimens preserved as natural molds, and gave a very adequate description (1945: 185–187). However, a third small specimen (USNM 165425) from the same locality (and collection?) was apparently never described. Robison (1965: 362–363) gave a short redescription of this species and assigned it to the genus *Gogia*. I studied latex castings of these three specimens that are redescribed below, but had virtually no success in trying to collect additional complete specimens from the apparent type locality in August, 1968.

Specific description. The calyx in *Gogia multibrachiatus* is very large, subglobular to barrel-shaped with a flattened summit, and has numerous irregular plates. Holotype USNM 108556a is about 33–35 mm long and 16–18 mm wide (the paratype has about the same length but a somewhat greater width), giving a calyx L/W ratio of about 1.8–2.0. There are between 80–120 calyx plates per side in these 2 specimens. These calyx plates are largest near the middle of the calyx, smaller near the base, and much smaller near the summit. The calyx plates are ornamented with moderately spaced pustules scattered over the surface (see Pl. 11, fig. 2). Many of the plates have depressed centers surrounded by the numerous epispires with prominent raised rims. Elliptical epispires are strongly developed over the entire calyx, with an epispire L/W ratio ranging from 3 to 12 and increasing toward the summit. The number of epispires per plate ranges from 6 to 24 in both type specimens.

The holdfast, which has not previously been described, is poorly preserved on all 3 of the known specimens. It appears to be a relatively large, globular structure attached to the base of the calyx. In the 2 specimens in which it is best preserved (Pl. 11, figs. 1–3), it ranges from about 12+ mm long and 13 mm wide to 22 mm long and 18 mm wide. It is apparently composed of many very small plates about 0.8–1.5 mm in size and lacks epispires. If these proportions are correct, then the HF/C length ratio is about 0.6–0.7 and the holdfast L/W ratio about 0.9–1.3. No attachment or distal tip features could be determined.

The brachioles are long, straight, relatively large, and very numerous. In the holotype these brachioles are at least 55 mm long (incomplete) and are about 0.6–0.8 mm high and wide except near the base where they gradually expand for attachment. One biserial set of small brachiolar cover plates is present with about 2.0–2.4 BCP/BP. A total of 24 brachioles is present on the negative counterpart of the holotype (Pl. 11, fig. 1), and close examination shows that all of these brachioles are attached to the same side of the calyx and represent only about 1/2–2/3 of the likely total number, as originally inferred by Kirk (1945: 186). Thus, the total number of brachioles was probably in the range of 36–48. These observed brachioles seem to be attached together in groups of 6–10 (see Pl. 11, fig. 4), but these groups appear to rim the entire oral surface instead of being attached to separate raised projections or spouts. Each of these groupings probably represents the terminus for one or more ambulacra radiating from the central(?) mouth on the oral surface.

The mouth, anal pyramid, and other features of the oral surface are still unknown from the three studied specimens.

Discussion. Gogia multibrachiatus is distinguished from other species by its large size, calyx plating and ornamentation, numerous very elliptical epispires, apparent globular holdfast, and very numerous, long, straight brachioles. It does not seem to be closely related to any of the other known species in this genus. Additional specimens would be most desirable.

Stratigraphic and geographic range. Bright Angel Shale, approximately 135 ft. above the base, Middle Cambrian (*Glossopleura* zone), Walcott locality 74e, Grand Canyon National Park, northern Arizona.

Studied specimens. Holotype, USNM 108556a (two counterparts), paratype, USNM 108556b (two counterparts), additional specimen (topotype?) unfigured by Kirk, USNM 165425.

Gogia spiralis Robison
Plates 12 and 13, Text-figure 5D

Gogia spiralis Robison, 1965: 363, pl. 52, figs. 1–4, text-fig. 3; Ubaghs, 1967b: S459, fig. 294.

This species was described by Robison (1965: 363) from 27 specimens (types USNM 139550–65) collected from the Wheeler Shale and overlying Marjum Formation in the House Range, western Utah. These type specimens were restudied in 1967 and several additional USNM specimens were also found in the Walcott Collection. In 1967 and 1968, I collected 117 additional specimens from the uppermost 80–100 feet of the Wheeler Shale at localities AS-1. and 2. near Wheeler Amphitheater in the House Range. This species is redescribed below, on the basis of this newly collected material and these additional USNM specimens.

Specific description. The calyx ranges in size from relatively small to relatively large. It usually has a rounded conical, ellipsoidal, or, more rarely, globular shape with a slightly domed summit. There are between 15–48 calyx plates per side, the average being about 34 plates for a medium-sized specimen. Relatively large plates are found in the center of the calyx, with medium-sized plates near the holdfast attachment and relatively small plates around the summit. There is almost no ornamentation on these calyx plates, and they are usually slightly convex with slightly domed centers and are relatively thick for their size. Because of the lack of ornament, the original echinoderm microstructure in the calcite often shows up on the smooth surfaces of these plates.

Epispires are well developed over the entire calyx. The number of epispires per plate ranges from 7–17, averaging about

12 for a relatively large plate in the middle of the calyx. When shared by 2 plates, these epispires usually have a moderately elliptical shape with the epispire L/W ratio ranging from 2 to 6. However, some epispires are located at the corners of 3 plates (see Pl. 13, fig. 6) and have a triangular shape. In young specimens these epispires are more rounded, and appear to be present (but not strongly developed) even in the smallest observed specimens.

The holdfast in *Gogia spiralis* shows more variation in shape (see Pl. 12, figs. 1–8) than in any other species of *Gogia*. It is usually of medium length and varies from cylindrical to moderately inflated and spindlelike in shape. The relative length is also quite variable, as shown by the wide range in the HF/C length ratio, from 0.65 to 1.5 (average about 1.05) in the 14 specimens measured. The holdfast L/W ratio ranges from 1.6 to 7.0, with an average of about 3.9; inflated holdfasts have the lower values, and cylindrical ones the higher values. The holdfast is made up of medium to very small plates usually having a moderately convex shape and often showing a slight "whorling" effect between plates of different sizes (Pl. 13, figs. 1–2). There are between 4–7 or more plates per 1/2 holdfast (higher in inflated holdfasts). The distal tip of the holdfast has many very tiny plates overlapping distally in definite whorls. In a few specimens with cylindrical holdfasts, the tips are expanded into a flat base (Pl. 12, fig. 3; Pl. 13, figs. 5 and 7); however, this was not observed in any of the specimens with inflated holdfasts. The transition between the calyx and holdfast is abrupt with a relatively large increase in plate size and the first appearance of epispires at this point, although there is only a moderate increase in calyx diameter. A few specimens with broken holdfasts show that the central lumen extends the length of the holdfast and occupies approximately 1/2–3/5 of the holdfast diameter.

At least 3 and perhaps as many as 5 specimens in my collection, and 2 excellent specimens in the Walcott Collection, were found attached to various fossil fragments (Pl. 12, figs. 1–5), including large trilobite cephalons, large *Ogygopsis*-like trilobite pygidia, and a possible sponge(?) or mud lump. Each attached specimen has a strongly flared distal tip on the holdfast that is expanded into a large, flat, pancakelike base approximately twice the holdfast diameter (Pl. 12, figs. 1–3). The tiny plates at this distal tip are extended to their maximum positions and do not appear to be imbricate. Only specimens with a cylindrical holdfast have been found in an attached position; specimens with an inflated holdfast have not been found attached and may possibly have had a different mode of life.

Gogia spiralis has a moderate number of long, medium-sized, spiralled brachioles. The observed number of brachioles ranges from 4 to 14, with a medium-sized specimen usually averaging about 10 brachioles. However, one of Robison's paratypes (USNM 139557), which has the brachioles extending to the edge of the slab, shows that there are at least 15–16 brachioles present in this specimen. The length of these brachioles varies from 16 to 39 mm, giving a BR/C length ratio ranging from 2.4 to 4.0 and averaging about 3.3. All of the brachioles observed in the studied specimens of *Gogia spiralis* are spiralled in a left-handed direction (Pl. 12, figs. 9–10). This spiralling has a relatively constant spiral "wavelength" along the entire brachiole in a single specimen, ranging from approximately 2.8 to 4.0 mm per spiral and averaging about 3.3 mm. This spiralling starts relatively close to the calyx, usually within 3–8 mm of the summit. Smaller specimens with shorter and smaller brachioles usually have a lower spiral wavelength. As many as 10 spirals per brachiole are found in the larger specimens having the most complete brachioles. A single set of relatively high domed biserial cover plates (BCP) covers the brachiolar food groove. Although the larger brachiolar plates (BP) appear to be normally developed and symmetrical, the brachiolar cover plates appear to be somewhat asymmetrical (see Text-fig. 5D and Pl. 12, figs. 9–10). Several specimens show that the brachiolar cover plates on the outside of the spiral appear to be larger and more strongly developed than the set on the inside of the spiral (Text-fig. 5D), perhaps for protection of the more exposed outside cover plates. There are approximately two BCP/BP in these specimens, although this ratio is very difficult to measure because of the spiralling. A large median canal between the brachiolar plates was observed in several specimens (Pl. 13, fig. 1) and it is possible that lateral canals may also be present. The brachioles are attached in groups of 2–5 to low projections on the calyx summit, and there may be as many as 5 of these groupings. The width and height of the brachioles increase appreciably near the attachment to the calyx.

The studied specimens yielded little information about the locations of the mouth and the development of the ambulacra on the calyx summit. At least one specimen shows that the anal pyramid is located on the side of the calyx below and between several groups of brachioles near the summit (Pl. 13, fig. 9). No other summit features are known at present.

Discussion. Gogia spiralis is a relatively distinctive species. It is one of three known species with spiralled brachioles, and is the only one with a holdfast ranging from medium length cylindrical to slightly inflated. It differs from other species, most notably *G. granulosa* and *G. guntheri* n. sp., in having a relatively small number of plates per side, no plate ornament, a cylindrical or slightly inflated holdfast, and an abrupt holdfast-calyx transition. Because of its occurrence in the *Bolaspidella* zone in the latest middle Cambrian, *G. spiralis* appears to be the youngest species of *Gogia* now known.

Stratigraphic and geographic range. Upper part of the Wheeler Shale (also from the basal part of the Marjum Formation), upper Middle Cambrian (*Bolaspidella* zone), localities AS-1. and AS-2. near Wheeler Amphitheater, House Range, west central Utah. Specimens have also been found at Marjum Pass in the House Range, just southwest of the above localities.

Studied specimens. Holotype and paratypes (16 specimens), USNM 139550–65; figured plesiotypes from the Walcott Collection, USNM 165421–22; figured plesiotypes MCZ 706–717; additional unfigured specimens, MCZ 730.

Gogia granulosa Robison
Plates 14 and 15

Eocrinus longidactylus (Walcott), Resser, 1939: 3–4, pl. 1, figs. 41–42.

Gogia granulosa Robison, 1965: 363–364, pl. 51, fig. 3.

This species was described by Robison (1965: 363–364) from a single complete holotype specimen (UU 1001). During the past five years many additional specimens have been found at Spence Shale localities near Calls Fort in northern Utah by Robison and several local collectors, especially Lloyd Gunther and his son Val, of Brigham City, Utah. I collected approximately 47 complete specimens from locality CF-1. in July, 1968, during a one-day visit with Robison. In addition, I borrowed approximately 25 specimens from Robison, 13 specimens from the Walcott Collection in the U. S. National Museum, and single specimens from A. R. Palmer, Kraig Derstler, and John Cutler. This species is redescribed here in greater detail on the basis of this new material.

Specific description. The calyx in this species has a globular (subspherical) to ellipsoidal shape with a domed oral surface. The specimens range in size from small to relatively large, but a great majority are of medium size. There are between 14–72 calyx plates per side, averaging about 45 plates for an average specimen. They range in size from small to relatively large, with the larger plates concentrated in the lower and middle portions of the calyx. Many of the calyx plates have slightly domed centers. The plate ornamentation, which is one of the most characteristic features of this species and from which the name was derived, consists of granular, radiating, often ridgelike pustules (see Pl. 15, figs. 1–2). This ornamentation is usually of moderate strength and shows little or no variation over the calyx; in many specimens the ornamentation also extends down onto the holdfast plates. Epispires are present over the entire calyx, although they are most strongly developed near the summit. The number of epispires per plate ranges from 5 to 20 and averages about 12 in larger plates. These epispires are slightly to moderately elliptical and have an epispire L/W ratio varying from 1.5 to 7. There is also some trace of absutural infilling on a few of the observed epispires. The smallest observed specimen with a calyx length of 2 mm apparently lacks epispires, but the next larger specimen (approximately 6 mm in size) does have them (Pl. 14, figs. 2 and 4).

The holdfast in *G. granulosa* is of medium length and has a cylindrical shape. It is made up of relatively small to medium-sized plates that usually have a relatively constant size on a single holdfast and show little trace of "whorling." The holdfast plates over most of the length have a polygonal to rounded shape, are moderately to slightly convex or bulged, and often show a pustular ornamentation similar to that in the calyx. The holdfast L/W ratio ranges from 2.0 to 6.5, averaging around 5.0, and the HF/C length ratio varies from 0.26 to 0.82, averaging around 0.5. There are approximately 5–7 plates per 1/2 circumference of the holdfast. The distal tip of the holdfast consists of many tiny distally imbricate plates surrounding a larger polygonal, perhaps imbricate, flat-plated surface in the center (see Pl. 15, fig. 1, left specimen). Approximately 1/3 of the specimens have this distal tip expanded; in these specimens both the holdfast L/W ratio and the HF/C ratio are near the low end of their ranges (compare Pl. 15, fig. 1 with figs. 5–8). No specimens with expanded distal tips are attached to objects, but a few specimens have this tip turned 90° from the long axis of the calyx as if they had been attached where they are now preserved. The transition between the holdfast and calyx is relatively abrupt, consisting of a moderate change in plating size and a relatively rapid expansion in calyx width. Some holdfast-sized plates continue up into the calyx for a short distance.

The brachioles in *Gogia granulosa* are very long, of medium size, and are all spiralled. The number of brachioles ranges from 2 to 13 or more in the studied specimens. All of the brachioles are spiralled in a left-handed direction (see Pl. 14, figs. 3 and 6), in contrast to the statement by Robison (1965: 363) that the brachioles in the holotype "appear to be straight rather than spiralled." Most brachioles begin spiralling relatively close to the calyx as in *G. spiralis*, but unlike *G. guntheri* from the same Spence localities. The BR/C length ratio varies from 2.7 to 4.1 and averages about 3.3. In the largest known specimen (Palmer Collection), unfortunately poorly preserved, the total number of spirals may range up to 15–16 in a brachiole at least 73 mm long. There is 1 spiral every 3–5 mm, and the spirals appear to be closer together both in small specimens and distally in large specimens with many brachiole spirals. Spiralling begins between 3–10 mm (usually within 3–6 mm) above the point where the brachioles are attached. Only 1 set of brachiolar cover plates (BCP) is present and these seem to be symmetrically developed. There are approximately 2.0–2.3 BCP/CP in the 2 specimens where this could be measured. Brachioles are attached to the calyx in groups of 2–5 on moderate-sized projections or spouts. In most specimens there appear to be 3–4 groupings or spouts on the calyx summit. As in many other eocrinoids, the brachiolar plates get appreciably shorter proximally near where they are attached; in addition, these plates in *G. granulosa* also become more concave on the sides near their proximal attachment point (Pl. 15, fig. 2).

The ambulacral system consists of 3 or more relatively wide and deep ambulacra protected by tiny cover plates (Pl. 14, fig. 1) leading out from the apparently central mouth to the spouts where the brachioles are attached. The anal pyramid, observed in several specimens, appears to be located on the side of the calyx below the brachioles. No other summit features are known in this species at present.

Discussion. Gogia granulosa differs from other species of *Gogia* in having spiralled brachioles with a great many spirals, a globular calyx shape, relatively constant moderately granular ornamentation over the entire calyx that often extends down onto the holdfast plates, and a medium length cylindrical holdfast, without whoriing.

Stratigraphic and geographic range. Spence Shale Member, Langston Formation, Middle Cambrian (*Glossopleura* to *Bathyuriscus-Elrathina* zones), from localities CF-1. and USGS 55e in northern Utah. John Cutler of Idaho State University, Pocatello, collected a single *Gogia* specimen (ISU 1440; Pl. 15, fig. 2) apparently belonging to this species from the Spence Shale on Mill Creek in the Bear River Range, southeastern Idaho. This locality is approximately 50–60 miles north of the CF-1. locality near Brigham City, Utah, but only five to six miles from the type locality for *G. palmeri* n. sp. Since the species of *Gogia* present at these two nearby localities are quite different, it is probable that they occur at different stratigraphic levels in the Spence Shale or in different shale tongues.

Studied specimens. Holotype UU 1001; plesiotype MCZ 732–738, UU 1010p, –w, and –x, UU 1011d, and UU 1040p, USNM 165433–165436, PE-214, and ISU 1440. Additional unfigured specimens include MCZ 739 and specimens in the USNM and UU collections.

Gogia palmeri new species
Plates 16, 17, and 18

This new species of *Gogia* from southeastern Idaho is represented by the largest collection of complete eocrinoid specimens that has ever been assembled from a single locality. A. R. Palmer and Colin Gatehouse discovered this locality (USGS locality 6201; my locality EC-1.) during the summer of 1967, and collected approximately 110 specimens during one day's work, about half of which are matched counterparts. I returned to this locality in June, 1968, and in three days of quarrying work collected an additional 201 specimens, over three-quarters of which are matched counterparts. Nearly all of the specimens were found in a small quarried exposure of sandy shale approximately two feet thick and eight feet long. In these beds the eocrinoids are more abundant than any other fossil, moderately to extremely gregarious, relatively well aligned when found together on the same slab face, and show a very wide variation in size. They seem to occur in definite bands representing sandier bedding surfaces spaced about two inches apart and separated by barren, nearly rectangularly jointed, shaly beds. The specimens were collected by quarrying out and splitting apart blocks of the sandy shale that yielded matched counterpart natural molds. These make excellent latex casts usually showing both sides of the specimen and sometimes part of the interior. These eocrinoids are completely leached and devoid of calcite up to about two feet back into the slope at this locality. At this depth calcite specimens begin to appear again, indicating that the natural molds are being produced by surface leaching during present-day weathering. Specimen USNM 165418 (Pl. 16, figs. 1–5) was chosen as holotype, and is described below along with 34 USNM and MCZ paratypes.

Specific description. The calyx ranges in size from very small to very large, with the average size being in the medium-large range. The shape in larger specimens is barrel-shaped to ellipsoidal; in smaller specimens the shape is rounded conical to subglobular. There are between 20–105 calyx plates per side, the average being about 75 for a large specimen. Very large plates occur just above the base and again in the upper middle portion of the calyx; medium-sized plates are scattered in between these larger ones; and small plates occur at the base of the calyx near the holdfast attachment, in between the larger ones over the rest of the calyx, and just below the brachioles near the summit (Pl. 16, fig. 5). The calyx plate ornament in *G. palmeri* shows the strongest variation over the calyx of any known *Gogia* species. From the base of the calyx up, the ornamentation varies from very strong to almost none. Larger plates in the lower half of the calyx are moderately to strongly convex in shape (sometimes almost hemispherical), very thick, and strongly ornamented with large, irregularly radiating pustules (Pl. 16, fig. 5; Pl. 17, figs. 4–5 and 10–11). Plates in the upper half of the calyx are thinner, slightly convex to slightly concave, and have subdued pustules or no ornament at all. Smaller specimens show little or no ornamentation, and have only a slight to moderate convexity in their lower calyx plates (Pl. 18, figs. 3–6). In some specimens the strong pustular ornament on the lower part of the calyx extends down onto the larger convex holdfast plates, giving them a slight radiating and stellate pattern (see Pl. 17, fig. 9).

Epispires are present over the entire calyx, although they are not strongly developed near the holdfast attachment. There are between 3 to 20+ epispires per plate, averaging approximately 12 for a medium-sized plate. They are slightly to very elliptical with an epispire L/W ratio of 1.0+ to 10+. All of these epispires have a prominent rim around the exterior and have a smooth rounded surface on the interior (see Pl. 18, figs. 1–2). Most epispires are shared by 2 plates, but some are present at the corners between three plates and have a triangular shape, while other epispires with an elliptical shape are shared by 3 plates in a "two-plus-one" combination (see Text-figs. 11A and Pl. 16, fig. 5). A few specimens also show that some of the epispires in the larger plates may have their absutural ends apparently filled in by secondary deposits to lower the epispire L/W ratio and confine the pore to the region along the suture. This infilling is built up slightly above the surface of the plate as a flat-topped area (see Pl. 18, fig. 11). Some of the largest plates show a possible "break off" of the plate limbs around the longest epispires to form new small plates (Pl. 16, fig. 5). The bridges of plate material between the epispires have well-developed slight depressions on their sutured surfaces (Text-fig. 11A and Pl. 16, fig. 5), apparently for muscles or ligaments to hold them together in place.

The holdfast in *Gogia palmeri* is cylindrical, of medium length, and relatively thin. The HF/C length ratio varies from 0.4 to 0.7, and averages about 0.57 for the 12 specimens measured. The holdfast L/W ratio varies from 2.3 to 7, with the ratio increasing during growth and averaging about 5.5 for medium-large specimens. The holdfast plates range in size from medium to very small. They are moderately to strongly convex (the larger ones are often hemispherical), rounded in shape, sometimes ornamented with pustules, and usually show a major alternation in plate size that gives an irregular or slightly diagonal "whorling" effect which is best developed on larger spcimens (Pl. 16, fig. 5). There are approximately 4–5 larger plates and 6–7 smaller holdfast plates per ½ circumference of the holdfast. The connection between the holdfast and the calyx is relatively abrupt; at this point there is a rapid increase in calyx width and the first appearance of larger calyx plates with a few epispires. However, holdfast-sized plates often continue a short distance up into the lower part of the calyx (Pl. 17, figs. 5 and 12). The distal tip of the holdfast is made up of tiny, distally imbricate plates arranged in strong whorls that resemble a Fibonacci spiral. Except in a few small specimens, most of these holdfast distal tips do not appear to be expanded. None of the observed specimens were found attached to any objects on the bottom. Finally, many of the holdfasts in this species are slightly to moderately curved or bent approximately 1/3–1/2 the distance down the holdfast (see especially Pl. 18, figs. 1–2). At present, no reason is known why this should occur, but it has also been observed in other species such as *G. granulosa* from northern Utah.

The brachioles in *G. palmeri* are very long, small to medium in size, and straight. There are 4–18 or more brachioles present, the average being about 13 brachioles in a medium-to-large specimen. These range up to 69+ mm long on the holotype specimen (Pl. 16, figs. 1–2), and the BR/C length ratio ranges from 2.4+ to 4.0 and averages about 3.2 for the seven complete specimens measured. This ratio seems to decrease with increasing size of the eocrinoid. All (except 1) of the studied brachioles are completely straight. The one exception to this was found in the lower part of 1 brachiole on paratype USNM 165419; here there is a single complete spiral before the brachiole becomes straight for the remainder of its length (Pl. 16, fig. 6). This type of isolated spiral has not been observed in any other specimens at this locality or in any other *Gogia* species.

The brachiolar cover plates (BCP) of *G. palmeri* are also somewhat unusual. Brachioles of the large holotype appear to have 2 sets of brachiolar cover plates proximally (Pl. 16, figs. 3–4), and this is the only known specimen of *Gogia* to show this. These sets seem to alternate on each side of the brachiole with a larger high cover plate followed by a smaller low one, and they may also be slightly imbricate distally (see Pl. 16, figs. 3–4). As these brachioles are traced distally, the low cover plate increases in size and becomes indistinguishable from the high one; therefore, only 1 type of brachiolar cover plate is present here. There are approximately 1.15–1.3 high BCP/BP proximally on these brachioles, one of the lowest ratios observed in any species of *Gogia*. However, this ratio doubles at the distal end, where only 1 set of brachiolar cover plates is present. A few specimens show that the brachioles have a median canal on the brachiolar plate sutures, and there may possibly also be 2 lateral canals or mounting areas for cover plates in the relatively wide food groove. The larger brachiolar cover plates are approximately 2/3 as high as the brachiolar plates, and, away from the calyx, the brachiole has a height of 0.4–0.5 mm and a width of approximately 0.33 mm. A brachiole of this size gradually expands to nearly double these dimensions near the calyx where it is attached.

The brachioles are attached to the calyx in groups of 2–5 and are mounted on relatively prominent "spouts" or projections on the summit of the calyx (see Pl. 17, figs. 6, 10–11, and 12–13). There are between 2–5 spouts around the rim of the summit. The mouth is apparently located in the center of the oral surface, and relatively wide and deep ambulacra with tiny cover plates run from this central location to the spouts where branches lead to all of the brachioles (Pl. 17, fig. 6). A small anal pyramid was observed on only 1 specimen (Pl. 17, fig. 13); it is located on the side of the calyx just below the summit. This pyramid is only about 2.5 mm in diameter, and is made up of numerous delicate tooth-like plates.

Discussion. Gogia palmeri is a relatively distinctive species of *Gogia*. It can be identified by its barrel-shaped to ellipsoidal calyx; its very elliptical epispires; the relatively large number of epispires per plate; its strong plate ornament, which shows a marked variation over the calyx and sometimes extends down onto the holdfast; its medium-length cylindrical holdfast with prominent whorling of both medium and very small plates; its very long, medium-sized, straight brachioles having two sets of unequal cover plates proximally; and, the way that the brachioles are mounted on relatively large spouts on the calyx summit. *Gogia palmeri* seems to be most closely related to such species as *G. granulosa* Robison, and perhaps *G. spiralis* Robison and *G. hobbsi* n. sp., but does not resemble any of these very closely. At present *G. palmeri* is the most abundant, best preserved, and perhaps best known species of *Gogia*.

Etymology. This species is named for A. R. Palmer, State University of New York, Stony Brook, who discovered this eocrinoid locality and collected the first specimens.

Stratigraphic and geographic range. "Spence Shale equivalent," Middle Cambrian (*Glossopleura* to *Bathyuriscus-Elrathina* zones), locality EC-1. (USGS locality 6201), Emigration Canyon, near Preston, southeastern Idaho.

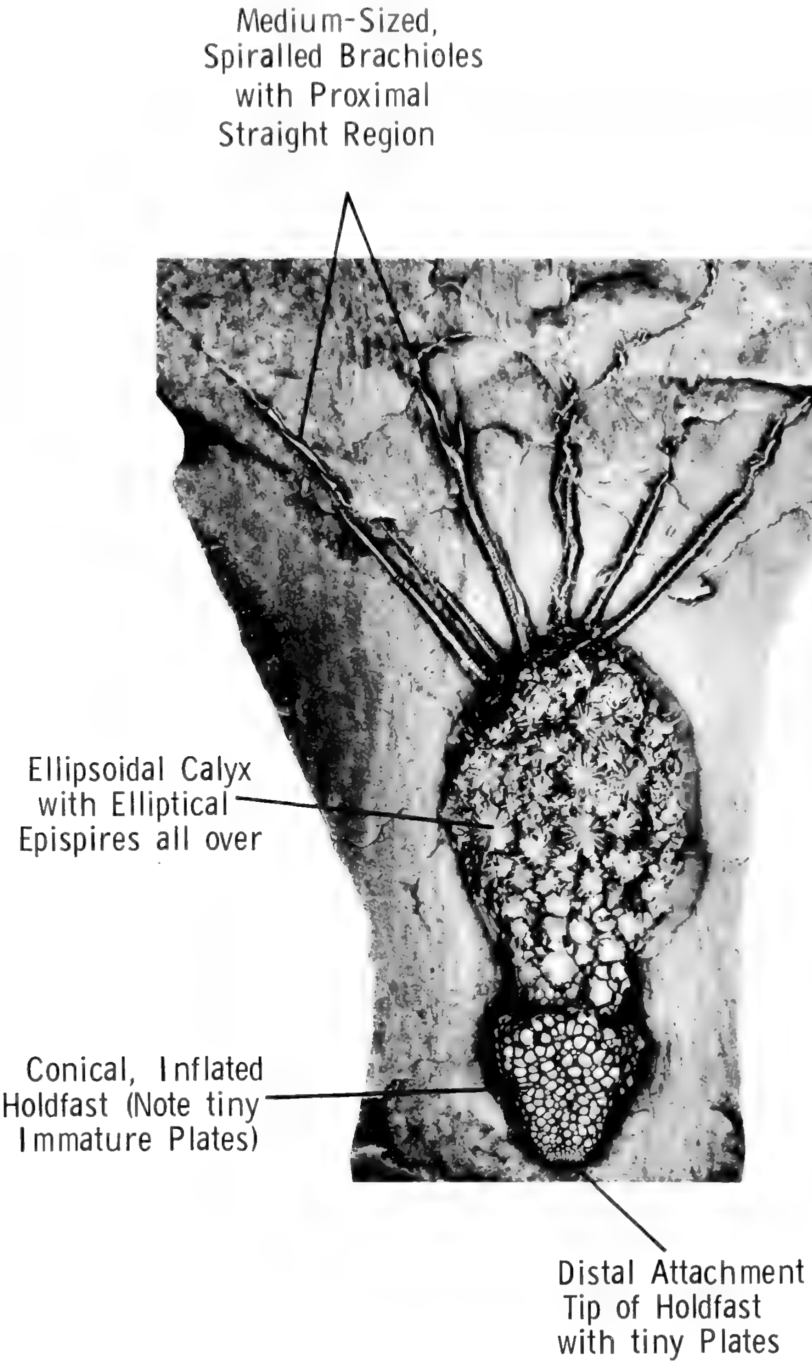
Studied specimens. Holotype USNM 165418A and B; figured paratypes USNM 165414–165417, 165419, and MCZ 676–689; unfigured paratypes USNM 165420 and MCZ 690.

Gogia guntheri new species
Plate 19; Text-figure 26

This unusual new species of *Gogia* was first recognized by Richard A. Robison of the University of Utah, Salt Lake City, from material originally collected by Lloyd Gunther and his son Val, of Brigham City, Utah. Robison was not able to describe this new material, and turned it over to me for study when I visited him in July, 1968. A total of 23 specimens were borrowed from Robison; five additional specimens were collected in the field during a one-day visit with Robison to locality CF-1., and two specimens were found in an old collection (perhaps made by Walcott) in the U. S. National Museum. Most of these specimens were collected from localities also yielding *Gogia granulosa*, but specimens of these two different species have not been found together on the same slab surface. Therefore, these two species probably occur in slightly different stratigraphic intervals in the Spence Shale. The following specific description is based on the 13 best preserved specimens.

Specific description. The calyx in this species usually is medium to large sized. The large, excellently preserved holotype (UU 1010a) is 23 mm long and 15 mm wide, with a calyx L/W ratio of about 1.5 (Text-fig. 26). The calyx shape is usually elongate ellipsoidal, although in some cases it varies from globular to almost barrel-shaped. The number of calyx plates per side varies from 25 to 90+, the average being approximately 55 for a medium to large specimen. These plates are largest in the middle of the calyx, relatively small around the summit, and very small to medium sized near the top of the holdfast. The calyx plates show almost no ornament in most of these specimens, and are slightly convex to slightly concave, and relatively thin for their size. However, some of the plates may have small areas of raised pustules in their centers; this was also observed in some of the holdfast plates (Pl. 19, fig. 5). Because the calyx plates are thin, it is difficult to uncover these plates during preparation of the buried calcite specimens by acid etching, and this is probably why the calyx is not especially well preserved in many of the studied specimens.

Epispires are present over the entire calyx, and also appear to extend down onto the upper cylindrical portion of the holdfast. They are most strongly developed in the middle and upper portion of the calyx. The number of epispires per plate ranges from 5 to 13, the average being about 9 for



Text-figure 26. Morphology of *Gogia guntheri* n. sp. Holotype specimen UU 1010a (collected by Lloyd Gunther and prepared by R. A. Robison) showing ellipsoidal calyx bearing elliptical epispires, spiralled brachioles with a proximal straight portion, and strongly inflated holdfast with tiny whorled plates at the distal tip.

a medium-sized plate. These epispires vary from slightly to widely elliptical with the epispire's L/W ratio ranging from 1.5 to 8. The lower values are usually found in smaller specimens and in epispires lower on the calyx. These epispires are shared by 2 plates, by 3 plates in a "two-plus-one" elliptical pattern such as is found in *G. palmeri* (see p. 91), and at the corners of 3 or more plates where they are more nearly circular.

The holdfast is the most distinctive feature in *Gogia guntheri*. It is moderately to strongly inflated and has a globular or rounded conical shape (Pl. 19, figs. 1–8). It is also very large (approximately 1/3–1/2 the size of the calyx); in the holotype (Text-fig. 26), the holdfast is 11.5 mm long and 9.5 mm wide. In 7 complete specimens the holdfast L/W ratio ranges from 1.05 to 1.40, the average being about 1.15, and the HF/C length ratio ranges from 0.4 to 0.6, the average being about 0.5. These inflated holdfasts have medium to small plates, and most of the plates in a single holdfast are approximately the same size. A few tiny and apparently new plates, however, may be present in between the larger ones on the holdfast (Text-fig. 26). These plates have a polygonal shape, are slightly to moderately convex, and in some specimens have raised centers with pustules. The number of holdfast plates per ½ circumference is very high because of the strong inflation, and usually ranges from 7 to 16+. The distal tips of these inflated holdfasts have whorls of tiny, distally overlapping, perhaps imbricate plates similar to other species of *Gogia* (Pl. 19, figs. 1, 4, 7, and 10). The implication may be that *G. guntheri* with its inflated holdfast was normally attached to objects on the bottom like other *Gogia* species. However, no specimens were found attached, and only one small specimen has the base of the holdfast flattened and turned 90° to the long axis of the calyx (Pl. 19, fig. 7). The transition between the holdfast and calyx is relatively gradual; calyx-sized plates with epispires at their corners appear lower than the gradual expansion for the calyx width.

Gogia guntheri has a moderate number of relatively large, medium to long, incompletely spiralled brachioles (see Pl. 19, fig. 9). None of the studied specimens has a complete complement of brachioles, but the apparent number may have ranged from 4 to 15(?), the average being about 8. The BR/C length ratio ranges from about 2.0 to 2.6+, again a minimal value. All of the observed brachioles are spiralled in a left-handed direction; however, this spiralling starts at a considerable distance above the calyx, much further than in any other species of *Gogia* with spiralled brachioles (see Pl. 19, fig. 9). Indeed, because of this delayed spiralling feature, badly weathered or buried specimens of *G. guntheri* can be distinguished from specimens of *G. granulosa* at the same outcrop even when no other calyx or holdfast features are visible. The brachioles are straight for a distance of between 6–25 mm above the calyx (average about 13 mm) before spiralling begins abruptly. In the spiralled portion of the brachioles there is about 1 spiral for every 3–5 mm. The total number of observed spirals ranges up to 8 or more in the studied specimens. Brachiolar cover plates on these brachioles are relatively large and prominent (Pl. 19, fig. 9), and only 1 symmetrically developed set of cover plates seems to be present. The number of BCP/BP ranges from 2.2 to 2.5. These spiralled brachioles are attached to the calyx in groups of 1–4, with the larger groups attached to relatively high spouts (Pl. 19, fig. 9).

The ambulacral system consists of 2–3 relatively large, wide, and deep ambulacra leading from the apparently central mouth to the larger brachiole groups. The anal pyramid is poorly preserved on 2 specimens, and is located on the side of the calyx just below the summit (Pl. 19, fig. 12). No other summit features are known for this species.

Discussion. *Gogia guntheri* is a relatively distinct new species. It is the only species now known to have a strongly inflated holdfast, although *G. multibrachiatus* from the Bright Angel Shale may also have this feature. Although two other species also have spiralled brachioles, *G. guntheri* is the only form with a relatively long straight portion proximally before the brachioles begin spiralling.

The strongly inflated holdfast is the most unusual feature in *G. guntheri* and there are several possible ways in which it may have been used. Specimens of *G. guntheri* may have buried the holdfast in soft sediment and used this as a base of support; however, the tiny whorled plates at the distal tip of the holdfast are nearly identical to those found in other *Gogia* species, which are thought to have been attached to objects lying on the sea floor. Epispires are also present on the upper part of the holdfast, the implication being that it could not have been very deeply buried, if at all. If normally attached, this inflated holdfast may have kept the eocrinoid from falling or being knocked over more than a certain angular distance (about 60° in most specimens). A gas-filled holdfast with an upside-down floating way of life is also a possibility, but the normal-looking distal attachment tip seems to argue against this. A final possibility is that this unusually shaped holdfast might represent a gall-like internal parasitic infection that caused an irregular enlargement in the holdfast. There is considerable variation in the shape of the inflated portion of the holdfast, ranging from rounded conical to almost spherical with a cylindrical portion at the bottom. However, all known specimens of *G. guntheri* have this strongly inflated holdfast, an unusual feature for a parasitic affliction, and this species is different enough from the associated *G. granulosa* that the absence of an inflated holdfast could easily be determined. Therefore, until further paleoecologic evidence becomes available, the exact way in which this unusual inflated holdfast was used cannot be conclusively determined.

Etymology. This new species is named for Lloyd Gunther, of Brigham City, Utah, who collected the first specimens of *G. guntheri* (including the holotype) and brought them to the attention of Richard A. Robison at the University of Utah. We thank Mr. Gunther and other members of his family for their assistance during this project.

Stratigraphic and geographic range. Spence Shale Member, Langston Formation, Middle Cambrian (*Glossopleura* to *Bathyuriscus-Elrathina* zones), locality CF-1., and nearby exposures in Miners Hollow and Cataract Canyon, west side of the Wasatch Range, just north of Brigham City, Utah.

Studied specimens. Holotype UU 1010a; figured paratypes UU 1010b, –h, and –s, UU 1040b and –f, and MCZ 739–741; unfigured paratypes USNM 189357, UU 1010c and –t, and UU 1040a; several additional unstudied specimens are filed under numbers UU 1010, 1011, 1040, 1041, and MCZ 742.

Gogia kitchnerensis new species
Plates 20 and 21; Text-figures 15 and 27

Gogia prolifica (Walcott), Harker and Hutchinson, 1953: 285–287, pl. 40.

(?)*Eocrinus* n. sp. Caster and Pope, 1960: 1840–1841.

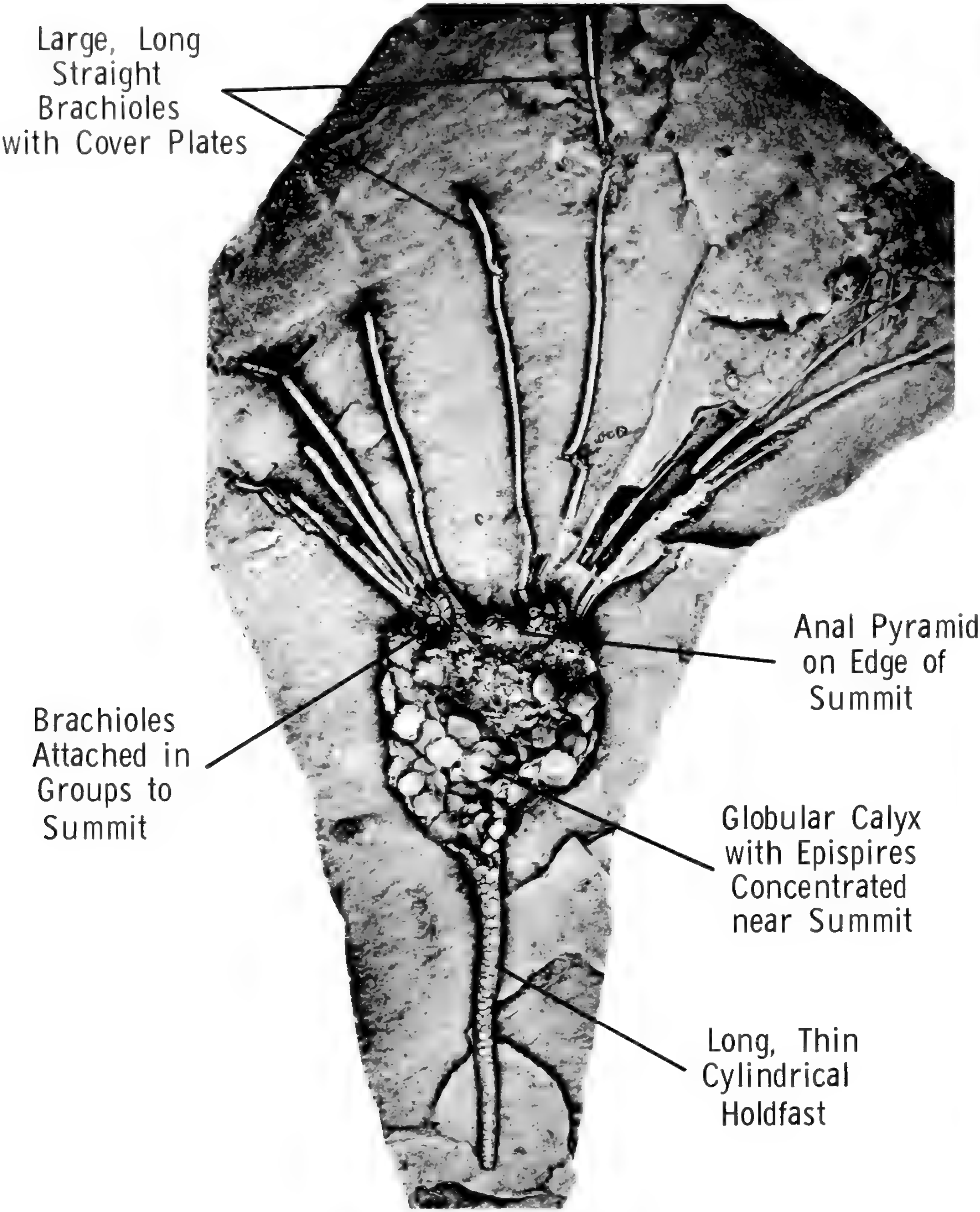
Harker and Hutchinson (1953: 285) reported the occurrence of *Gogia* in beds equivalent to the Stephen Formation on Mt. Kitchner, Jasper Park, Alberta. Several additional specimens were collected from this locality during the early 1950's by L. R. Laudon of the University of Wisconsin, who loaned them to me and also supplied information on how to reach this locality. One additional specimen from a nearby locality, which apparently was the basis for the abstract by Caster and Pope (1960: 1840–1841), was borrowed from Kenneth T. Caster of the University of

Cincinnati. I visited this locality (KT-1.) in July, 1968, with a national park permit, and in two days of work collected approximately 154 complete specimens. The partially weathered calcite specimens come from thin (1/8–1/2 in.), yellowish orange, shale partings in thin-bedded, gray limestones of the "Stephen Formation" both in outcrop and in large talus piles near the summer snowline on the eastward-facing dip slope of Mt. Kitchner. They were prepared either by scrubbing off the thin layer of soft shale around slightly weathered calcite specimens, or, if the specimen was badly weathered and the surrounding shale thick enough, by dissolving away the remaining calcite plates and then casting the artificial mold in latex rubber.

Both Harker and Hutchinson (1953: 286) and Robison (1965: 360) considered that the *Gogias* from Mt. Kitchner belonged to *G. prolifica* Walcott (1917b: 68–69), even though the Kitchner locality is three zones higher in the middle Cambrian (see Text-fig. 24). Apparently neither author was able to directly compare prepared material from both localities. After doing this, I have concluded that the Mt. Kitchner occurrence is sufficiently different to warrant a new species, here named *Gogia kitchnerensis*. Specimen GSC 25934 is here chosen as holotype, and is described below along with 16 paratypes.

Specific description. The specimens range in size from small to relatively large. The calyx has a rounded conical to subglobular shape, usually with a flattened summit. There are between 40–85 calyx plates per side, the average being about 70, with relatively large plates near the center of the calyx and smaller ones near the holdfast and summit. There is very little if any ornament on the calyx plates, although some of the larger specimens have plates with a slightly raised central knob and very faint radiating ridges. In most specimens, the epispires are strongly restricted to the adoral 1/4–1/2 of the calyx; this is much different from the arrangement found in *G. prolifica,* but is similar to that in *G. longidactylus* from Nevada. A few of the largest specimens, including holotype GSC 25934 (Text-fig. 27), have a few scattered epispires lower on the calyx, but these are not strongly developed. This restriction of epispires is probably the main reason why Harker and Hutchinson (1953: 286) reported "thecal pores lacking" in their specimens, although they noted that the margins of some of the larger adoral plates were "folded and crenulate." Near the center of the calyx the epispires are nearly circular (epispire L/W = 1.0), but nearer the summit they are moderately elliptical (L/W up to 4.0) with strongly developed raised rims. There are between 5–15 epispires per plate, and they seem to be present near the summit at all observed calyx sizes.

The holdfast in *G. kitchnerensis* is long, thin, and slowly tapering. In holotype GSC 25934, which has a calyx 21 mm long, it is 28 mm long and slowly tapers from 2.5 mm proximally to 1.0 mm at the distal tip. In other mature specimens the holdfast length varies from 9 to 31 mm, giving a HF/C length ratio varying between 0.6–1.3, with an average of about 0.9–1.0. Since the holdfast shows a considerable variation in length compared to the calyx (see Pl. 20, figs. 1 and 9), this ratio has an unusually large range. The holdfast L/W ratio ranges from 8 to 12 and averages about 9.5. The holdfast has small to moderate-sized plates, usually more or less similar in size in any one specimen. These plates are relatively thick, polygonal in shape, slightly convex on the exterior, and enclose a lumen occupying about 1/3 of the holdfast diameter. There are 3–4 holdfast plates per ½ circumference in most specimens (Pl. 20, fig. 7). There is a relatively rapid transition where the holdfast is attached to the calyx, involving a rapid increase in plate size and a moderate to very rapid increase in calyx width (most prominent in larger specimens). The distal attachment tip of the holdfast (Pl. 20, fig. 7) has very tiny plates



Text-figure 27. Morphology of *Gogia kitchnerensis* n. sp. Holotype GSC 25934 showing rounded conical calyx, partial restriction of epispires to summit portion, long cylindrical holdfast with tiny plates on distal tip, numerous long straight brachioles attached in groups to summit, and excellent anal pyramid at edge of summit between brachioles.

perhaps arranged in whorls and slightly overlapping distally. No specimens in this collection were found attached, and none had the holdfast tip expanded.

The brachioles in *G. kitchnerensis* are relatively numerous, of large size, relatively long, and straight. The observed number of brachioles ranges from 3 to 5 in the smallest specimens, up to 11–14 in the largest ones; the total number may have been considerably larger, perhaps as many as 20. In holotype GSC 25934, the brachioles are incomplete and at least 55 mm long (attached to a calyx 21.0 mm long). The brachiole/calyx length ratio ranges from 1.8 to 2.7, the average being about 2.2. These brachioles are about 1.0 mm high and 0.5–0.7 mm wide along most of their length, with the single set of high domed brachiolar cover plates (BCP) over the food grooves almost as high as the brachiolar plates (BP) themselves. There are between 1.8–2.1 BCP/BP along each brachiole. These brachioles are attached to low raised areas around the edge of the summit in groups of 1 or 2–5. Raised attachment areas or "spouts" are not strongly developed in this species.

Several of the collected specimens of *G. kitchnerensis* (especially GSC 25935) show relatively complete summit areas, a very rare occurrence in *Gogia*. The mouth appears to be central and to have 5 unequal ambulacral grooves radiating from it (see Text-fig. 15). Three of these ambulacral grooves (apparently ambulacra "A," "C," and "D" using the position of the anal pyramid in interradius "CD") extend from the elongate mouth to groupings containing 3–4 brachioles at the edge of the summit. The other two ambulacral grooves, "B" and "E," branch off from ambulacra "C" and "D" respectively, near the mouth and extend out to areas containing only 1–2 brachioles. This difference in ambulacral size probably results from the later development of the 2 smaller ambulacra during ontogeny. Therefore, although pentameral symmetry is present in the ambulacral system, it is not perfectly developed in this species of *Gogia*, but shows a possible origin from an earlier triradiate symmetry. Both the food grooves and the brachioles appear to be located on relatively large, but only slightly modified calyx plates. These ambulacral grooves were probably covered in life by tiny cover plates, but these have not been preserved.

The anal pyramid is located laterally at the edge of the flattened oral surface at or just below the level where the brachioles branch off the calyx (Pl. 20, figs. 2 and 5). This anal pyramid is large and strongly domed, about 3.0 mm in diameter and 1.0–1.5 mm high in the holotype. It consists of about 10–12 elongate tooth-shaped plates, with an area of tiny polygonal plates surrounding them, perhaps to form a periproctal area (Pl. 20, fig. 5). At present no other summit structures are known.

Discussion. Gogia kitchnerensis is most closely related to *G. longidactylus* from Nevada, but differs from this species by having somewhat less restricted epispires, fewer brachioles, fewer and larger calyx plates, and a somewhat shorter holdfast with considerably fewer and larger plates around the circumference. *G. kitchnerensis* differs from *G. prolifica* and other species by having the epispires restricted to the upper portion of the calyx, a long cylindrical holdfast strongly differentiated from the calyx, and by the arrangement of the ambulacral system and brachioles, which are not mounted on appreciably raised spoutlike areas.

Most of the specimens appear to be lying on their sides in bedding planes, but a few (including most of the specimens showing the oral surface) appear to be normal to bedding and may have been preserved in an upright position. None of the studied specimens show any attachment, and the strong association of most of the specimens with thin red or yellow shale partings between thicker limestone beds implies a possible mud slide origin (see p. 51). The smaller specimens are highly gregarious

(Pl. 21, fig. 1), but the largest ones are almost never found with any other specimens nearby (in one case no other fossils were found within a radius of 10–12 ft.). Other associated fossils, including large and small trilobites and rare inarticulate brachiopods and hyolithids, are very seldom found on the same bedding surfaces as the eocrinoids.

Several circular "lumps" about 25–30 mm in diameter and filled with trilobite "hash" (including meraspid growth stages) and disarticulated *Gogia* plates (Pl. 21, fig. 7) have also been found at this locality. These may represent fecal or regurgitation wads of indigestible skeletal material perhaps from some large wormlike animal, arthropod, or chordate(?) that fed on living or dead trilobites and echinoderms. These wads have been observed at other *Gogia* localities in the Rockies (especially CF-1.), but seem to be particularly abundant here.

Stratigraphic and geographic range. "Stephen Formation," Middle Cambrian (*Bathyuriscus-Elrathina* zone), locality KT-1., dip slope of Mt. Kitchner above the Sunwapta River, Jasper Park, Alberta, western Canada.

Studied specimens. Holotype GSC 25934; paratypes GSC 25935–25961 (17 specimens), GSC 10088a–b (Harker and Hutchinson's specimens), and UC 24691; additional specimens collected in 1968 (GSC collection), four specimens at the University of Wisconsin (Laudon Collection), and six specimens in GSC collection 10088c–h.

Gogia hobbsi new species
Plates 22 and 23

Gogia sp. Palmer, *in* Hobbs, Hays, and Ross, 1968: J19.

While mapping a window of deformed Paleozoic sediments surrounded by Challis Volcanics of Tertiary age in central Idaho, S. Warren Hobbs of the U. S. Geological Survey, Denver, discovered an isolated Cambrian fossil locality at the top of the Cash Creek Quartzite near Clayton, Idaho (USGS locality 5462). Material from this locality was sent to A. R. Palmer, then of the U. S. Geological Survey in Washington, for identification and age assignment; among the fossils he identified were specimens of *Gogia* sp. (Palmer *in* Hobbs, Hays, and Ross, 1968: J19). In July, 1968, I revisited this locality, which I have designated CL-1., with Hobbs and we collected 97 specimens during a four-hour visit. These specimens represent a new species of *Gogia*, which I have named after Hobbs in recognition of his original discovery of this material and the assistance he gave me during my thesis field work. Specimen MCZ 631 is here chosen as holotype along with 34 other paratype specimens, ten of which are figured in Plates 22–23.

Specific description. The specimens are all relatively small and preserved as weathered natural molds. The calyx ranges from 4 to 11 mm in length (holotype MCZ 631 is 10.5 mm long), and usually has a rounded conical shape, showing some variation from club-shaped to globular. There are between 24–26 relatively large calyx plates on the exposed side of the holotype (Pl. 22, fig. 1); other specimens have between 12–28 plates per side. The largest plates are near the center of the calyx, with somewhat smaller ones aborally near the holdfast and much smaller ones near the summit and between the brachioles. Epispires are present between all of the calyx plates and even occur at the top of the holdfast. There are between 5–14 epispires per calyx plate, with the epispires having an elliptical shape (epispire L/W = 2.0–8.0) and prominent raised rims on the exterior. The calyx plates are only slightly ornamented with tiny granules on their exterior surface (see Pl. 22, fig. 2).

Gogia hobbsi has a very short cylindrical holdfast attached to the aboral end of the calyx. In holotype MCZ 631, which has a calyx length of 10.5 mm, the holdfast is about 3.0–3.5 mm long and 1.0–1.5 mm in diameter. In this and other specimens the

HF/C length ratio varies from 0.29–0.40, while the holdfast L/W ratio ranges between 2.5–3.2. The holdfast plates are moderately large in size, often longer than wide (Pl. 23, fig. 8), and grade into very small plates distally. They have a smooth, moderately convex or "bulged" exterior surface. The adoral connection of the holdfast to the calyx is gradational and this region is occupied by plates of intermediate size with few epispires. The distal attachment tip of the holdfast is usually flattened and sometimes bulged laterally (Pl. 22, figs. 4–5), and is made up of rows, perhaps spiralled, of very tiny plates. Five of the studied specimens of *G. hobbsi* in this collection are attached to other fossils; 3 are attached to trilobite cephalons (molts?) (see Pl. 23, figs. 1–5), 1 to an inarticulate brachiopod valve (Pl. 23, fig. 6), and 1 to a possible hyolithid(?). It is unusual to find this many well-preserved *Gogia* specimens (5 out of 97) apparently attached in their normal life positions.

The brachioles in *G. hobbsi* are few in number, relatively short, and have a small diameter. The number of brachioles ranges from 4 to 8, with an average of about 5–6. Holotype MCZ 631 has several apparently complete brachioles about 16.0 mm long; these are the longest brachioles observed. Several other smaller specimens have brachioles about 14–15 mm long, giving a BR/C length ratio of 1.2 to 1.6+. These brachioles are relatively small (usually about 0.5–0.6 mm wide and high) and taper slowly in a distal direction. They appear to be straight and not spiralled, although 1 poorly preserved specimen shows some curvature and possible spiralling near the distal tips of a few brachioles (Pl. 22, fig. 5). The brachioles have biserial brachiolar plates (BP) about 0.2 mm long and high, as well as a biserial set of small, domed, brachiolar cover plates (BCP) of about the same height. There are approximately 1.6 BCP/BP near the middle of a brachiole. The brachioles appear to be attached to low raised areas on the summit of the calyx either singly or in groups of 2; there may be as many as 4–5 of these groups.

Little is known about the ambulacral system in *Gogia hobbsi;* the mouth is inferred to have been central on the summit, with short ambulacral grooves leading to the areas on which the brachioles are mounted. Holotype MCZ 631 shows a poorly preserved region of small plates that may be the anal pyramid on the upper part of the calyx just below the brachioles (Pl. 22, fig. 2). Little is known about other structures on the calyx summit.

Discussion. *Gogia hobbsi* differs from all other species by its small calyx size, few calyx plates, very short cylindrical holdfast, and its relatively few, small brachioles. Although many of the 97 specimens appear to be mature, none has a calyx longer than 12 mm, making this the smallest species of *Gogia* now known. The small size of these *Gogias* (and many of the other fossils at this locality) probably cannot be ascribed to "dwarfing" because a few large trilobite pygidia (30–40 mm wide), perhaps belonging to *Ogygopsis*(?), are also present. The five attached specimens indicate that *G. hobbsi* probably used its short holdfast to attach to small fossil fragments lying on the sea bottom, and this was probably the normal mode of life.

Stratigraphic and geographic range. Found in reddish silty shales at the top of the Cash Creek Quartzite at locality CL-1. (USGS 5462), central Idaho. Trilobites in these beds indicate an early to middle middle Cambrian age (Palmer *in* Hobbs, Hays, and Ross, 1968: J19), perhaps in the *Albertella*(?) zone (A. R. Palmer, personal communication, 4 September 1969).

Studied specimens. Holotype MCZ 631; figured paratypes MCZ 632–641; unfigured paratypes MCZ 642 (24 specimens); and 62 additional specimens under number MCZ 643. Other small collections of *Gogia hobbsi* are located in the U. S. Geological Survey collections in Denver (USGS locality 5462) and Washington (same locality).

Gogia(?) *radiata* new species
Plate 24, figures 1–7

During the recent reopening of Walcott's famous Burgess Shale Quarry above Field, British Columbia, in 1966, a single, small, poorly preserved calyx apparently belonging to *Gogia* was found. In 1967 in the U. S. National Museum collections in Washington, I discovered a small group of unstudied echinoderms apparently dating from Walcott's original Burgess Shale work. These specimens include another small, poorly preserved calyx similar to the one above, a tiny but poorly preserved complete specimen, several large holdfast fragments, and a partially preserved specimen from the small accessory quarry (designated 35k/10) about 75 feet above Walcott's main quarry (locality 35k). Since this last specimen was preserved as partially weathered and partially buried calcite plates in a hard noncalcareous shale, I prepared it by dissolving away the remaining calcite plates with HCl and then making latex casts of the resulting artificial mold. This last specimen, representing the lower part of a large calyx with a long attached holdfast segment, proved to be well enough preserved and so different from all other known *Gogia* species in its ornamentation and holdfast size that I have decided to describe it as a new species, here named *G.*(?) *radiata* (Pl. 24, fig. 1). Because there is some question of whether this large incomplete specimen lacking appendages and the other smaller, more poorly preserved, complete calyces with appendages represent the same taxon, I have questionably referred this species to *Gogia*. This incomplete prepared specimen (USNM 165399) was selected as holotype, and is described below along with these four additional paratypes (USNM 165400–165402 and GSC 25954).

Specific description. The holotype has a large globular to bowl-shaped incomplete calyx with a very large cylindrical holdfast attached to it. The preserved calyx, apparently representing only the lower 1/2–2/3, is 16 mm long and 18 mm wide. It expands rapidly from the contact with the holdfast and has at least 43 medium-large plates visible on the preserved portion; this indicates that there were between 60–100 calyx plates per side total. Most of the larger plates have prominent raised ridges radiating from their centers or crossing them (Pl. 24, fig. 1). These ridges radiate to the sutured sides of the plates, and there may be as many as 7 ridges per plate. Some of the smaller plates have only a single ridge crossing the center of the plate. Epispires appear to be present over the entire calyx along the plate sutures in the deltoid-shaped areas between these ridges, although they are not prominent near the base. These epispires are slightly to moderately elliptical (L/W = 1.5–5) with slightly raised rims, and on some of the larger plates there may have been as many as nine epispires per plate.

The incomplete holdfast attached to this calyx is long, cylindrical, and very large in diameter (Pl. 24, fig. 1). This holdfast was perhaps as much as 2–5(?) times longer than this originally. As presently preserved, it is 21 mm long and 4.0–4.5 mm in diameter (slightly crushed); the original uncrushed diameter was probably about 3.5–4.0 mm at this proximal end. The holdfast plating consists of irregular oblique rows of larger (1.0–1.3 mm) strongly convex plates with a nearly circular outline alternating with smaller (0.5–0.8 mm) plates of the same shape; this alternation of plate types gives an irregular "whorling" to the holdfast plating (Pl. 24, fig. 1). There are between 5–8 plates per ½ circumference of the holdfast. This holdfast is strongly differentiated from the calyx by an abrupt plating change and a very rapid increase in width. A single rectangular plate much wider than long and ornamented with vertical ridges is exposed at the point where the holdfast is attached to the calyx (Pl. 1, fig. 24); there may have been as many as 4–5 of these plates around the entire circumference.

The upper part of the calyx, oral surface, and appendages are all missing from this specimen. Two tiny plates perhaps representing brachiolar plates (?) are present on the upper left-hand side of this slab about 8–10 mm above the preserved top of the calyx (Pl. 1, fig. 24). Because of this incomplete preservation, this holotype specimen (USNM 165399) cannot be assigned to the genus *Gogia* with complete certainty until more complete, similar specimens are found.

Paratypes USNM 165400 and GSC 25954 are very much alike in appearance and preservation (Pl. 24, figs. 2–3 and 5–6), and very probably belong to *G.*(?) *radiata.* Both specimens are represented by matched positive and negative counterparts. Each has a much smaller calyx about 11–12 mm wide with several relatively short brachioles. These specimens have between 20–32 relatively large calyx plates per side, with strongly raised centers, possible low ridges, and epispires on the plate sutures over the entire calyx. Paratype GSC 25954 has some plates with as many as 7–11 relatively elongate (L/W = 6+) epispires on their margins (Pl. 24, fig. 5). The other paratype USNM 165400 has at least 3–4 brachioles ranging up to about 17 mm long (Pl. 24, figs. 2–3). These brachioles are straight, biserially plated, and have relatively high cover plates with about 2.0 BCP/BP. There is a cylindrical structure about 6.0 mm long and 1.0 mm in diameter lying beside the base of paratype GSC 25954 that might be a partially complete holdfast (Pl. 24, fig. 5); however, there is no trace of plates in this structure and its identity remains obscure. Because definite ridges are not strongly developed on the calyx plates, these 2 smaller specimens (plus the following smallest paratype) could possibly represent a different taxon than the holotype, but this seems unlikely.

The smallest specimen (paratype USNM 165401) has a poorly preserved calyx, holdfast, and several brachioles. The calyx is globular and about 4.0 mm long and 4.5 mm wide, but is too poorly preserved (it is the mold counterpart of a missing covered specimen) to show any features of the calyx plating or epispires. A long cylindrical holdfast with numerous tiny plates approximately 9 mm long and 0.6–1.0 mm in diameter is attached to the calyx; this holdfast may possibly be incomplete distally. Three to five poor brachioles ranging up to 4–5 mm long are attached to the other end of the calyx. This specimen is of primary interest because it shows the likely proportions of the calyx, holdfast, and brachioles in *G.*(?) *radiata* during early ontogeny.

The last specimen, paratype USNM 165402, represents the longest holdfast ever observed in a possible eocrinoid (Pl. 24, fig. 7). This holdfast is at least 85 mm long, 4 mm (crushed) in diameter proximally(?) and 2.5–3.0 mm in diameter distally(?), and may be incomplete at one or both ends. It has numerous small convex calcite plates, usually about 4–5 per ½ circumference of the holdfast, and a possible flared attachment area about 6.0 mm wide at its present distal end. Although somewhat smaller in diameter than the holdfast in holotype USNM 165399, it is very similar in plating and almost certainly belongs to *G.*(?) *radiata.* When scaled to this specimen, the holotype may have had a holdfast more than 100 mm in total length. Two additional specimens in this collection, USNM 165403 (a partially disarticulated holdfast) and USNM 165404 (a deeply buried calyx?) may also belong to this taxon but they are too poorly preserved to warrant further description here.

Discussion. Gogia(?) *radiata* differs from all other species of *Gogia* by having strongly ridged calyx plates and a very long and large cylindrical holdfast. Other differences may eventually become evident when additional complete specimens of this taxon are collected.

Stratigraphic and geographic range. Burgess Shale Member, Stephen Formation, Middle Cambrian (*Bathyuriscus-Elrathina* zone), Walcott's localities 35k/10 and 35k (1966 specimen from zone between 6′7½″–7′3″), Burgess Shale Quarries, near Field, British Columbia, Canada.

Studied specimens. Holotype USNM 165399, paratypes USNM 165400–165402 and GSC 25954; possible additional specimens USNM 165403–4.

Gogia species 1
Plate 25, figures 1–7

Gogia sp. Robison, 1965: 364.

This form, represented by a single nearly complete specimen, USNM 165411 (Pl. 25, fig. 1), was collected by A. R. Palmer from USGS locality 4148 CO (my locality FC-1.) in the Carrara Formation in Echo Canyon, Death Valley, California. I returned to this locality in August, 1968, but could not find any additional complete specimens although I did find a single 4–6-inch bed packed with silicified *Gogia* plates apparently belonging to this form. This complete specimen at the U. S. National Museum was cast after being hardened with Alvar, but unfortunately the cast is not perfect and the specimen is also somewhat incomplete. It has a rounded conical calyx of medium size, relatively few plates, strongly developed epispires only near the summit where the calyx is incomplete, and a calyx L/W ratio of approximately 1.4. The complete holdfast is long and cylindrical. It is approximately 16 mm long and 0.6–1.0 mm wide, giving a holdfast L/W ratio of approximately 20 and HF/C length ratio of approximately 1.2. There are only 3–4 plates per ½ circumference in this holdfast and these plates are small and moderately convex. Only a short section of one brachiole is present. It is apparently straight, relatively large, and at least 17 mm from the calyx. There are approximately 1.6 BCP/BP in this brachiole segment. The separate silicified plates (Pl. 25, figs. 2–7) are large and relatively thick, many have well-developed epispires on the sutured margins (sometimes only on one sutured margin), and show little ornament on their exterior.

This species, which comes from the *Plagiura-Poliella* zone (early middle Cambrian), cannot be specifically identified at present even after casting the one complete specimen. It resembles *G. prolifica* from the same zone in southeastern British Columbia in many respects except that there are few epispires in the lower portion of the calyx. This form might possibly represent a young specimen of *G. longidactylus* except for the relatively few holdfast plates and the much earlier age. When additional specimens are collected, it may turn out to be a new species.

Gogia species 2
Plate 25, figure 8

Eocystites? sp. Walcott, 1917a: 25, pl. 4, fig. 2.

Walcott (1917a: 25) reported and figured a single eocrinoid specimen from the Ptarmigan Formation (*Albertella* zone), near Ross Lake, British Columbia. He could not specifically identify the specimen because of its poor preservation. I restudied this single known specimen (USNM 63712) with the hopes of identifying it and learning more about its morphology. This specimen almost certainly belongs to the genus *Gogia,* but is so incomplete and heavily recrystallized with pyrite that it cannot be identified specifically at the present time.

The specimen consists of an incomplete calyx and at least eight brachioles. No holdfast is preserved. The calyx is ellipsoidal and at least 16 mm long and 8+ mm wide. There is little evidence of original calcite plating because of the extensive replacement with cubic pyrite crystals. The presence, number, and shape of epispires, and their possible restriction to adoral parts of the calyx (like *G. kitchnerensis* n. sp.), cannot be determined from this specimen. The brachioles are at least 7+ mm long, relatively large, and apparently unspiralled. They are also replaced by large pyrite crystals, so that the original calcite plating has been completely lost. No other diagnostic features could be observed on this specimen.

This specimen could belong to either of the known Canadian *Gogia* species (*G. prolifica* from the underlying *Plagiura-Poliella* zone, or *G. kitchnerensis* n. sp., from the higher *Bathyuriscus-Elrathina* zone), or it could represent a new species. However, a complete identification will have to await the collection of additional better-preserved material. At present, it is of interest primarily because of its age; it is the only *Gogia* known for certain to occur in the *Albertella* zone (*G. hobbsi* n. sp. from central Idaho may possibly occur in this zone also).

Acanthocystites Barrande, 1887

Type species, Acanthocystites briareus Barrande, 1887

Generic diagnosis. Eocrinoids with a large, elongate, irregularly plated calyx having modified epispires (sutural pores) and very numerous long brachioles attached to the rim of the summit. Base of calyx and possible attachment appendage (holdfast or stem) unknown. Numerous epispires are modified by having a central thin lid apparently on the plate interior(?) that closes off the center of the epispire while leaving the 2 ends open. Brachioles apparently normal, at least 16 in number, with 1 set of toothed and imbricate cover plates present. Calyx plates irregularly arranged with no evidence of pentameral symmetry; arrangement of ambulacral system and other summit structures unknown. Middle Cambrian, Jince Beds, Czechoslovakia.

Discussion. Only a single specimen of this middle Cambrian eocrinoid genus and species is known to exist. This specimen is preserved as an incomplete natural mold that is missing the base of the calyx and any attachment appendage; the preserved portion of the calyx also has the plates strongly disarticulated. Unfortunately, no latex casts of this specimen were available for study during this project, and the information presented here is therefore based on examination of several excellent photographs and a drawing from a latex cast presented by Ubaghs (1967b: S467, S479). From the arrangement of brachioles, calyx plating, and epispires, *Acanthocystites* seems most closely related to the North American genus *Gogia*, also from the middle Cambrian. It differs from *Gogia* in having distally imbricate brachiolar cover plates with only about 1.0 BCP/BP, and in the unusual partial closure of the epispires; in addition, *Acanthocystites* may not have had a holdfast like that in *Gogia*. Because of these differences, *Acanthocystites* and *Gogia* seem to be quite distinct and separate genera.

I have carefully examined Ubaghs' published photographs and drawing of the epispires in *Acanthocystites*, but I am not certain that I agree with his interpretation of the covered epispires as being "protected externally by a thin sheet of stereom" (1967b: S466). I think that this protective sheet may have been internal and not external, since the specimen appears to be broken, and may show the interior of the opposite wall near the base of the calyx where these structures are best preserved (Ubaghs, 1967b: S479, fig. 307, 1b). Without studying a latex cast of this specimen, however, it is impossible to tell whether this inference is correct or not.

Akadocrinus Prokop, 1962

Type species, Akadocrinus jani Prokop, 1962

Diagnosis. Eocrinoids having an elongate, flat-topped, irregularly multiplated calyx bearing epispires (sutural pores) medially, numerous biserial brachioles branching off the summit in groups, and a long, large-diameter stem having a few irregularly wedge-shaped columnals proximally, a large diameter lumen, and a rounded, irregularly plated, attachment disk at the distal end. Middle Cambrian (*Paradoxides gracilis* zone), Jince Beds, Czechoslovakia.

Akadocrinus jani Prokop
Plate 26

Akadocrinus jani Prokop, 1962: 32–34, pl. 1, figs. 1–2, text-figs. 1, 2a; Ubaghs, 1967b: S480, fig. 307, 2a.

Akadocrinus nuntius Prokop, 1962: 34–35, pls. 2–3, text-fig. 2b; Ubaghs, 1967b: S480, figs. 304, 305, 307, 2b–c.

Prokop (1962: 31–36; English summary pp. 37–39) described two species of *Akadocrinus*, differentiating them on calyx shape (p. 35, fig. 2) and other minor differences in the calyx, stem, and brachioles. Although he did not cast the five figured specimens that are preserved as natural molds, he gave relatively adequate morphologic descriptions except for calling the appendages "arms" and not brachioles. Also, the counterpart figured on his plate 1, figure 2 should not have been designated a paratype because it represents the other half of the holotype specimen. Ubaghs (1967b: S480) redescribed the two species and figured excellent latex casts of several of the type specimens (unfortunately, he did not include the holotype of *A. jani;* casts of this specimen were not available during my study either). He also figured a drawing of the irregularly plated attachment disk at the distal tip of the stem.

Latex casts of the types and a few other specimens from the Caster Collection at the University of Cincinnati and from A. R. Palmer at the State University of New York, Stony Brook, were studied during this project. Some of these are figured in Plate 26, figures 1–6. I have concluded that Prokop's two species, *Akadocrinus jani* and *A. nuntius,* are very likely synonyms, with the former name having page priority. Only about seven or eight specimens of this genus are known to exist at present, making it difficult to assess the amount of morphologic variation present in these species. However, using as a guide the large populations of different *Gogia* species collected from the Rocky Mountains, I feel that the difference shown by these few specimens of *Akadocrinus* could easily be explained by individual variation, ontogeny, and slight preservational differences. By using the difference in shape figured by Prokop (1962: 35, fig. 2), I have concluded that the holotype of *A. nuntius* occurs on the same slab with an apparent specimen of *A. jani* (see Pl. 26, figs. 1–3). Yet these two specimens are almost identical except for a size difference and slightly different modes of crushing.

Little additional information was obtained from the studied latex casts of *A. jani.* A counterpart (Pl. 26, fig. 6) of one of the specimens figured by Ubaghs shows that only a single biserial set of brachiolar cover plates may be present, arranged in a distally imbricating pattern. This would be similar to the pattern of brachiolar cover plates observed in *Kinzercystis,* but different from that found in the many species of *Gogia.* The largest number of brachioles observed in any of the specimens of *A. jani* is 12–14, and all of the brachioles appear to be straight and nonspiralled.

The epispires seem to be confined to the middle portion of the calyx. They are greatly reduced or absent just above the stem facet and also appear to die out just below the edge of the flat summit where the brachioles are attached (Pl. 26, fig. 5).

Only one specimen has the basal attachment disk preserved at the distal end of the stem. This structure may have been cemented down to some object on the sea floor, or if it was spherical instead of disklike, may have been a float type of buoyancy organ. The stem of *A. jani* in general is advanced for a middle Cambrian eocrinoid, showing only a small amount of irregularity (incomplete fusular rings) in the columnal plating (Pl. 26, figs. 2–4). *Akadocrinus* is one of the earliest echinoderms with a well-developed stem.

The location and morphology of the

mouth, anal pyramid, and other structures on the calyx still remain unknown.

Studied specimens. Latex casts E62 (a slab with two specimens), E40 (two counterparts), and E41 (a specimen figured by Barrande and Ubaghs), Caster Collection, University of Cincinnati. Two other latex casts (500–501) were borrowed from A. R. Palmer. All of these casts were made from specimens in the National Museum, Prague, Czechoslovakia.

Eocrinoid(?) Plates from the Poleta Formation Plate 25, figures 9–22

J. Wyatt Durham has reported the occurrence of "eocrinoid plates" possibly belonging to "*Eocystites* (= *Gogia*)" in the upper part of the Poleta Formation in the Westgard Pass area of eastern California (Durham and Caster, 1963: 820; Durham, 1964: 24; 1966: 98). In August, 1967, Durham and I visited the best exposed of these eocrinoid plate localities (WP-1A.), and in 1968 I intensively collected at this (and other) localities for three and a half days. A careful survey of this locality indicates that the 40–80 feet of beds containing eocrinoid plates at WP-1A. are separated from the helicoplacoid-bearing beds (WP-1.) by about 75–100 feet of section containing small archaeocyathid patch reefs but no echinoderms. Eocrinoid and helicoplacoid plates are not usually found in the same beds, and although the entire area is intensely faulted on a small scale, it appears that the eocrinoid plates are lower in the Poleta Formation than the helicoplacoids. Unfortunately, no complete eocrinoids were found at locality WP-1A. in four and a half days of collecting, although the entire area is littered with shale slabs bearing abundant separate plates. The several different types of observed plates are described below.

Description. A few of the smaller polygonal plates have straight margins with no epispires. These plates are slightly convex and have fine rugose ornament on the exterior surface. These plates most likely developed epispires gradually during their growth and changed into the next described type.

Perhaps 25–30 percent of the Poleta eocrinoid(?) plates are relatively large, thin, polygonal, and slightly convex, and have well-developed circular or elliptical epispires on their sutured margins (Pl. 25, figs. 9–11, and 19). These plates are usually smooth on the interior but have coarse pustules or low radiating ridges on the exterior surface. Sometimes the ridges seem to radiate from the plate center to the sutural epispires, perhaps representing earlier filled-in portions of the epispire openings. The epispires penetrate through the entire plate thickness, have a slightly raised rim on the exterior surface, and probably had an original epispire L/W ratio ranging from 1.0+ to 6.0. On some plate margins there are as many as 6 epispires (Pl. 25, fig. 19), although the usual number is between 1–3. These plates are very much like those in many early eocrinoids, especially the middle Cambrian genus *Gogia*.

A third type of plate comprises about 20–25 percent of the Poleta material studied. These plates are characterized by a smooth slanted region occupying between 1/3–2/3 of the plate surface and bearing 2 or more deep elliptical depressions (Pl. 25, figs. 14 and 17). The remainder of the plate usually has coarse granular ornament and normally developed epispires. These depressions are the same size or slightly larger than the sutural epispires, but they do not penetrate to the interior and are arranged along the center of this smooth area. A few plates have been found having intersecting smooth areas with depressions on two of the sutured margins (Pl. 25, fig. 18). These smooth regions appear to represent half ambulacral areas as discussed in the following sections.

A fourth very characteristic type of plate makes up about 15 percent of the Poleta material studied. These plates have a "double" smooth region bearing two rows of depressions running over their surface (Pl. 25, figs. 20, 21 and 22). Outside this area, the plate has normal rugose ornament and sutured margins sometimes bearing epispires (but never at the edges of the smooth areas). Both lateral margins of the smooth area usually consist of medium-sized ridges, and the centers may be either slightly depressed or raised. The depressions do not penetrate to the plate interior and appear to be alternately arranged in a biserial pattern (Pl. 25, fig. 20). They do not seem to be connected with the center of the smooth area, but often show a gradual increase in size towards one end of the plate.

These smooth areas with depressions described above appear to represent ambulacral areas extending over the surface of the calyx plates. The entire width of the ambulacrum may either lie entirely on one plate (type four), or be shared by two plates across a sutured margin (type three). It is not known how long these ambulacral areas were in the original complete specimens, whether they were covered with secondary flooring plates or cover plates (no sutures for these were seen), or whether they led to groupings of brachioles, as in *Gogia* and other eocrinoids, or to other structures. The depressions on these ambulacral areas could be either sockets for cover plates (as in many rhombiferan cystoids and blastoids), or locations for mounting the tube feet or their ampullae. However, they do not strongly resemble either of these structures in other early echinoderms, and their exact function is therefore unknown. Plates with ambulacral structures like these are not known at present in *Gogia* or other early eocrinoids.

A fifth type of plate has an oblique thickened edge with deeply embayed epispire-like pores on it (Pl. 25, figs. 12 and 13). These pores are best developed on the interior of the plate, but seem to penetrate to the exterior surface.

A sixth type of small pentagonal plate (rare) has two large knobs at one edge of the interior(?) surface. However, the exterior surface of this type of plate has not been observed. Several other small plates, including a few that resemble arm ossicles, have also been observed but are not common. No plates resembling biserial brachiolar plates were found.

Discussion. Because this Poleta material is known only from separate plates, a conclusive assignment to the eocrinoids cannot be made at the present time. Some of the simple plates with epispires are very similar to those found in other early and middle Cambrian eocrinoids, but others are quite different from any of the known eocrinoids. Since several other echinoderms with epispires are also known from the early and middle Cambrian (edrioasteroids, carpoids, *Cigaria*, etc.), the presence of epispires cannot be used as an exclusive diagnostic character for eocrinoids. In addition, no definite brachiolar plates were observed in any of the material studied. Indeed, I am not even certain that only one echinoderm taxon is present in this Poleta plate material, but since contrary information is lacking, this seems to be a reasonable assumption. This taxon probably represents a new genus and species no matter where it is assigned, but at present it does not seem warranted to name it on the basis of the incomplete material now known. More complete specimens of this Poleta echinoderm will be necessary before it can be assigned to any group with certainty.

Stratigraphic and geographic range. Basal 40–80 feet of brownish shale and thin-bedded limestones in upper Poleta Formation, middle Lower Cambrian (*Holmia-Nevadella* zone), locality WP-1A., Westgard Pass, eastcentral California.

Family LICHENOIDIDAE Jaekel, 1918

Diagnosis. Eocrinoids with a reduced, highly organized calyx having three major rows of plates with relatively good pentameral symmetry, sutural epispires present between all of the plate sets, an ambulacral system developed as five simple covered food grooves extending down over the two adoral sets of calyx plates to long erect brachioles, and no stem or holdfast at the aboral end of the calyx.

Genus *Lichenoides* Barrande, 1846

Type species, Lichenoides priscus Barrande, 1846

Diagnosis. Calyx highly organized, consisting of only 3 rows of large plates showing good pentameral symmetry. Five deltoid-shaped radials(?) surround central mouth on the upper part of the calyx; 5 large laterals(?) alternate with these and make up the middle of the calyx; 5 large unequal basals (plus several small accessory plates at the aboral pole) make up the base of the calyx. Most of basals and lower portions of laterals(?) strongly inflated (either solid calcite or possibly gas-filled). Ambulacral system consists of 5 covered food grooves from central mouth leading to groups of 1–2 brachioles attached to the radial(?) and lateral(?) plates. Food grooves show alternate branching to brachiole facets. Brachioles long, unspiralled, and normally plated except right at the base where only a single plate may be present; 1 set of imbricate brachiolar cover plates protect food groove. Very elongate sutural epispires strongly developed between all calyx plates, with longest pores apparently on interradial(?) sutures. Location of anal pyramid unknown. No holdfast or stem present. Middle Cambrian, Czechoslovakia.

Discussion. Only the type species of this genus is known. In many of its features, *Lichenoides* seems to be a specialized eocrinoid. The strongly reduced plating, development of pentameral symmetry, food grooves extending down over the calyx to the erect brachioles, and absence of a stem or holdfast indicate that *Lichenoides* has diverged considerably from other genera belonging in the same order. It is the earliest "pelmatozoan" echinoderm to show a high degree of pentameral symmetry in its calyx plate organization.

Lichenoides priscus Barrande
Plate 27, figures 1–6

Discussion. Lichenoides priscus was redescribed in detail by Ubaghs (1953a); he has more recently given a short redescription (Ubaghs, 1967b: S481) and has presented a new reconstruction based on several illustrated specimens. I examined approximately 24 latex casts (Caster Collection) of specimens originally collected and described by Barrande. Several of the better preserved specimens in this group are figured on Plate 27. My main interest was in the arrangement of the ambulacral system and brachioles, and in attempting to locate the position of the anal pyramid.

The five ambulacral food grooves extend from the central mouth on the summit down over approximately one-third of the calyx to brachiole facets on the radial(?) and lateral(?) plates. One specimen (BC 141B; Pl. 27, fig. 5) shows a complete, but unfortunately poorly preserved summit view of the calyx; in this specimen, the ambulacral grooves show a standard "2–1–2" pattern around the mouth, and both the mouth and the adoral portions of the ambulacral grooves are protected by tiny cover plates. Although the "CD" interradius can be identified in this specimen, it is not fully exposed and no anal pyramid was observed here or in any of the other studied specimens. These ambulacral grooves lead directly to a single brachiole facet mounted on the center of each radial(?), but then each sends off a lateral branch to the left (looking aborally) that crosses the oblique radial(?)-lateral(?) suture and leads to one or two additional brachioles mounted on the center of each lateral(?). If two facets are present here, the lower one is usually on the right (looking aborally), the implication possibly being that a heterotomous branching pattern (see Ubaghs, 1967b: S470) was present in these food grooves.

This arrangement of the ambulacral system suggests that the present designation of calyx plates may not be correct. The two adoral sets of plates, now designated as radials and laterals (Ubaghs, 1967b: S481), may perhaps represent deltoid (or oral) plates and radials. Since the ambulacral grooves show a zig-zag pattern and extend to the centers of two sets of alternating plates in *Lichenoides*, it is difficult in this case to give a conclusive definition of the terms "radial" and "interradial" (see p. 11). Since radials are by definition "radial" in position, and laterals and deltoids usually interradial, there is a definite problem in applying these terms to the unusual plating arrangement found in *Lichenoides*. The adoralmost set of plates (either five or six[?] in number) appears to abut the oral opening (Ubaghs, 1967b: S467, fig. 301, 1c), a feature not known to occur in the radial plates of other blastozoans. Also, radials in other highly organized echinoderms are usually in the center of the calyx and are often the largest plates, and both of these conditions are met by the second set of plates (previously called laterals) in *Lichenoides*. Although this alternate system of plate designation cannot be proven at present, it may perhaps help to explain some of the plating problems mentioned above.

Brachioles were examined in several specimens of *Lichenoides* (Pl. 28, figs. 2, 4, and 6). These brachioles seem to have normal alternate biserial plating over most of their length, but near the attached proximal end the plating seems to change rapidly to opposite biserial (see Pl. 28, fig. 4) and perhaps for the extreme basal plate to uniserial. The facets on the calyx plates are symmetrical, without one side being deeper than the other (see Text-fig. 4). These brachioles have a small adoral food groove protected by small distally imbricate cover plates, with about 1.0 BCP/BP. The brachioles in *Lichenoides* appear to be relatively long, at least twice the calyx length in a few specimens.

Stratigraphic and geographic range. Jince Beds, upper Middle Cambrian, several localities in Czechoslovakia.

Studied specimens. Latex casts E 11, E 12, E 17, E 21, E 25, E 26, E 27, E 66, E 70A, and BC 141A, all from the Caster Collection, University of Cincinnati. Many of the original specimens (natural molds) from which these latex casts were made were studied by Barrande (1887) and are in the National Museum, Prague.

Family RHOPALOCYSTIDAE Ubaghs, 1967

Diagnosis. Eocrinoids with a conical calyx, relatively numerous thick calyx plates showing fairly good pentameral symmetry and having epispires on many of the sutures, a rounded oral surface having 5 ambulacra with single plates bearing long biserial brachioles, and a long slowly tapering aboral attachment stem. Early Ordovician.

Genus *Rhopalocystis* Ubaghs, 1963

Type species, Rhopalocystis destombesi Ubaghs, 1963

Diagnosis. Calyx conical to club-shaped, composed of numerous thick adjacent plates showing fairly good pentameral symmetry and bearing circular or slightly elliptical epispires on their margins. Single very thick basal plate at base of calyx. Domed oral surface consists of central mouth, lateral anal pyramid, and 5 relatively short ambulacra with single plates bearing long biserial brachioles. Long, slowly tapering stem with 1-piece columnals attached to base of calyx. Early Ordovician (Upper Tremadocian), Morocco.

Discussion. The original description of *Rhopalocystis destombesi* by Ubaghs (1963: 26–39) is very complete and excellently done, and little can be added here. I examined latex casts from Ubaghs of three large slabs of specimens, many of which are jumbled together and partially disaggregated. There is some evidence of partial alignment by current action, but this is not strongly developed in most places on these slabs. The occurrence seems to be autochthonous and probably represents a natural death assemblage of a large colony or "garden." Some specimens still have a few of the brachioles and the stem attached, but when present these have usually become partially disarticulated. This indicates that these specimens were not buried almost instantly like many of the *Gogias* studied (see p. 80), but lay on the bottom for a time before being buried. The brachioles are normal and appear to have one (or perhaps two) sets of brachiolar cover plates (BCP) over the food groove, with about 1.3 BCP/BP. The adoral thinner-plated and enlarged portion of the conical calyx is often crushed, apparently by compaction during diagenesis.

Rhopalocystis is the latest eocrinoid in the fossil record (early Ordovician) to have epispires present. A few slightly elongate epispires were found inside plate margins, and these are somewhat reminiscent of diploporan cystoids. The presence of epispires, a partially organized calyx with relatively numerous plates but fairly good pentameral symmetry, and the presence of five ambulacra with single brachiole mounting plates and normal brachioles puts *Rhopalocystis* in the same order as more primitive genera such as *Akadocrinus* and *Gogia*. *Rhopalocystis* is probably most closely related to *Akadocrinus* from the middle Cambrian, and differs from this genus by having better pentameral symmetry with more standardized plating, more highly developed ambulacra, and perhaps a better organized stem.

Family INDETERMINATE

"Archaeocyathids" from Poland

A. R. Palmer of the State University of New York at Stony Brook brought to my attention several specimens of presumed archaeocyathids figured by Orlowski (1959, 1964) from the middle Cambrian of the Holy Cross Mountains, Poland. Palmer suspected that these were echinoderm calyces and not archaeocyathid fragments (personal communication, 24 October 1969), and sent me several silicone replicas of latex casts of these fossils from his personal collection. The specimens of "*Syringocyathus* sp." as well as "*Syringosnema* sp." and "*Ajacicyathus* sp." (Orlowski, 1959: pl. 1, pl. 2, figs. 1–5; 1964: pl. 11, figs. 7–8 and 9–10) are almost certainly echinoderms, although they are incomplete and not especially well preserved. Specimens of the first two genera, studied from Palmer's casts 770 and 774, are portions of large incomplete calyces with numerous adjacent plates bearing nearly round epispires. The calyx plates and epispires are very similar to those on the oral surface of *Kinzercystis* (see Text-fig. 22) or those in the calyx of several *Gogia* species from North America. However, no other diagnostic features are present in these casts, and they could also represent edrioasteroids or some other epispire-bearing echinoderm. The specimens of *Ajacicyathus* sp. (Palmer casts 771 and 773) are small, apparently complete specimens of a flattened, plated echinoderm bearing some resemblance to specimens of the recently described class Ctenocystoidea (Robison and Sprinkle, 1969) or other carpoid classes. Unfortunately, it was not possible to study this material in more detail or prepare illustrations because of preservation problems and lack of time.

UNNAMED ORDER #2

Diagnosis. Globular eocrinoids with adjacent calyx plates lacking epispires, a columnal-bearing stem (or in one case a multiplated holdfast), and normal brachioles mounted separately on ambulacral or modified calyx plates on the calyx summit. Middle Cambrian—middle Ordovician.

Discussion. This provisional order containing eocrinoids that have a normal calyx and brachioles, but no epispires, may turn out to be polyphyletic when the included genera become known in more detail. Members include the genera *Pareocrinus*, *Eustypocystis* n. gen., *Nolichuckia* n. gen., *Ascocystites*, and possibly *Cryptocrinites*, *Bockia*, and *Macrocystella*. Other poorly known genera may also belong here.

Family INDETERMINATE

Genus *Pareocrinus* Yakovlev, 1956

Type species, Pareocrinus ljubzovi Yakovlev, 1956

Diagnosis. Incompletely known eocrinoids having an elongate globular calyx with 5–6 rows of large polygonal plates lacking epispires, a long columnal-bearing stem, and numerous brachioles attached around the edge of the summit. The anal opening may lie at the edge of the summit outside the ring of brachioles. Late middle Cambrian or early late Cambrian, Siberia, U.S.S.R.

Discussion. This genus, based on only a single complete specimen, was originally described by Yakovlev (1956: 726–727) and recently reviewed by Ubaghs (1967b: S493). No material was available for study, so no additional information can be added here. Several features of the morphology, such as the brachiole plating, location of the mouth and anus, and presence of ambulacra, remain unknown. *Pareocrinus* seems most closely related to *Eustypocystis*, *Nolichuckia*, *Cryptocrinites*, and possibly *Akadocrinus*, but differs from these genera in the arrangement of relatively few calyx plates in definite rows, the lack of epispires, the well-developed stem, and the way in which the brachioles are attached to the calyx.

Genus *Eustypocystis* new genus

Type species, Eustypocystis minor new species

Diagnosis. Small eocrinoids with a cylindrical calyx, few brachioles, a true stem, and no epispires. The small calyx has an elongate cylindrical shape with rounded ends, and is composed of 60–100 small, thin, irregularly arranged, polygonal plates lacking ornament. Epispires (sutural pores) appear to be completely absent from all parts of the calyx. The mouth is centrally located on the summit and a small anal pyramid is apparently present about 2/5 of the way down the side of the calyx. At least 3 (and possibly 5) biserial brachioles are attached together on the summit around the mouth. They are relatively short and apparently have tiny imbricate cover plates. A short tapering stem composed of 1-piece disklike columnals with a round lumen occupying 1/4–1/2 the diameter is attached to the base of the calyx. No terminal stem attachment known. Secret Canyon Formation, upper Middle Cambrian (*Bolaspidella* zone), central Nevada.

Etymology. The name is derived from *eu* (Gr.)—early, primitive, and *stypos* (Gr.)—stem, referring to the fact that this genus now represents the earliest stemmed eochinoderm known from North America.

Discussion. Eustypocystis is the earliest eocrinoid in North America to lose the respiratory epispires and develop a true stem. It is similar to *Gogia, Acanthocystites, Akadocrinus, Pareocrinus, Trachelocrinus, Nolichuckia, Bockia,* and *Cryptocrinites. Eustypocystis* differs from the first three genera (all middle Cambrian) in completely lacking respiratory epispires, while it differs from the following three genera (all late Cambrian?) in having a much smaller calyx with numerous calyx plates, and relatively few small brachioles without branches. It differs from the middle Ordovician genus *Cryptocrinites* in its calyx size, shape, and plating, and possibly in its appendages. *Eustypocystis* closely resembles the early-middle Ordovician genus *Bockia* in its calyx shape, plating, and anal pyramid location, but *Bockia* is several times larger, has ridged plates and a large projection on the summit probably for the attachment of all the food-gathering appendages together, and occurs much later in time. *Eustypocystis* could have been ancestral to several late Cambrian eocrinoids such as *Pareocrinus* and perhaps *Trachelocrinus* if certain modifications in the calyx plating and food-gathering appendages had occurred.

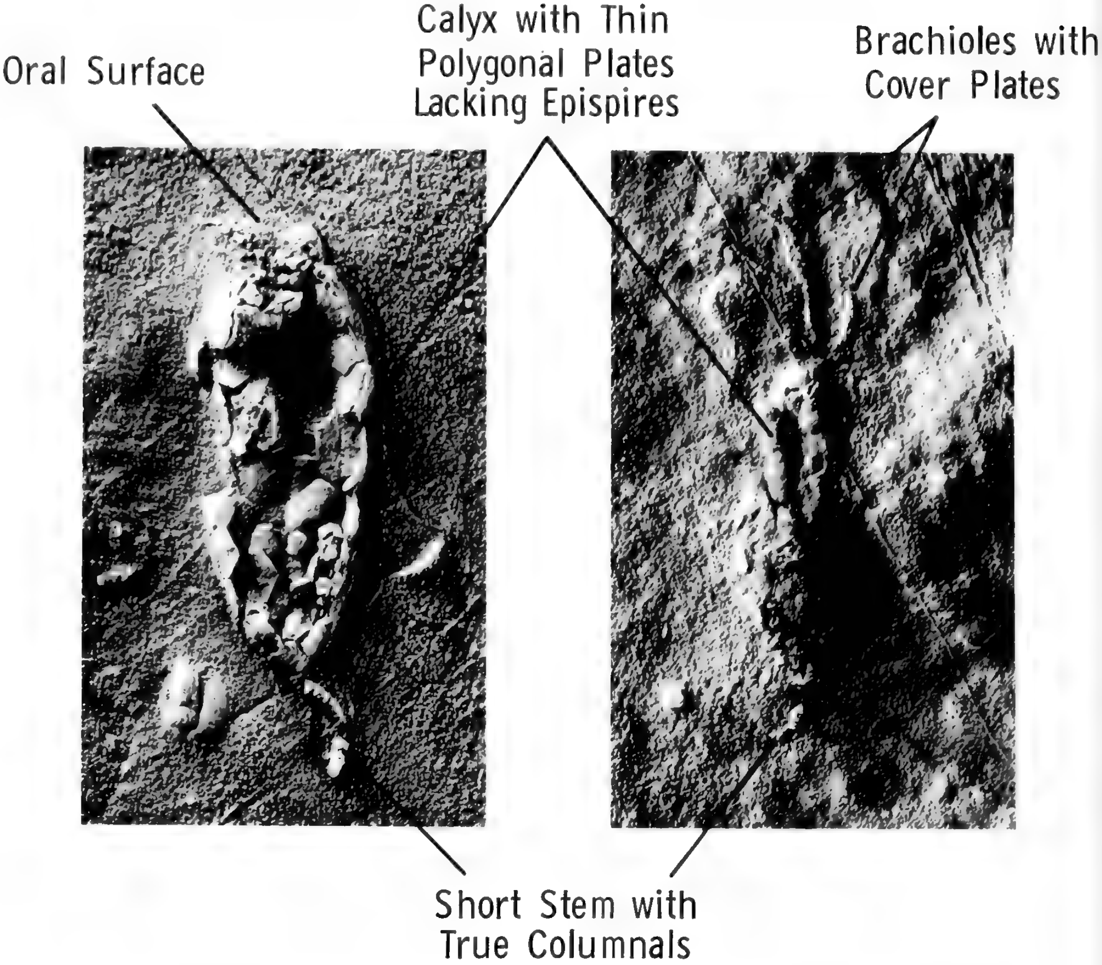
Eustypocystis minor new species
Plate 28; Text-figure 28

During the late 1930's, three specimens of this taxon were collected by Thomas Nolan, Joshua Bridge, and G. Arthur Cooper at two localities in Secret Canyon, near Eureka, central Nevada. These specimens were sent to the U. S. National Museum and were apparently prepared by Edwin Kirk during the 1940's, but never described. In 1967 I discovered these specimens in the USNM collections and borrowed them for study. In July, 1968, I visited the Eureka area in central Nevada and, after considerable difficulty, managed to relocate the Secret Canyon localities where these original specimens had been found. A moderate-sized collection of echinoderms (also including an undescribed carpoid-like form) was assembled from these localities and from two additional nearby localities in the same formation. In all, 17 specimens of *Eustypocystis minor* were collected during this field work, of which nine are well enough preserved to be described here in addition to the three USNM specimens (Pl. 28, figs. 1–11). Specimen MCZ 719 is here selected as holotype along with paratypes MCZ 720–727 and USNM 165423–24.

Specific description. The calyx in *Eustypocystis* is very small and has an elongate cylindrical or barrel shape with rounded ends. The collected specimens range from 3.5 mm long and 2.5 mm wide to about 13.0 mm long and 6.0 mm wide. Many of the specimens are crushed, which has increased the apparent width (see Text-fig. 28A), and in addition some have been badly disarticulated, probably by compaction and burrowing activity. There are between 25–50 small polygonal plates on each side of the calyx, the number probably increasing during ontogeny. These plates are relatively thin, usually 5–7-sided, somewhat larger toward the center of the calyx, and are smooth on the exterior (and interior) without any trace of ornament or growth lines. Epispires appear to be completely absent from all parts of the calyx in *Eustypocystis*. Respiration apparently took place across the entire surface of the thin calyx plates in these small echinoderms, and no specialized calyx respiratory structures were needed.

The summit of the calyx with the mouth and food-gathering appendages is not shown very well by any of the studied specimens. At least three brachiole-like appendages are attached close together near the center of the summit (Text-fig. 28B). These appendages are about 6.5–7.0 mm long and 0.25–0.40 mm high, and 1 specimen (Pl. 28, fig. 1) shows that they have biserial plating near their attachment point and probably along their entire length. A biserial set of tiny cover plates, apparently overlapping distally, appears to cover the food groove on the adoral side (Text-fig. 28B). Because they are small, biserially plated, and unbranched, these appendages are probably true brachioles. These brachioles appear to be attached together in a group perhaps to a single raised area near the center of the summit (Pl. 28, figs. 1 and 6). The mouth was probably located in the center of this grouping of brachioles. At least 1 specimen (Pl. 28, fig. 4) shows what appears to be a small anal pyramid made up of tiny wedge-shaped plates about 2/5 of the way down the side of the calyx from the summit.

The attachment appendage in *Eustypocystis* is a short true stem with well-developed columnals. In the larger specimens, this stem is about 4.0 mm long (incomplete), and tapers from about 0.5 mm proximally to 0.25 mm distally. The rounded, 1-piece columnals are thin (0.1 mm or less) with crenulae apparently ab-



Text-figure 28. Morphology of *Eustypocystis minor* n. gen., n. sp. Holotype MCZ 719 (left) and paratype MCZ 722 (right) showing elongate cylindrical calyx with thin plates lacking epispires, small columnal-bearing stem, and at least three apparent brachioles with biserial cover plates.

sent, and the central lumen occupies 1/4–1/2 of the columnal diameter. Some slab surfaces in the Secret Canyon Formation are covered by scattered separate columnals as much as 1.5–2.0 mm in diameter with a lumen occupying 2/3 of this diameter, but no columnals this large were found attached to any of the complete specimens. All of the stems appear to be incomplete, and no attachment structures were observed at the distal end of any of the stems. One small specimen (Pl. 28, fig. 4) is lying on top of a large unidentified echinoderm, but does not appear to be attached to this specimen. This occurrence now represents the earliest known stem-bearing echinoderm in North America, and it marks the first appearance of echinoderm columnals as calcarenite debris.

Etymology. The specific name refers to the characteristic small size of these eocrinoids.

Stratigraphic and geographic range. Most of the specimens come from the upper part of the Secret Canyon Formation (a few may possibly be from the base of the overlying Hamburg Dolomite), upper Middle Cambrian (*Bolaspidella* zone), localities SC-1., SC-3., SC-4., and SC-4A.; and USGS localities 834 (= SC-4A?) and 835 (= SC-4.?), Eureka District, central Nevada.

Studied specimens. Holotype MCZ 719; figured paratypes MCZ 720–27 and USNM 165423–4 (three specimens); plus eight poorly preserved specimens filed under MCZ 728.

Genus *Nolichuckia* new genus

Type species, Nolichuckia casteri new species

Diagnosis. Eocrinoids(?) having a large, thin-plated, globular calyx lacking epispires, several very large, long, biserially plated brachioles(?) attached separately(?) to the summit, and a relatively short, thin, irregularly plated attachment holdfast. The calyx consists of numerous, large, irregularly arranged, thin, polygonal plates lacking epispires. Four to six very large and long, biserially plated brachioles(?) are present, branching off spoutlike projections on the calyx summit. Two types of cover plates are present over most of the brachiole length with 1 set of cover plates per brachiolar plate. Wedge-shaped gaps for ligaments (or muscles) are present near the base of each brachiole. Attachment holdfast relatively short and thin, irregularly plated, with a relatively small lumen; distal attachment tip unknown. Calyx food grooves, mouth, anal opening, and other structures unknown. Nolichucky Formation, lower Upper Cambrian (*Cedaria* zone), Virginia and Tennessee.

Etymology. The genus is named after the Upper Cambrian Nolichucky Formation where its disarticulated plates are usually the most abundant fossils.

Discussion. The taxonomic position of *Nolichuckia* depends primarily on whether its large appendages are interpreted as arms (implying crinozan affinities) or brachioles (implying blastozoan affinities). None of the other calyx and holdfast morphologic features of *Nolichuckia* are diagnostic of either group, although the age might suggest eocrinoid affinities. After a study of the appendages in the holotype, I have concluded that they are most likely brachioles, and that *Nolichuckia* is a true blastozoan belonging in the eocrinoids. The fixed biserial plating, lack of branching, arrangement of cover plates, and lack of canals in these appendages all support an interpretation as brachioles. No crinoid with biserial arms is known until at least the middle Ordovician. However, these appendages are very large (see Text-fig. 29), about two to three times the size of most other brachioles, and the food groove is large enough to have enclosed an extension of the water vascular system if one had been present. Nevertheless, at least a few other blastozoan echinoderms, such as the Ordovician bottom-living rhombiferan cystoid *Pleurocystites*, have normal brachioles as large as those in *Nolichuckia*. There is also no trace of a water vascular system in these appendages. If this interpretation is correct, then *Nolichuckia* is an early late Cambrian eocrinoid and represents the last known member of this group to have a multiplated holdfast.

Nolichuckia is only the second eocrinoid known from the late Cambrian of North America. It seems to be most closely related to the new genus *Eustypocystis* from the late middle Cambrian of Nevada, and *Pareocrinus* (Yakovlev, 1956) from the middle(?) or late Cambrian of Siberia. *Nolichuckia* resembles these other genera in having a globular calyx with thin plates lacking epispires, but differs from them in having an irregularly plated holdfast instead of a columnal-bearing stem, a large calyx with numerous irregular plates, and a few very large brachioles attached separately(?) to the summit.

Scattered *Nolichuckia* plates are very common in the Nolichucky Formation of southwestern Virginia and northeastern Tennessee and at least one has been figured as a "cystid or crinoid plate" (Butts, 1941: 12). However, even partially complete fragments seem to be quite rare; only two incomplete holdfast segments as well as a disarticulated holdfast and lower calyx are known in addition to the partially complete holotype. The very thin calyx plates of *Nolichuckia* probably were not strongly sutured together, and disarticulated rapidly after death. The fine grained matrix implies relatively quiet water and slow sedimentation, which would allow the dead echinoderms to become disaggregated before being buried.

Nolichuckia casteri new species
Plate 29; Text-figures 5B and 29

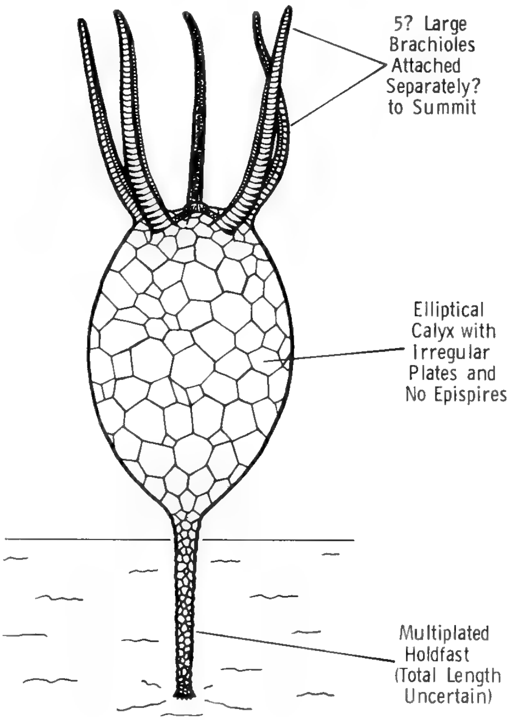
"Cystid or crinoid plate," Butts, 1941: pl. 66, fig. 27.

The holotype specimen, MCZ 616, was apparently collected by P. E. Raymond of Harvard University about 1925, and prepared for study by Kenneth E. Caster of the University of Cincinnati in the early 1960's. A short holdfast segment, a disarticulated lower calyx and holdfast, and several small collections of separate plates collected in 1967 and 1968 were also studied.

Specific description. The holotype and only known relatively complete specimen (Pl. 29, fig. 1) is spread out on a large slab of olive green, hard shale along with several other scattered plates. It is about 2/3 complete as now preserved, and has been extensively excavated to uncover the appendages. The calyx is only about half complete, with most of the summit and left side weathered off. It has a globular to ellipsoidal shape and is very large in size, approximately 50–52 mm long and at least 28 mm wide. Although the calyx appears to have been crushed flat during post-burial compaction, it originally may also have been somewhat flattened or lens-shaped, as in some paracrinoids. Most of the calyx plates are somewhat disarticulated and are slightly weathered; 62+ plates are now exposed on this incomplete side of the calyx. These plates are relatively large (4–5 mm in size), mostly 5–8-sided, and irregularly arranged with no indication of plate "columns" as in *Trachelocrinus* or *Pareocrinus*. The plates are very thin over most of the calyx, approximately .01–.02 mm thick, and there are no epispires (sutural pores) present between the plates anywhere on the preserved portion of this specimen. A few of the calyx plates near the base are only slightly weathered, and show traces of pustular ornament; however, this ornament may have been confined to this part of the calyx. The calyx-to-holdfast transition appears to be relatively abrupt (Pl. 29, fig. 3), with few if any intermediate-sized plates present. Five to six plates are apparently present around the base of the calyx where the holdfast is attached. None of the preserved calyx plates in this holotype specimen show any trace of growth lines. However, many of the separate plates in the Nolichucky, preserved as natural external or internal molds, show prominent growth "bands" (Pl. 29, figs. 5–6), which may have been seasonal in nature. The primary growth in these separate plates appears to have been holoperipheral in nature.

The curved holdfast in holotype MCZ 616 is approximately 18–19 mm long and tapers from about 2.5 mm in diameter at the proximal end down to less than 1.0 mm near the apparent distal tip (Pl. 29, fig. 3). It is made up of numerous, very small (0.4–0.6 mm), irregularly arranged, slightly convex plates. Near the proximal end of the holdfast there are 4–5 plates per ½ circumference. The distal portion of this holdfast is too poorly preserved to tell anything about the plating arrangement (Pl. 29, fig. 3); it is also possible that the holdfast is incomplete as preserved and originally was somewhat longer. This holdfast probably had an expandable distal tip similar to that in *Gogia*, where there are circlets of very tiny plates for attachment to objects on the sea bottom. The isolated holdfast segments (MCZ 617–618) are similar to the preserved holdfast on the holotype. In addition, MCZ 617 shows that the holdfast plates are relatively thick and that the central cavity or lumen of the holdfast represents less than 1/3 of the total holdfast diameter (Pl. 29, fig. 4).

The very large brachioles(?) of *Nolichuckia casteri* are one of the most characteristic features of this taxon. They are preserved only on the holotype specimen where at least 4 and possibly as many as 6 brachioles are present. The exact number is uncertain because these brachioles are somewhat broken, mostly unattached to the calyx, and at least 1 emerges from the edge of the slab where it may possibly have been attached to another specimen. Five brachioles are shown on the reconstruction of *Nolichuckia casteri* (Text-fig. 29), but this represents only an educated guess about the probable original number. These brachioles are biserially plated, unbranched, and relatively massive in construction (Pl. 29, figs. 7–9). The largest is 34 mm long and about 3.0 mm high by 1.8 mm wide near the base. These brachioles slowly taper distally to a blunt tip. The larger series of brachiolar plates (BP) have a biserial arrangement along the entire length, form an elongate heart-shaped cross section for the brachiole, and bear the food groove adorally (see Text-fig. 5B). Each of these brachiolar plates is about 0.55 mm long, 1.9 mm high, and 0.9 mm wide. There are prominent wedge-shaped gaps aborally between the 10–12 most proximal brachiolar plates (Pl. 29, fig. 7). These probably served for the attachment of ligaments (or muscles) for flexing this lower portion of the brachioles, as in many crinoids and some other eocrinoids (see *Ascocystites* p. 119). The adoral food groove in these brachioles is protected by a biserial series of domed brachiolar cover plates (BCP). Near the proximal end, only 1 type of rectangular cover plate is present, but after about 10 brachiolar plates, the cover plates become differentiated into 2 distinct types, a smaller triangular plate with a wide base, and a larger elongate-pentagonal plate, which intermeshes with the larger cover plates from the other side of the brachiole (see Pl. 29, fig. 8, and Text-fig. 5B). These larger cover plates are approximately 1.1 mm high and 0.40–0.55 mm long. Along the entire distal portion of the brachiole, there is 1 set of these 2 differentiated cover plates for each brachiolar plate; near the proximal end where only 1 type of cover plate is present, the ratio is about 1.4 BCP/BP. These high domed cover plates enclose a relatively large food groove; however, no canals were observed in the bottom of this food groove or in the large brachiolar plates themselves.



Text-figure 29. Reconstruction of *Nolichuckia casteri*, n. gen., n. sp. based on the holotype specimen. Relative proportions of calyx, attachment of large brachioles on summit, and total length of holdfast are all uncertain.

One of these brachioles appears to be attached at its base to a "spoutlike" projection of the calyx. Three to four very thick calyx plates extend out to form a projecting platform on which the brachiole is mounted. Unfortunately, this projection is isolated from the rest of the calyx, and it is now impossible to tell whether each brachiole was attached separately, or all were attached together to one large projection. The plates are probably thicker here than elsewhere in the calyx to help support the weight of the large brachiole. Specialized plated ambulacra for mounting these brachioles were apparently absent. The location and structure of calyx food grooves, mouth and anus, and other summit structures are all unknown at the present time.

Etymology. The species is named for Kenneth E. Caster of the University of Cincinnati, who prepared the holotype specimen and allowed me to study it during this project. He also aided me considerably during other portions of my work on American and European eocrinoids.

Stratigraphic and geographic range. Nolichucky Formation, lower Upper Cambrian (*Cedaria* zone), my localities HL-1. (MCZ 618–619) and TH-1., Walcott's locality 103a (USNM 165410), all in southwestern Virginia or northeastern Tennessee, and a locality listed as "Nolichucky Fm., 1 mi NE of Bristol, SW Va." (holotype MCZ 616 and MCZ 617). *Nolichuckia* may also occur in the Upper Cambrian of northwestern Georgia and northern Alabama.

Studied specimens. Holotype MCZ 616, figured paratypes MCZ 617–619 and USNM 165410. Other fragmentary material is present in USNM collection 103a and MCZ 630a–b.

Family ASCOCYSTITIDAE Ubaghs, 1967

Diagnosis. Eocrinoids with a large spindle-shaped calyx bearing strong vertical ridges, numerous calyx plates not arranged in circlets, a flat, tegmenlike, oral surface with 5 ambulacra bearing numerous brachioles ringing the oral surface, and a columnal-bearing stem. Middle Ordovician.

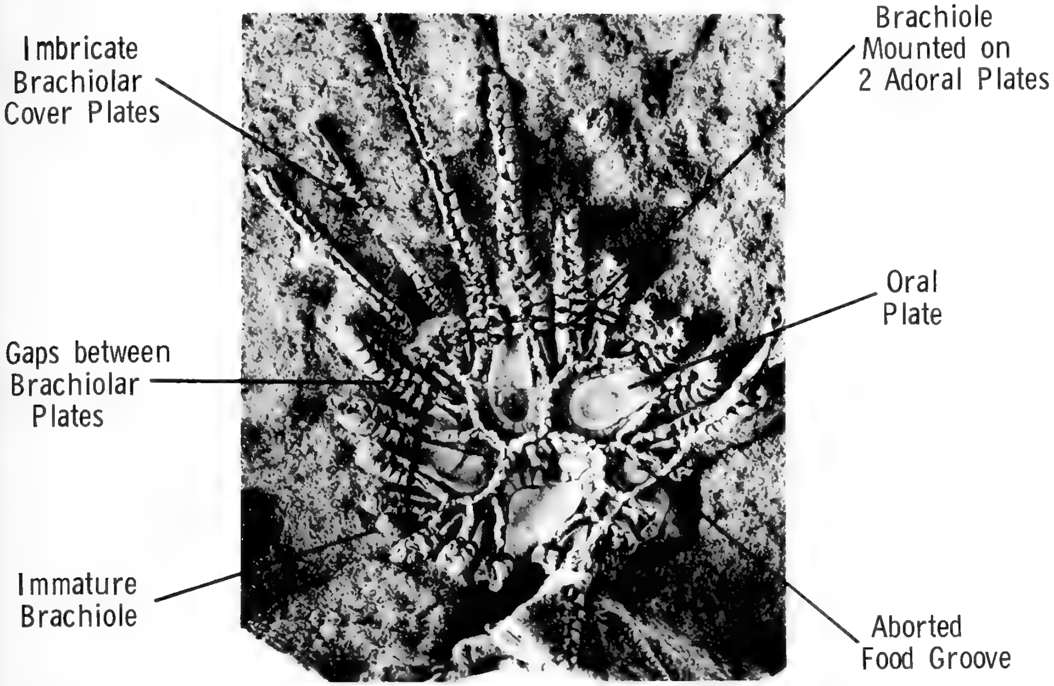
Genus *Ascocystites* Barrande, 1887

Type species, Ascocystites drabowensis Barrande, 1887

Diagnosis. Calyx large and elongate, made up of numerous irregularly arranged large and small ridged calyx plates. Six large vertical ridges run the length of the calyx. No epispires present between calyx plates, but external ridges developed as hollow grooves on interior. Stem long and well developed with some alternation of columnals. Oral surfaces flattened and tegmen-like, bearing the central mouth, ambulacral system with 20–30 brachioles, and lozenge-shaped oral and adoral plates. Five ambulacra with two sets of cover plates present, showing strong "2–1–2" pattern; side food grooves to brachioles change from exotomous to heterotomous branching pattern during ontogeny. Each brachiole mounted on 2 adoral plates (or 1 adoral and 1 oral) at edge of oral surface; earliest formed brachioles largest. Brachioles long, biserially plated with one set of large distally overlapping cover plates; gaps present between proximal brachiolar plates for muscle (or ligament) insertions. Anus unknown, on side of calyx; hydropore possibly present in "CD" interradius near mouth. Middle Ordovician, Czechoslovakia.

Ascocystites drabowensis Barrande
Text-figure 30

Discussion. This genus and species has recently been redescribed by Ubaghs (1967b: S483). I studied several latex casts of specimens originally figured by Barrande from the Caster Collection at the University of Cincinnati. New information was derived from only one specimen, cast KR–2; this specimen was also figured and photographed by Ubaghs (1967b: fig. 299,



Text-figure 30. Oral surface morphology in *Ascocystites drabowensis.* Latex cast KR 2 (Caster Collection, University of Cincinnati) showing well-preserved oral surface with brachioles; note strongly developed "2-1-2" pattern of ambulacra around central mouth, two sets of cover plates on main food grooves, variation in size of brachioles from oldest (largest) to youngest (smallest), distally imbricate cover plates over brachiolar food groove, aborted ambulacral branch in "B" ambulacrum, and lack of anal opening on oral surface.

2; fig. 311, 2). This cast of a large specimen shows an oral surface with excellently preserved ambulacra and brachioles (Text-fig. 30); it yielded additional information on brachiole morphology, cover plates, growth of the ambulacral system and brachioles, and the relationship between the brachioles and the oral plates.

At least 26 brachioles are present in this specimen, including at least four immature brachioles (in ambulacra "A," "C," "D," and "E") not figured by Ubaghs in his reconstruction of this specimen (1967b: fig. 211, 2). This is one of the few blastozoan echinoderms in which I have seen immature brachioles, and because of their size difference, they appear to be in slightly different stages of growth. All of the brachioles show a moderate gradation in size in each ambulacral area from the largest one, which comes off the first branch from the main ambulacral groove (therefore the oldest brachiole in this ambulacrum), down to the smallest and newest immature ones. These brachioles are very long (the longest is 29 mm and incomplete), range in width from 0.3 to 1.5 mm, and have distally imbricate cover plates (BCP) protecting the adoral brachiolar food groove (Text-fig. 30) with between 1.0–1.4 BCP/BP. The brachiolar plates are relatively massive and show a marked decrease in length near the proximal end of each brachiole where it is attached to the calyx. Adoral and aboral gaps appear between the brachiolar plates in this proximal region, apparently for the insertion of muscles or ligaments to bend the brachiole (see Ubaghs, 1967b: fig. 303). However, these gaps extend only about

8–12 brachiolar plates up from the attached proximal end; the brachiolar plates beyond that have nearly flush sutures. There appears to be no opening into the body cavity where the brachioles are attached to the calyx plates at the edge of the oral surface.

The five ambulacra from "A" to "E" have five, three, five, six, and six food grooves with brachioles, respectively. Ambulacrum "B" probably has a considerably lower number than the others (and no immature brachiole) because an "aborted" food groove is present here (see Text-fig. 30) that never developed a brachiole, apparently inhibiting the growth of this ambulacrum. This aborted food groove is well inside the edge of the oral surface where the other brachioles are located and appears to be located in the third branching position. This irregularity in ambulacral development probably occurred either because this food groove branched off the main food groove too far from the edge of the oral surface for its aboral plates and brachioles to be inserted, or because it may have been injured during its early growth so that it did not develop normally.

This abnormality and an examination of the rest of the oral surface with its ambulacra suggests how growth occurred in the ambulacral system of *Ascocystites*. The five primary ambulacral branches, each with a single brachiole, the central set of ambulacral cover plates, and the five main oral plates are probably the earliest formed parts of the system. These five earliest brachioles continue to grow in size and perhaps length and become the largest ones in a mature specimen. As the eocrinoid grows, it requires more food-gathering surface than is provided by a single growing brachiole in each ambulacrum. An ambulacral branch then forms on the right (looking aborally down each ambulacrum) near the edge of the oral surface, and a portion of the oral plate on this side of the previous brachiole "buds off" or is inserted as a new adoral. This new ambulacral branch grows along this new oral-adoral suture to the edge of the oral surface where a new brachiole is formed and mounted on the suture between these two plates. New food grooves (and brachioles) are added in an exotomous manner (all branching to the right as described above) until the third or fourth branch; at this point the branching changes to heterotomous (determined from position of branching and relative brachiole size) and new ambulacral branches, adoral plates, and brachioles are added between older ones in each ambulacrum. The oral and adoral plates continue to grow laterally and apparently adorally to increase the size of the oral surface and its perimeter so that additional room for new ambulacral branches and brachioles is produced. The main ambulacral grooves must also become wider to accommodate the increased supply of food being moved to the mouth; therefore, a second set of ambulacral cover plates is apparently added outside the central set sometime during growth. This lateral set of cover plates dies out as each branch comes off the main food groove, and only the central set continues out to and up each brachiole as imbricate brachiolar cover plates (see Text-fig. 30). Ubaghs 1967b: S464, fig. 299, 2) showed a possible hydropore in the "CD" interradius in these lateral cover plates, but although the plates are slightly displaced here, no definite opening was observed in the cast that I studied.

The observed ambulacral morphology and growth features of *Ascocystites* described above suggests that the two-plate ambulacral sets supporting the brachioles in later eocrinoids, rhombiferans, and blastoids evolved from the multiplication or budding of somewhat specialized calyx plates surrounding the mouth in early eocrinoids. *Ascocystites* has already reached an early but characteristic stage in this development where the oral and adoral plates have in fact become ambulacral supporting plates. If this arrangement was modified so that these ambulacral areas extended further down the calyx either in a sinus between other calyx plates (or a sinus in a single plate), or were mounted on the exterior surface of other calyx plates, an arrangement identical to that found in more advanced blastozoans would be produced. This derivation suggests that erect brachioles are specialized structures of earlier and different origin from their supporting ambulacra.

No additional information was learned about the location of the anus in *Ascocystites* (it must be somewhere on the side of the calyx), or about the calyx plating just below the oral surface.

Family INDETERMINATE

Genus *Cambrocrinus* Orlowski, 1968

Type species, Cambrocrinus regularis Orlowski, 1968

Diagnosis. Imperfectly known eocrinoids(?) with an elongate cylindrical calyx bearing 6 or more rows of alternating(?) plates in a partially regular arrangement. Epispires apparently absent, and plates have large ridges radiating from the plate centers to the corners. Attachment stem present; stem expands proximally and has disklike columnals as well as some that appear to be wedge shaped. Food-gathering appendages and summit features unknown at present. *Olenus* beds, Upper Cambrian, Holy Cross Mountains, Poland.

Discussion. Cambrocrinus was proposed as a new eocrinoid genus by Orlowski (1968: 265–266) who based his proposal on approximately 50 partially complete specimens preserved as internal and external molds. The preservation is not very good in these specimens, and none of them have the oral surface or food-gathering appendages well enough preserved for comparison with other eocrinoids. Georges Ubaghs of the University of Liège, Belgium, sent me photographs of several latex casts made from Orlowski's type specimens. The calyx plate sutures in these specimens are very indistinct and are overshadowed by the large external ridges radiating from the plate centers to the corners. The arrangement of these ridges is different from that found in some other eocrinoids such as *Macrocystella* and *Gogia*(?) *radiata,* but is similar to the arrangement of ridges in the plates of *Eocystites* from the middle Cambrian. Orlowski (1968: fig. 3) seems to have been correct in his method of determining calyx plate suture location from the arrangement of ridges on the plates; points where five to seven ridges come together are almost certainly plate centers, while points with three radiating ridges are very likely "3-plate corners." The inferred calyx plating does not seem to be as regular as illustrated by Orlowski, although the rows of plates do seem to alternate in most cases. It is impossible to tell at present whether pentameral symmetry was strongly developed.

The stem attached to many of the calyces seems to bear both normal disk-shaped columnals and wedge-shaped ones, similar to those found in *Akadocrinus* (p. 106). The stem seems to expand in diameter somewhat near its attachment to the calyx, as it does in many early rhombiferan cystoids.

The summit of the calyx with its food-gathering appendages is not well enough preserved in any of the figured specimens to determine anything about its morphology. Since brachioles are not known for certain to be present in *Cambrocrinus,* this genus cannot at present be assigned to the eocrinoids with complete certainty. However, it very likely belongs here, judging from its age and other morphologic features.

Genus *Eocystites* Billings, 1868

Type species, Eocystites primaevus Billings, 1868

Discussion. Eocystites is based on poorly known ridged calyx plates from Middle Cambrian strata near Saint John, New Brunswick, eastern Canada. Ubaghs, (1967b: S493) discussed and figured examples of these plates at the end of the eocrinoid chapter in the Treatise, and provisionally included them in this class. I have seen several collections of plate material belonging to this taxon, including the apparent type specimens that are currently on loan from Cornell University to the University of Cincinnati, but I have no additional information to add to Ubaghs' description. These separate plates probably belong to some unknown eocrinoid (or other echinoderm) lacking epispires, but more complete material has not been found. Similar plates have been reported from other Cambrian localities in Europe and North Africa, but these may very well belong to other taxa. *Eocystites* is left in the eocrinoids here for lack of a better place to assign it.

Family MACROCYSTELLIDAE Bather, 1899

Diagnosis. Eocrinoids(?) having fixed calyx plating nearly identical to that in glyptocystitid rhombiferan cystoids (but without pectinirhombs), ridged plates with internal folds extending out under the ridges, a large periproctal area on one side of the calyx, a flattened summit containing 5 short ambulacra around a central mouth with nearby hydropore and gonopore, long biserial food-gathering brachioles with distally imbricate cover plates, and a long stem with a proximal expanded portion consisting of 2 types of interlocking columnals. Early–middle Ordovician, England, Czechoslovakia, France, and other areas.

Genus *Macrocystella* Callaway, 1877

Type species, Macrocystella mariae Callaway, 1877

Discussion. Macrocystella and the very similar *Mimocystites* (type species *M. bohemicus* Barrande, 1887) were briefly reviewed by Ubaghs (1967b: S483–S485), who concluded that the two genera are very closely related and are probably eocrinoids. However, Paul (1968a: 580–600) in a major review of both genera concluded that *Mimocystites* is a junior synonym of *Macrocystella* (his p. 582) and that *Macrocystella* should be assigned to the class Rhombifera even though it had not yet developed the pectinirhombs characteristic of this class (his p. 599). *Macrocystella* has calyx plating, ridge structures, stem morphology, and brachiole development very similar to the slightly later rhombiferan cystoid genus *Cheirocrinus*. *Macrocystella* differs from *Cheirocrinus* primarily in lacking pectinirhombs and in having instead much thinner calyx plates with more pronounced external ridges, apparently allowing respiration to take place over much of the plate surface (Paul, 1968a: 594).

I agree with Paul in his morphological analysis and his interpretation that *Macrocystella* is probably directly ancestral to the rhombiferan *Cheirocrinus*, but disagree on the final point that *Macrocystella* should be assigned to the Rhombifera. The class Rhombifera is defined by a variety of features (see p. 170), the most important of which is the development of characteristic rhombiform respiratory structures (pectinirhombs or cryptorhombs). *Macrocystella* had not yet developed these critical defining structures when it appeared in the fossil record, although it already had many of the plating and stem features found in true glyptocystitid rhombiferans. Therefore, I would consider that *Macrocystella* was one of the last eocrinoid ancestors leading to the earliest glyptocystitid rhombiferans, and that it represents a true intermediate between eocrinoids and at least one major group of rhombiferan cystoids.

Paul's comparison of the systematic problem of *Macrocystella* with that of *Amecystis*, another rhombiferan without pectinirhombs, is well stated for his proposed systematic assignment (1968: 594), but actually involves a somewhat different phylogenetic situation. *Amecystis* is closely related to *Pleurocystites*, a specialized bottom-living mobile rhombiferan usually having three pectinirhombs. However, several species of *Pleurocystites* have reduced the number of rhombs to two probably because of water recirculation problems, as pointed out by Paul himself in another paper (1967c: 122–123), and a related Devonian genus (*Regulaecystis*) has reduced the number of rhombs to one. It seems reasonable to postulate that *Amecystis* is a specialized and somewhat aberrant pleurocystitid rhombiferan that has completely lost the pectinirhombs once possessed by its *Pleurocystites*-like ancestors. *Macrocystella*, however, represents a different situation because neither it nor its ancestors *ever* had the characteristic pectinirhombs that were developed by its later rhombiferan descendants. This is why I consider *Macrocystella* a pre-rhombiferan eocrinoid that was directly transitional between these two classes.

Order **INDETERMINATE**

Family TRACHELOCRINIDAE new family

Diagnosis. Eocrinoids(?) with an irregular globular calyx lacking epispires, well-developed columnal-bearing stem, and unusual food-gathering appendages consisting of 3–5 biserial "arms" (= ambulacra?) bearing biserial "pinnules" (= brachioles?) attached together to a single projection containing the mouth on the calyx summit. Middle(?)–late Cambrian.

Discussion. This new family contains two aberrant taxa with very unusual food-gathering appendages: *Trachelocrinus* from the late Cambrian, known from a single complete specimen and fragmentary columnal and plate material; and several pinnule-bearing "arms" without calyces from the Middle Cambrian Burgess Shale. The unusual appendages in these taxa appear to represent erect armlike ambulacra bearing pinnulelike brachioles, an arrangement similar to that found in the later rhombiferan *Caryocrinites* (see p. 20). If true, then these forms are true eocrinoids although they are different from most other representatives of this class.

Genus *Trachelocrinus* Ulrich, 1929

Type species, Trachelocrinus resseri Ulrich, 1929

Diagnosis. Eocrinoids(?) with 5 erect ambulacra(?) bearing brachioles(?), a globular, thin-plated calyx without epispires, and a long columnal-bearing stem. The calyx is large and globular with many thin polygonal plates arranged in partially regular rows; no epispires present. Food-gathering appendages apparently 5 in number, all attached to a large raised spoutlike projection on the summit of the calyx. Appendages very long, biserially plated, and bearing smaller biserial branches coming off alternately(?) every third appendage plate. This food-gathering system of branching appendages appears to represent erect ambulacra bearing normal brachioles. Stem long and well developed, apparently made up of 1-piece(?), flanged, and spine-bearing columnals with a small lumen. Diameter of columnals increases only slightly near calyx. Mouth, anus, and other calyx openings unknown. Snowy Range Formation, middle Upper Cambrian, Wyoming and Montana.

Discussion. Trachelocrinus has been an enigmatic echinoderm ever since it was first described by Ulrich in 1929. He assigned it (his p. 63) to the crinoids, although he had some difficulty finding a suitable place for it within this class. Bassler and Moodey (1943: 3, 193) assigned *Trachelocrinus* to the family Eocystitidae of the class Cystoidea, a grouping containing many forms now included in the eocrinoids. Moore (1952: 341) stated flatly that this genus was a cystoid and not a crinoid, but did not explain his reasoning. Finally, Ubaghs (1967b: S493) questionably listed *Trachelocrinus* without additional information with the unassigned forms at the end of the eocrinoid section in Treatise. Since this genus is one of the very few relatively well known late Cambrian attached echinoderms, it might yield important information about the transition between one or more groups of middle Cambrian and early Ordovician echinoderms. The main problem is deciphering its true phylogenetic position from its somewhat puzzling morphology.

The calyx and stem features of *Trachelocrinus* are not distinctive either of crinozoan or blastozoan echinoderms. The "arms," however, are relatively complex and unusual for a primitive echinoderm, and are probably the most distinctive feature in this genus. Biserial "arms" with biserial, alternately branching "pinnules" are unknown in Paleozoic crinozoans and are not present for certain in blastozoans until the middle Ordovician or early Silurian with the appearance of the rhombiferan cystoid *Caryocrinites* and its relatives (see p. 20). However, similar "arms with pinnules" of unknown affinities have also been found in the Middle Cambrian Burgess Shale (see next section); although no other calyx or stem structures are preserved, this poorly known Burgess Shale taxon may possibly have been ancestral to *Trachelocrinus*.

After I wrote to him about my interpretation of the "arms" in *Caryocrinites*, Georges Ubaghs of the University of Liège suggested to me (personal communication, March 1, 1969) that the "arms with pinnules" of *Trachelocrinus* might have had a similar origin from recumbent ambulacra with brachioles. I have gone back and restudied the type specimen of *Trachelocrinus* with this suggestion in mind, and have concluded that this suggestion is probably the most reasonable explanation of the known morphology. If the "arms with pinnules" in *Trachelocrinus* do represent modified ambulacra bearing brachioles, then this genus is certainly a late Cambrian eocrinoid. Because no later known eocrinoid has "arms" like this, the implication is that *Trachelocrinus* probably represents an evolutionary "dead end" in the eocrinoids, although there is a slight possibility it may have been ancestral to one group of rhombiferan cystoids (see p. 171).

Trachelocrinus resseri Ulrich, 1929
Plate 30

Trachelocrinus resseri Ulrich, 1929: 63–66, text-figures 1–2; Bassler and Moodey, 1943: 3, 193; Moore, 1952: 341; Ubaghs, 1967b: S493.

Ulrich's original 1929 description and reconstruction appear to be relatively adequate. My examination of the holotype and additional fragmentary material produced only a few slight corrections and additions.

I studied the holotype and only known complete specimen of *Trachelocrinus resseri* (USNM 80490) in 1966 and again in 1969. Although relatively complete, it is not perfectly preserved, and additional material would be very desirable. In July, 1967, I visited the type locality but could find no additional complete specimens. However, separate calyx plates and columnals apparently belonging to this genus are very abundant here and at several other Snowy Range localities in southwestern Montana.

Specific description. The type specimen occurs on a slab of shaly limestone containing a few flat limestone pebbles and relatively abundant trilobite and echinoderm fragments. The stem, calyx, and arms are all somewhat incomplete, and the specimen is partially weathered (Pl. 30, fig. 3). The preserved stem is approximately 25 mm long, and is made up of disklike columnals having a relatively small lumen occupying about 1/3–1/2 of the stem diameter. The exposed distal tip of the stem has been sectioned with a saw (cut off portion now missing); however, I was not able to confirm that each columnal is made up of 5 segments, as reported by Ulrich (1929: 64). The stem shows an alternation between flanged columnals with approximately 10 short spines mounted on each flange and unornamented columnals (Pl. 30, fig. 4). This stem does not expand appreciably near the calyx, as it does in some early rhombiferan cystoids (see p. 170).

The calyx plates in *Trachelocrinus* are thin, arranged in partially regular rows, and have no epispires (sutural pores). The calyx is apparently globular in shape, but it has been badly crushed. The calyx summit bears a spoutlike projection supporting all the "arms." The mouth was probably located in the center of this spoutlike projection, but no other calyx openings are known. Portions of 3 arms are now preserved, and it seems likely from their spacing that the specimen originally had a total of 5. Each of these preserved arms has biserial plating all the way to its termination, but only 1 is well preserved and nearly complete. This arm is at least 40 mm long and slowly tapers along its entire length from a maximum width of about 1.5 mm near its base (Pl. 30, figs. 1 and 3). It has smaller biserial brachioles branching off the exposed side every third arm plate except at one place where a single brachiole branches off from the second arm plate (Pl. 30, fig. 1). Unfortunately, only one side of this arm is exposed, but it seems likely that the brachioles probably branch off alternately from opposite sides of the arm. These brachioles are approximately 1/3–1/2 the size of the arm, and several of them are at least 9–10 mm long. Each brachiole is attached to 2 arm plates, with the basal brachiolar plate having the deepest facet located proximally (adorally) on the arm and the next biserial plate located distally. This attachment pattern is also present in many blastoids and rhombiferan cystoids (see Text-fig. 4). Since the brachioles are attached to 2 arm plates and branch off every third arm plate, 1 arm plate in each series of 3 on both sides of the arm has no brachiole attached to it (Pl. 30, fig. 1). This may represent an additional "filler" plate, unlike other blastozoan echinoderms in which every ambulacral or arm plate bears either one or one-half brachiole. No other morphologic features could be observed.

Discussion. At Republic Creek and other localities, large thin calyx plates and spiny columnals are relatively common, and many of these probably belong to *Trachelocrinus.* Most of the observed columnals have a relatively large lumen, and usually five spines; sometimes these spines are relatively long, unlike the columnals found attached to the type specimen of *Trachelocrinus.* However, other blastozoan or crinozoan echinoderms may also be present in the Snowy Range fauna, although no complete specimens have yet been found.

Stratigraphic and geographic range. Snowy Range Formation (*Conaspis* to *Prosaukia* zones), middle Upper Cambrian, Walcott locality 37o, my locality RP-1.; along Republic Creek, northwestern Wyoming. Plates and columnals apparently from *Trachelocrinus* have also been found in the Snowy Range Formation just above the top of the Pilgrim Formation at localities SD-1. and SA-1. in southwestern Montana.

Studied specimens. Holotype USNM 80490; additional plates and columnals, MCZ 624–626.

Burgess Shale "Arms"
Plate 24, figures 8–16

"Pinnule-bearing arms" belonging to an otherwise unknown echinoderm occur in the Middle Cambrian Burgess Shale of western Canada. Several specimens were found in the U. S. National Museum collections (with specimens of *Echmatocrinus* and *Gogia*(?) *radiata*) dating from Walcott's original quarrying work (1911–1917), and in July, 1966, an additional specimen was collected during the reopening of the Burgess Shale quarry. This last specimen came from beds between 8′4″ and 8′7″ in the quarried sequence. These arms most likely belong to some unknown blastozoan eocrinoid that had erect armlike ambulacra with brachioles, an arrangement similar to that found in *Trachelocrinus* from the late Cambrian. There is a remote possibility that these arms might belong to the same taxon as the holotype specimen of *Gogia*(?) *radiata* n. sp., which lacks appendages, but this seems rather unlikely. Five specimens (mostly pyritized, partially buried, and represented by matched counterparts) were available for study, and are briefly described below.

These "arms" consist of a long, slightly curved main branch sending off multiple smaller "pinnules" on one or both sides. The main arm ranges up to about 20–25 mm in length and as many as 14–15 pinnules branch off in this distance (Pl. 24, figs. 8–9). It appears that two sets of pinnules are present, one lying in front of the other, since more pinnules can be counted away from the arm than can be seen attached on the exposed side. These pinnules in the larger specimens seem to be as much as 30–34 mm long (Pl. 24, fig. 16). Large portions of both the arms and pinnules have been pyritized, destroying the original plating, but the pinnules appear to be biserially plated with tiny biserial cover plates in the best specimen (Pl. 24, fig. 9). These pinnules are attached close together along the length of the arm, so that there is probably one pinnule per arm plate. The arms themselves are too poorly exposed and too highly recrystallized to determine any information about their plating, but if two sets of pinnules are in fact present, these arms would most likely be biserial. All of the arms are apparently incomplete in a proximal direction, and no trace of a calyx or other echinoderm structures was found associated with them.

All the figured specimens (USNM 165428–31 and GSC 25963) come from the Burgess Shale Member, Stephen Formation (*Bathyuriscus-Elrathina* zone), Middle Cambrian, Burgess Shale Quarry (USNM locality 35k), near Field, British Columbia.

Discussion. The biserial plating in the pinnules, and the possibly biserial(?) plating in the arms both suggest that this unknown echinoderm is a blastozoan most likely related to the late Cambrian eocrinoid *Trachelocrinus*. This would imply that the "pinnules" are true brachioles and that the "arm" represents an erect ambulacrum. Biserial pinnules are unknown in crinozoan forms, and neither plated pinnules nor biserial arm plating is present in crinoids until early in the middle Ordovician. This taxon differs from *Trachelocrinus* in apparently having the brachioles branching off every arm plate, instead of having gaps where "filler" plates are present. It is not known whether this Burgess Shale echinoderm was similar in its other morphological features to *Trachelocrinus*.

Order **INDETERMINATE**

Family CRYPTOCRINITIDAE Bassler, 1938

Diagnosis. Eocrinoids(?) with a globular calyx composed of 4 slightly irregular circlets of smooth polygonal calyx plates lacking epispires. Mouth and ambulacral system central on summit, anus lateral in "BC" interradius, and 2 small accessory openings also present. Five short ambulacral grooves each lead to 1–2 small appendage facets mounted on single plates. Food-gathering appendages unknown (brachioles?); stem present but also unknown. Middle Ordovician.

Genus *Cryptocrinites* von Buch, 1840

Type species, Echinospherites laevis Pander, 1830

Diagnosis. Same as for family above.

Discussion. Cryptocrinites is a puzzling genus which is only provisionally kept in the eocrinoids here. Ubaghs (1967b: S487–8, fig. 316) gave a very adequate short review of the known morphology, and after examining a small collection of specimens, two of which are figured in Plate 33, figures 12–13, I cannot add any additional morphologic information. Unfortunately, the food-gathering appendages are still unknown and this is the major reason why *Cryptocrinites* cannot be assigned with certainty to any class. The calyx morphology is more similar to known eocrinoids than to members of any other class. *Cryptocrinites* specifically lacks several features that would indicate paracrinoid affinities, such as the stem facet opposite the anus, and strongly asymmetric appendage facets. Until specimens are found with the food-gathering appendages preserved, it is probably best to leave *Cryptocrinites* assigned to the eocrinoids.

Family INDETERMINATE
Genus *Bockia* Hecker, 1938

Type species, Bockia neglecta Hecker, 1938

Diagnosis. Eocrinoids(?) with an elongate cylindrical calyx composed of numerous irregularly arranged, slightly ridged plates lacking epispires. Large central "spout" or proboscis on summit apparently contains mouth and ambulacral system; food-gathering appendages unknown. Anal pyramid on side of calyx about 1/4 of way down from summit. Stem unknown but probably present. Lower–Middle Ordovician, U.S.S.R. and Sweden.

Discussion. Bockia is another genus here provisionally included in the eocrinoids. Hecker (1938: 423; 1940: 30–43) originally described this genus, and it was briefly reviewed by Ubaghs (1967b: S486, fig. 314). The calyx shape resembles *Eustypocystis* n. gen. from the Middle Cambrian, but this earlier genus has a much smaller calyx with smooth plates and possibly a different type of attachment for its brachioles. Although much of the morphology is still unknown, *Bockia* does not have any of the features characteristic of paracrinoids. No specimens were available for study during this project.

Order **INDETERMINATE**
Family LINGULOCYSTIDAE Ubaghs, 1960

Diagnosis. Eocrinoids with an elongate, flattened, and paddle-shaped calyx consisting of a marginal frame bearing short, thick, U-shaped marginal plates enclosing large central areas made up of numerous tiny polygonal central plates and several longitudinal ridges for reinforcement. Flattened oral surface bears central mouth and 2 lateral ambulacra bearing long normally plated brachioles on both sides. Anus at edge of central area at about 1/3 of distance to base. Attachment stem long and columnal-bearing. Early Ordovician, France.

Genus *Lingulocystis* Thoral, 1935

Type species, Lingulocystis elongata Thoral, 1935

Diagnosis. Same as for family above.

Discussion. Lingulocystis is a quite distinct eocrinoid that has many carpoid-like features. It was originally described by Thoral in 1935 and revised in a major paper by Ubaghs (1960: 81–116). *Lingulocystis* is the only known flattened eocrinoid (see Table 3) to have a small-plated central area that was probably quite flexible. Since this genus has a normal columnal-bearing stem, it could have lived either in an upright position or directly on the sea bottom. The brachioles are also long and normally plated and do not show any of the modifications found in several other flattened eocrinoids. Because of the recent excellent redescription by Ubaghs, I did not study any specimens of *Lingulocystis* during this project.

Family INDETERMINATE
Genus *Cardiocystites* Barrande, 1887

Type species, Cardiocystites bohemicus Barrande, 1887

Diagnosis. Eocrinoids with a flattened asymmetrical calyx made up of thick rounded marginal plates surrounding a few large thin central plates, both sets of plates roughly arranged in two transverse rows. Ambulacral system confined to the calyx summit, consisting of at least 3 and probably 5 stubby, heavily plated, biserial

TABLE 3. COMPARISON OF MORPHOLOGY IN THE FIVE KNOWN FLATTENED EOCRINOIDS

Genus	Age	Central plates	Brachioles	Stem	Anus location
Lingulocystis	Early Ordovician	very numerous, much smaller than marginals	normal, long	normal	in central area at side of calyx
Cardiocystites	Middle Ordovician	large and few (3–4 per side)	normal?; stubby and heavily muscled	normal, spiny	unknown
Rhipidocystis	Early-Middle Ordovician	very few (1–4 per side), large	strongly modified to uniserial (with suppressed suture)	normal? short and tapering	uncertain—on margin near summit?
Batherocystis	Middle Ordovician	relatively few (4–8 per side), large	unknown, modified?	3–5 wide and flattened columnals	on margin near summit
Petalocystites n. gen.	Middle Ordovician	large and few ($3^{\pm}$ per side)	normal except near proximal end where partially modified	1–2 large ellipsoidal columnals	at edge of central area near summit

brachioles(?) attached to a flattened central platform. A long columnal-bearing stem with flanges and spines is attached aborally. Middle Ordovician, Czechoslovakia.

Discussion. *Cardiocystites* has been briefly reviewed recently by Ubaghs (1967b: S491–2) and included with the unclassified genera at the end of the eocrinoid chapter. Because of its flattened calyx shape, normal stem, and brachiole-like appendages mounted on the summit, this genus apparently represents an eocrinoid related to the other four known flattened eocrinoid genera (Table 3). In several features, *Cardiocystites* is similar to *Lingulocystis*, which also has normal (but longer) brachioles and a well-developed stem, but *Lingulocystis* has very numerous central plates and many more marginal plates than *Cardiocystites*. *Rhipidocystis, Batherocystis,* and *Petalocystites* n. gen. all have relatively similar calyces with few marginals and central plates, but these forms have a modified stem made up of a few elongate elliptical columnals, and partially or completely modified brachioles in which the plating has changed to "opposite biserial."

Cardiocystites bohemicus Barrande, 1887
Plate 27, figures 7–9

Specific description. Casts of the 2 known type specimens, E 39 and E 51 from the Caster Collection, University of Cincinnati, were studied during this project. The calyx in *Cardiocystites* is flattened or depressed, heart-shaped, and strongly rimmed by a margin of more massive plates extending into upper and lower flat surfaces as thin limbs. There are 2 different kinds of plates present in the calyx, marginals and centrals, and these plates are arranged in 2 transverse rows on the same exposed side in the 2 known specimens. The proximal or lower row consists of 2 marginals linked together at the base to form a stem facet, and a modified triangular central (Pl. 27, fig. 7). The lower left marginal may possibly be divided into 2 plates along the rounded rim, but this is not well shown in either specimen and cannot be confirmed. The upper row consists of 4 plates, 2 marginals, and 2 modified rectangular centrals. In the central area there are 2 relatively prominent ridges running longitudinally across this area, apparently for strengthening. They diverge slightly, running from the edge of the lower left marginal across the lower central plate and then across a large portion of the 2 upper centrals almost to the summit. There are also traces of small ridges running along the rounded marginal rim on the left and right sides.

On the summit of the calyx there is a series of projections and a central area to which the appendages are attached. On the left side of the summit the central (or perhaps another plate with a well-developed suture) is extended into a high, rounded projection which then falls off to the summit area (Pl. 27, fig. 8). On the right side of the calyx, the marginal is developed into a lower serrated projecting crest which also falls off into the central area.

The central portion of the summit is apparently composed of a flat-topped, raised and rounded platform made up by the two upper centrals on this side of the calyx. The appendages are mounted in the center of this flat-topped area (Pl. 27, fig. 8). Three appendages are present on the exposed portions of the best preserved specimen, and it appears that the total number may have been 5. These appendages appear to be normal brachioles; they are relatively short and massively plated, apparently biserial, and have a large brachiolar food groove. The plating consists of biserially arranged, fusular or ring-shaped, brachiolar plates (Pl. 27, fig. 8). Some of these brachiolar plates are scattered around above one of the type specimens, associated with tiny rectangular plates that may have been covering plates for these appendages. These brachioles have large gaps between adjacent brachiolar plates, and the enclosed food groove is very large.

The mouth was apparently located at the center of the summit and all of the brachioles appear to have been attached together around it (Pl. 27, fig. 8). Neither of the 2 known specimens has an anal pyramid preserved anywhere on the exposed side of the calyx.

The stem in both specimens is long and very well developed. Near the calyx, it is made up of alternating large, thin, flanged and unflanged columnals. Distally, this alternation dies out and the columnals change in shape, apparently by increasing their thickness while maintaining approximately the same width. These distal columnals are flanged and bear circlets of small spines both above and below the central flange. Approximately 6–7 spines are visible on each side of the columnal.

Both type specimens are from the Middle Ordovician (D_4) of Czechoslovakia. No other specimens are known to exist.

Family RHIPIDOCYSTIDAE Jaekel, 1901

Diagnosis. Eocrinoids with an elongate flattened calyx, relatively few thick marginals and thin central plates, a central mouth and two short ambulacra on the summit bearing long, completely or partially modified brachioles, an anal pyramid laterally near the summit, and a reduced stem attached aborally. Three genera; early–middle Ordovician.

Genus *Rhipidocystis* Jaekel, 1901 (emended Hecker, 1938; 1940)

Type species, Rhipidocystis gigas Jaekel, 1901

Diagnosis. Calyx flattened and elliptical, with slightly depressed top and bottom central areas made up of few large thin central plates surrounded by a thickened rim of more numerous U-shaped marginal plates. Summit (oral surface) slightly flattened, bearing central mouth and 2 short ambulacra leading to groups of 6–12 modified brachioles slightly longer than calyx. Brachioles strongly modified along entire length to an apparently uniserial plating, probably representing an "opposite biserial" arrangement with a suppressed aboral suture. Anal opening unknown; tiny accessory pores present on adoral and lateral marginals. Stem short and small but normally plated(?) with disklike columnals; usually attached to 1 basal marginal plate. Early middle Ordovician, U.S.S.R.

Discussion. The history of *Rhipidocystis* has recently been briefly reviewed by Ubaghs (1967b: S489). Jaekel described a variety of echinoderms under this generic name, but it was restricted to flattened "carpoids" (order Digitata) by Hecker (1938: 421–422; 1940: 7–22), who assigned the other forms to new genera and described several new species. No material definitely belonging to this genus was available for study, and J. W. Durham (personal communication, 20 November 1969) is currently studying this genus in connection with a new rhipidocystid occurrence in Maryland (see Text-fig. 5C). *Rhipidocystis* appears to be very closely related to *Batherocystis,* differing primarily in the type of stem, possible location of the anus, number of central plates, and number and arrangement of brachioles. The two genera may possibly be synonyms, but complete specimens of *Batherocystis appressa* Bassler, the type species, must be found with brachioles and a complete stem attached before this can be determined. *Rhipidocystis* is also related to *Petalocystites* n. gen., and may have descended from this form or a common ancestor. It seems likely that several of the species described by Jaekel and Hecker are synonyms of *R. gigas.*

Genus *Batherocystis* Bassler, 1950

Type species, Batherocystis appressa Bassler, 1950

Diagnosis. Calyx strongly flattened, elongate-elliptical in shape, and plated with relatively few thin central plates covering the top and bottom surfaces, surrounded by a massive rim made up of relatively few thick U-shaped marginal plates. Mouth central(?) on flattened summit with 2 ambulacra leading to 6–24(?) brachioles that are probably somewhat longer than the calyx and may be modified to apparently uniserial plating(?) with a suppressed brachiolar suture. Anal pyramid lateral on edge of rim near summit and surrounded by 3(?) marginals. Stem strongly modified, attached to two basal marginals and consisting of 1–4 inflated "pillow-shaped" columnals. Middle Ordovician (Black Riveran), eastern United States.

Discussion. This genus is currently being studied by R. L. Parsley (personal communication, 6 September 1969) and by J. W. Durham (see previous section). *Batherocystis* seems to be closely related to *Rhipidocystis* (it may be a synonym), and to *Petalocystites* n. gen., from which it differs primarily in its unusual stem, brachiole morphology, and location of its anal pyramid.

Genus *Petalocystites* new genus

Type species, Petalocystites ikecanensis new species

Diagnosis. Calyx flattened, elliptical to elongate heart-shaped with a flattened summit; made up of depressed top and bottom central areas with few, very large, thin, central plates, and surrounded by a raised and thickened rim with 8–12 U-shaped marginal plates extending part way into the central areas. Summit (oral surface) constricted and slanted, composed of marginals and small accessory plates (orals?) bearing central mouth and 2 short lateral ambulacra leading to 16–20 brachioles about 1½ times as long as the calyx. Brachioles normally plated (biserial alternate) over most of length, but at proximal end plating is modified to biserial opposite for first 5–10 brachiolar plates. Anal pyramid below summit at lateral edge of central area, surrounded by 3 marginals and 1 central. Stem reduced, consisting of 1 or 2(?) inflated globular or rounded-conical columnals attached to 2–3(?) basal marginals. Early middle Ordovician (Whiterockian), central Nevada.

Etymology. The generic name is derived from *petalos* (Gr.)—broad, flat, referring to the characteristic flattened calyx in this eocrinoid.

Discussion. Petalocystites n. gen. is closely related to both *Rhipidocystis* and *Batherocystis;* these three genera form a closely knit group of flattened Ordovician eocrinoids in the family Rhipidocystidae. *Petalocystites* differs from both genera by having only slightly modified biserial brachioles, by having the anal pyramid at the edge of the central area on one side and not on the edge of the rim, by having a somewhat different type of reduced stem, and by having an intermediate number of central plates (Table 3). *Petalocystites* could be directly ancestral to *Batherocystis,* and perhaps also to *Rhipidocystis* if the stem (poorly known in this latter genus) is different from that shown in Hecker's reconstruction (1938: 422). The most primitive feature in *Petalocystites* compared to these other genera is the slightly modified brachiole plating which apparently is just beginning to show the modified uniserial arrangement. *Petalocystites* is the first rhipidocystid genus known from the Cordilleran region in North America, but it (or a closely related form—see the following section) is probably widespread here because of the occurrence of isolated silicified U-shaped marginal plates at many localities.

Petalocystites also seems to be related to *Lingulocystis* and *Cardiocystites,* differing from the former by having considerably fewer and larger marginal and central plates, a much reduced stem, and partially modified brachioles. It differs from the latter by having much longer, thinner, more numerous, and partially modified brachioles, a considerably reduced stem, and a somewhat different calyx shape.

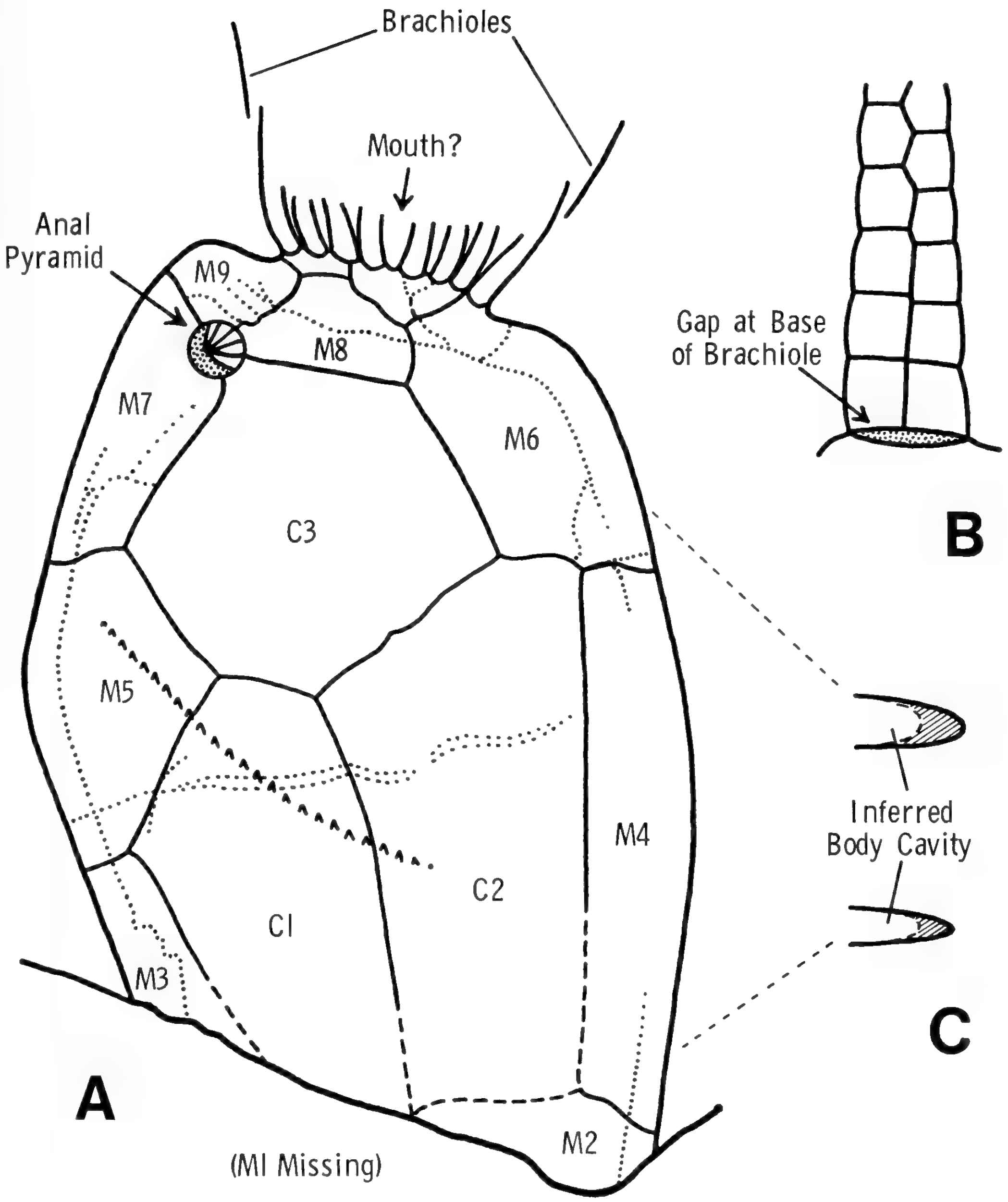
Petalocystites ikecanensis new species

Plates 31 and 32, figures 1–3; Text-figure 31

Four partially complete specimens of this new rhipidocystid species are known. Two specimens on a single limestone slab from the Antelope Valley Limestone were found on a talus slope on the south side of Ikes Canyon, Toquima Range, central Nevada in July, 1967. The matrix in this slab was traced up to the outcrop above this slope (IK-2.), and a third specimen (the holotype) was dug out in place from this exposure. The famous "Sponge Beds" in the Antelope Valley Limestone appear about 75–100 feet further up the slope, the implication being that these specimens come from Kay's "faunule b" (Kay, 1962: 1422, 1424), or from the "slabby beds" in the lower part of the *Orthidiella* zone (Ross and Ingham, 1970: table 1). The fourth, poorly preserved specimen was found across the canyon within the "Sponge Beds" (IK-3.). None of these specimens is entirely complete or exposed, but fortunately two of them have well-preserved brachioles. The following description is based on the holotype (MCZ 646) and the two better preserved paratypes (MCZ 647–648), all of which were partially cleaned with an air abrasive unit before study.

Specific description. The calyx is large, elongate, and strongly flattened. Complete paratype MCZ 647 is approximately 68 mm long and 40 mm wide (greatest width at approximately 3/5 of length), while holotype MCZ 646 is at least 46 mm long (incomplete) and 37 mm wide. The calyx has a massive thickened frame or margin that encloses 2 thin-plated, flat, central areas. The frame is composed of at least 8–9 massive U-shaped marginal plates with relatively long thin projections extending part way into the central area apparently on both sides (Text-fig. 31A and C). The base of the calyx seems to be made up of only 2 plates (Pl. 31, fig. 3), although only one side has been observed and additional plates might also be present. Marginal plates (M1–9) extend up to the flattened but oblique summit where they support 1–2 of the brachioles and several smaller plates (orals?, ambulacral flooring plates?), on which the rest of the brachioles are mounted (Pl. 32, fig. 1). Three large central plates cover the flat central area on the only known side of the calyx (Text-fig. 31A). The 2 aboral ones (C1 and C2) are relatively elongate and side-by-side; the third adoral central (C3) is roughly hexagonal and has a small edge abutting the anus. A possible low ridge, perhaps for strengthening, crosses the central area obliquely (Text-fig. 31A). The anal opening is located adorally and laterally at the edge of the central area and is surrounded by 3 marginals (M7, M9, M8) and 1 central (C3) (Text-fig 31A). It is a nearly circular opening about 2.5 mm in diameter, with a few small crushed anal pyramid plates still preserved on the holotype (Pl. 32, fig. 3). In life the anal pyramid probably consisted of a low dome with 12–16 wedge-shaped plates.

The stem appears to be considerably reduced and perhaps vestigial in *Petalocystites ikecanensis*. It is clearly shown only on paratype MCZ 648 (an incomplete calyx base), although it is also present (but buried) on complete paratype MCZ 647 (Pl. 31, figs. 2–3). Only a single elongate ovoid columnal is present in these two specimens. This columnal has pustular ornament and is about 6 mm long and 4–5 mm in diameter. It appears to be a solid calcite structure attached equally to the 2 basal plates, and no facet was observed at its distal end for the attachment of additional columnals. This arrangement is very similar to that found in a new rhipidocystid from Maryland (J. W. Durham, personal communication, 20 November 1969). However, it is somewhat different from abundant silicified rhipidocystid basal and columnal plates from nearby beds at IK-2. (see the following section), from *Batherocystis appressa* (see Ubaghs, 1967b: S489),



Text-figure 31. Calyx and brachiole morphology of *Petalocystites ikecanensis* n. gen., n. sp. A, nearly complete holotype MCZ 646 showing nine marginal plates (M1–9) and three central plates (C1–3) on exposed side of calyx (other side would have same marginals but different centrals), brachioles attached to central portion of summit, and anal opening with partially preserved pyramid. B, enlargement of leftmost brachiole attached to summit in holotype showing change from normal biserial alternate plating to biserial opposite near base as well as gap for muscles at attachment. C, cross sections of calyx margin near summit and base; note relatively sharp edge in both cases.

and much different from figured specimens of *Rhipidocystis* (see Hecker, 1940: 15).

The ambulacral system with its long brachioles occupies the central portion of the slanting summit area (Text-fig. 31A). Complete and relatively well-preserved brachioles are present only on the holotype, although paratype MCZ 647 also has some partially silicified and weathered brachioles. At least 16–17 brachioles are present on the holotype (Pl. 31, fig. 1), arranged in 2 ambulacral groupings extending out from the apparently central mouth. Several brachioles are mounted on marginal plates (M6 and perhaps M9), but most are mounted on smaller oral or ambulacral(?) plates sitting on the marginals; brachioles are apparently attached to both sides of the 2 ambulacra extending out from the mouth. On the holotype the brachioles are at least 70–72 mm long by 1.0 mm high and 0.8–1.0 mm wide. They are straight and have normal biserial plating along most of their length (Pl. 32, fig. 2). However, at the proximal attachment end, the 5–10 basal brachiolar plates are altered to a biserial opposite arrangement (Text-fig. 31B; Pl. 32, fig. 3). The median suture between these basal plates is apparently well developed and not suppressed as in other rhipidocystid genera. At the very base of the brachiole there is a prominent gap between the first 2 brachiolar plates and the underlying plate (Text-fig. 31B), apparently for the insertion of muscles or ligaments to move the brachiole. Two sets of relatively large brachiolar cover plates (BCP) appear to be present (Pl. 32, fig. 3), occupying nearly half the brachiole height. The larger set is elongate diamond-shaped with a small flat base; these are biserially arranged over the brachiolar food groove and appear to slant slightly in a distal direction. The smaller set is only about 1/3 as high and fills in triangular gaps at the base of the larger one along much of the brachiole length. There are between 1.7–1.8 larger BCP/BP along the entire length of the brachiole. The brachioles expand in size somewhat near their proximal attachment, but maintain about the same width along most of their length until 10–15 mm from the distal tip, where they taper gradually to a blunt tip (Pl. 31, fig. 1). No internal canals were observed in any of these brachioles.

No other features of the summit or ambulacral system are known at present.

Discussion. Petalocystites ikecanensis appears to be the most primitive rhipidocystid now known. Although the calyx shape and plating are already characteristic of this family, it is just beginning to show the change from normal to modified brachioles, and this change is apparently occurring first at the proximal (earliest formed) end. The anal pyramid is in an early stage in its apparent migration from the central area to the edge of the lateral rim, as found in later species of *Batherocystis* and perhaps *Rhipidocystis.* The stem has been reduced to one apparent "columnal," and may not have been used to attach the calyx in an upright position. As in Hecker's reconstruction of *Rhipidocystis* (1940: 16), I believe that *Petalocystites ikecanensis* probably lay on one of its flattened sides (probably the one opposite the anus) on the sea bottom.

Etymology. The specific name is derived from the name of the collecting locality, Ikes Canyon, Nevada, where this new form was first discovered.

Stratigraphic and geographic range. Lower member of the Antelope Valley Limestone (*Orthidiella* zone), Middle Ordovician (Whiterockian), localities IK-2. and IK-3., Ikes Canyon, Toquima Range, west-central Nevada.

Studied specimens. Holotype MCZ 646, paratypes MCZ 647–649. The separate rhipidocystid plates described in the next section may possibly belong to this taxon, but cannot be assigned with certainty.

Antelope Valley Rhipidocystid Plates

Separate silicified marginal, basal, and columnal plates apparently belonging to another rhipidocystid and not *Petalocystites ikecanensis* n. gen., n. sp. have been found in the Antelope Valley Formation at Ikes Canyon and other localities in Nevada. These plates, especially combinations of the massive basal marginals and first columnal (Pl. 32, figs. 9–10 and 17–18), are especially abundant on the talus slope below locality IK-2. where the first specimens of *P. ikecanensis* were found. This broken up plate material appears to have been derived from the Antelope Valley beds just below the zone where *P. ikecanensis* occurs. Several large collections of marginals, basal sets, and columnals were borrowed for study from R. J. Ross, Jr. of the U. S. Geological Survey, Denver. These separate plates are described below.

The complete basal and columnal sets are probably the most distinctive combinations in this material. The marginal frame of this unknown rhipidocystid terminates in a three-plate base (Pl. 32, figs. 4–5, 8, and 14–16). Two of these basal plates, one on each side of the calyx, send long U-shaped limbs adorally to form the characteristic marginal frame of the calyx (Pl. 32, figs. 17–18). The third plate is a small wedge-shaped "filler" that fits in between these other two basal marginals on one side (Pl. 32, figs. 4–5, 8, and 17). All three of these basal plates form a wide concave facet with a central elliptical lumen for the attachment of the basal columnal (Pl. 32, fig. 5).

The basal columnals are large, globular to ellipsoidal in shape and apparently solid calcite (many specimens in the field still have a solid calcite interior surrounded by a thin silicified "skin"). They are truncated proximally by the large facets for the basal marginals, and opposite this there is a small round facet with a tiny circular lumen apparently for the attachment of one or more additional columnals (Pl. 32, figs. 6–8 and 10). However, these additional columnals have not been found attached to these basal combinations, although smaller spherical columnals with round facets are common in some of the acid residues.

Other marginal plates from higher in the calyx also occur sometimes with these basal combinations and are common in other collections (Pl. 32, figs. 11–13). These are U-shaped plates with slight rugose exterior ornament and concave end sutures where ligaments or muscles were inserted. They may have had thin top and bottom projections extending into the central area like other rhipidocystids, but these are now clearly broken off (Pl. 32, fig. 11). No other plates from this rhipidocystid are known at present.

Figured specimens include MCZ 671–675 from the talus slope below locality IK-2., Ikes Canyon, central Nevada, and USNM 165412–3 from locality USGS D719i CO, Frenchman Lake Quadrangle, Nuclear Test site, southwestern Nevada. All material is apparently from the lower part of the Antelope Valley Limestone (*Orthidiella* zone) of early middle Ordovician age.

Discussion. This rhipidocystid plate material differs from *Petalocystites ikecanensis* n. gen., n. sp. in the following points: 1) the basal columnal has a different shape (globular vs. elongate ovoid) and different ornament (smooth vs. rugose); 2) this rhipidocystid apparently had additional columnals attached to the basal columnal, whereas no facet for additional columnals is present in the type specimens of *P. ikecanensis;* 3) only two marginal plates form the exposed side of the base in *P. ikecanensis* versus three in these plates; and 4) these separate marginal plates are not known for certain to have had thin top and bottom projections like *P. ikecanensis.* These differences may only be of specific value, but complete specimens of this fragmentary form will have to be collected before this can be determined.

The occurrence of this fragmentary rhipidocystid material in the Antelope Valley Limestone is very similar to that of the strange middle Cambrian echinoderms *Cymbionites* and *Peridionites* described by

Whitehouse (1941: 5–16). I suspect that his material may also represent current-accumulated, heavily calcified, basal "cups" of some otherwise unknown eocrinoid(?) having more delicate (and now missing) plates higher in the calyx.

Forms Provisionally or Definitely Removed from the Eocrinoids

The following genera or families either definitely belong to other classes (*Cigaria*(?), Springerocystidae, and *Archaeocystites*) or cannot be assigned to the eocrinoids with any degree of certainty at present because they are so poorly known or have unusual morphology (*Palaeocystites* and *Lysocystites*). They are therefore grouped together in this section and briefly described with comments on their phylogenetic assignment.

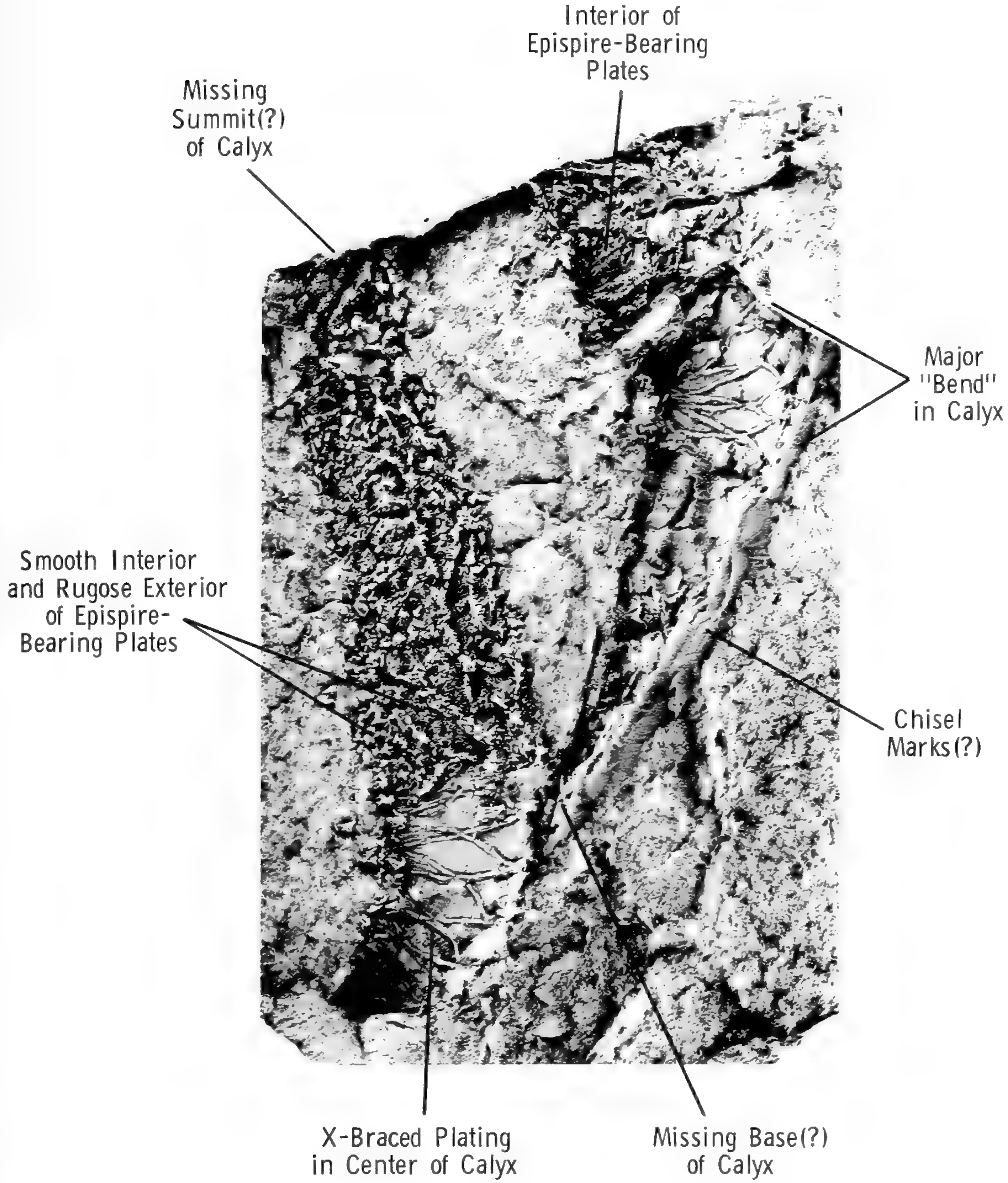
Genus *Cigaria* Barrande, 1887

Type species, Cigaria dusli Barrande, 1887

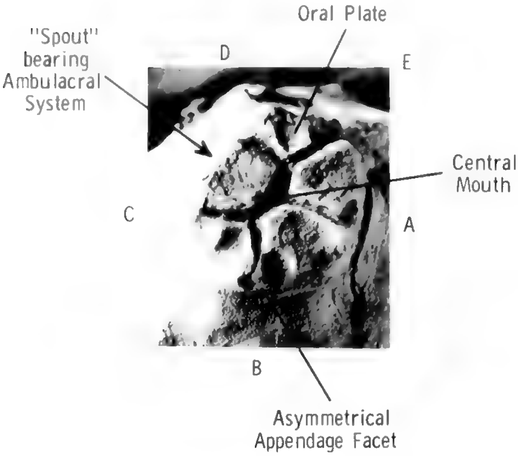
Discussion. This genus, represented by only two specimens (both incomplete) on a single slab of matrix, comes from the Middle Cambrian Jince Beds of Czechoslovakia. These specimens were originally collected and described by Barrande, reviewed by Bather and Jaekel, and recently redescribed by Ubaghs in Treatise volume S (1967b: S492–3), in which this taxon was questionably included at the end of the eocrinoid chapter. I studied a latex cast (E 35) of this only known slab of type specimens from the Caster Collection, University of Cincinnati (Text-fig. 32). The two specimens on this slab are oriented in the same direction, and show somewhat different portions of the calyx. This strange echinoderm has an elongate biconical calyx with a prominent bend of approximately 40° near the middle. As described by Ubaghs (p. S493), the body is divided into three general regions with different plating. The "third" (probably adoral) region of the calyx consists of many small rugose plates bearing rounded epispires. Probably the most unusual feature of this echinoderm is the prominent X-bracing or tight lattice structure present in the bent middle portion of the calyx (Text-fig. 32). This region (preserved as an internal cast) consists of thin elongate plates that cross in X-shaped patterns. These X-shaped braces enclose wide diamond-shaped areas that were probably plated with very thin calcite sheets, but may possibly have been covered only by soft membranes. No sediment has entered the interior of the calyx through these diamond-shaped areas because they are still sharply delineated. The lower (aboral?) portion of the calyx is poorly preserved but appears to be plated with large rugose, perhaps imbricate(?), plates lacking epispires. Unfortunately, neither of the *Cigaria* specimens on this slab is complete at either of the extremities, and no appendages are attached to any of the preserved portions of the calyx.

At the present time, it appears best to remove *Cigaria* from the eocrinoids. The only feature possibly indicating any eocrinoid affinities are the epispires between some of the calyx plates. However, epispires are also present in several other classes of early echinoderms, including edrioasteroids and stylophoran and homostelean carpoids. The unusual X-braced plating in the middle portion of the calyx is completely unknown in eocrinoids and in nearly all other early Paleozoic echinoderms. The only group of echinoderms having structures at all similar to these are some of the early stylophoran carpoids. I would predict that when more complete specimens of *Cigaria* are found, biserial brachioles will not be present.

The most puzzling question is where to assign *Cigaria* if it is removed from the eocrinoids. This taxon may possibly be a very early and perhaps aberrant type of stylophoran carpoid or even an early holothurian, but it is quite unlike most later members of these two classes. I have considered the possibility that *Cigaria dusli* might represent a single occurrence of



Text-figure 32. Morphology of *Cigaria dusli.* Latex cast (E 35, Caster Collection, Univ. of Cincinnati) of the only two specimens of this taxon now known; note that different portions of bent calyx are preserved in these two specimens, but that both summit(?) and base(?) are still incomplete. Note rugose, epispire-bearing plates in upper(?) part of calyx, X-braced plating in bent center portion (interior view?), and large, perhaps imbricate(?), rugose plates in lower portion. (× 1.9)



Text-figure 33. Asymmetrical appendage facets in *Columbocystis typica.* Holotype specimen USNM 93407 showing spout-like oral surface with its central mouth, "2-1-2" arrangement of ambulacral grooves, and asymmetrical facets where arms (unknown but also asymmetrical) are attached to calyx. This last feature implies that *Columbocystis* (and other related genera) are true paracrinoids. Much enlarged.

another new class of early echinoderms. However, because of the imperfectly known material, I do not feel justified in setting up a new class for this taxon at present.

Family SPRINGEROCYSTIDAE Bassler, 1950

Discussion. Ubaghs (1967b: S486) assigned this family, which contains four Ordovician genera, to the Eocrinoidea, although two of the genera were questionably included. The genus *Bockia* is removed from this family and discussed on page 127; it is considerably different in morphology from the other members of this family and probably represents an eocrinoid. The other three genera (*Springerocystis, Columbocystis,* and *Foerstecystis*) all come from the Benbolt Formation ("Ottosee") of the southern Appalachians, and are relatively similar (in fact *Columbocystis* and *Springerocystis* may possibly be synonyms). They have a globular and slightly asymmetrical calyx with irregularly arranged polygonal plates, no epispires, ambulacral system developed as an oral protuberance with a central mouth surrounded by facets for erect "arms" (possibly short recumbent ambulacra(?) in *Foerstecystis*), a stem facet almost opposite the anus, and pentameral symmetry present only in the ambulacral system. Some of these features strongly suggest paracrinoid affinities.

I examined the type specimens of these Benbolt genera in 1966, and studied the holotype of *Columbocystis typica* (USNM 93407) in detail in 1967 and 1969. This specimen has definite asymmetric facets for the arms around the mouth (Text-fig. 33), the implication being that the arms were also asymmetrical. These facets show the same type of asymmetry (called "left lateral"—see p. 185) found in other true paracrinoids with erect arms and recumbent ambulacra. Therefore, *Columbocystis* and very likely *Springerocystis* and *Foerstecystis* are true paracrinoids and not eocrinoids; thus, the family Springerocystidae with these three genera (but not *Bockia*) is here transferred to the Paracrinoidea.

Genus *Archaeocystites* Barrande, 1887

Type species, *Archaeocystites medusa* Barrande, 1887

Discussion. This poorly known taxon, originally described by Barrande (1887: 94–95), was questionably referred without redescription to the eocrinoids by Ubaghs (1967b: S491). Two latex casts were available for study from the Caster Collection, University of Cincinnati; E 32 is a complete but poorly preserved calyx with appendages (holotype), and E 33 is a set of similar appendages apparently from the same species. These two specimens show that *Archaeocystites* has long uniserial pinnules and not biserial brachioles (Pl. 33, figs. 9–10). The calyx is relatively large, globular to squat bowl-shaped, and has numerous poorly preserved plates apparently without epispires. A stem bearing numerous thin columnals with spines is also present.

Since *Archaeocystites* has uniserial pinnules, this genus is probably not an eocrinoid or other blastozoan echinoderm. However, until better preserved specimens become available, it is difficult to determine where this taxon should be assigned. It may possibly be a paracrinoid or diploporan cystoid.

Genus *Palaeocystites* Billings, 1859

Type species, Palaeocystites dawsoni Billings, 1859

Discussion. Ubaghs (1967b: S482; figs. 301, 3a–c; 309, 1–2) gave a short redescription of this genus and assigned it to the eocrinoids. I briefly examined the two syntypes of the type species of this genus (GSC 1021a–b) in September, 1967. I am not convinced that this genus belongs in the eocrinoids, and since the appendages around the mouth are unknown at present, it seems best to provisionally remove it from this class. The apparent "epithecal respiratory canals" (Hudson, 1911: 251; Ubaghs, 1967b: S467) are very similar to structures found in several Ordovician crinoid genera, especially *Palaeocrinus*, several rhombiferan cystoids, and a few paracrinoids. Somewhat similar structures are also found in a few eocrinoids (*Ascocystites, Macrocystella*), although they are nowhere near as strongly developed. *Palaeocystites* could belong in the Crinoidea, Paracrinoidea, Rhombifera, or Eocrinoidea, but conclusive evidence that might resolve this problem is lacking at present.

Plates very similar (but perhaps not identical) to those found in *Palaeocystites* are common in the Benbolt Formation of the southern Appalachians (perhaps belonging to *Ulrichocystis*(?)), the Bromide Formation of Oklahoma, and the Antelope Valley Limestone of Nevada and eastern California. Complete specimens are lacking at most of these other localities, and the assignment of these plates must remain provisional.

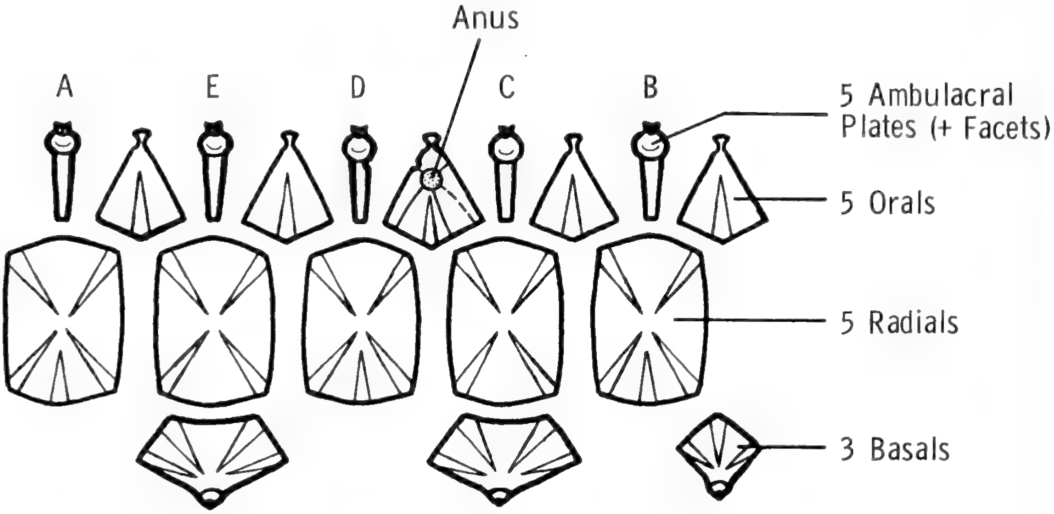
Genus *Lysocystites* Miller, 1889

Type species, Echinocystites nodosus Hall, 1864

Lysocystites is an unusual and puzzling echinoderm from the Middle Silurian Laurel Limestone of southeastern Indiana and Racine Dolomite of southeastern Wisconsin. S. A. Miller proposed this genus in 1889 for material described and illustrated by Hall in 1864. Foerste (1920: 44–48) redescribed the two species, and Springer (1926: 142–143) reviewed this genus in his work on Silurian crinoids, concluding that *Lysocystites* probably belonged in the cystoids. Bassler and Moodey (1943: 6) put *Lysocystites* in the family Cryptocrinitidae and included it in the rhombiferan cystoids with a group of genera now assigned to the eocrinoids. Most recently Ubaghs (1967b: S488) has assigned this genus to the eocrinoids without further comment.

I studied four plesiotype specimens (S3163) in the Springer Collection of the U. S. National Museum that Springer had originally used in his 1926 redescription. Using these specimens, I have concluded that *Lysocystites* is probably not an eocrinoid. However, I have been unable to assign this genus with certainty to any other class of blastozoan or crinozoan echinoderm because of the unusual calyx morphology and the still unknown appendages. Its tentative removal from the eocrinoids reduces the latest well-documented occurrence of this class from middle Silurian to middle Ordovician. Because previous authors have apparently incorrectly interpreted both the plating arrangement (see Text-fig. 34) and the nature of the unusual respiratory structures (see Text-fig. 36), I have included a redescription of these plesiotype specimens below.

Specific description. The calyx in *Lysocystites sculptus* is relatively large, globular in shape, and composed of four major sets of highly ornamented plates. Three unequal basals make up the conical base of the calyx. Two basals are relatively



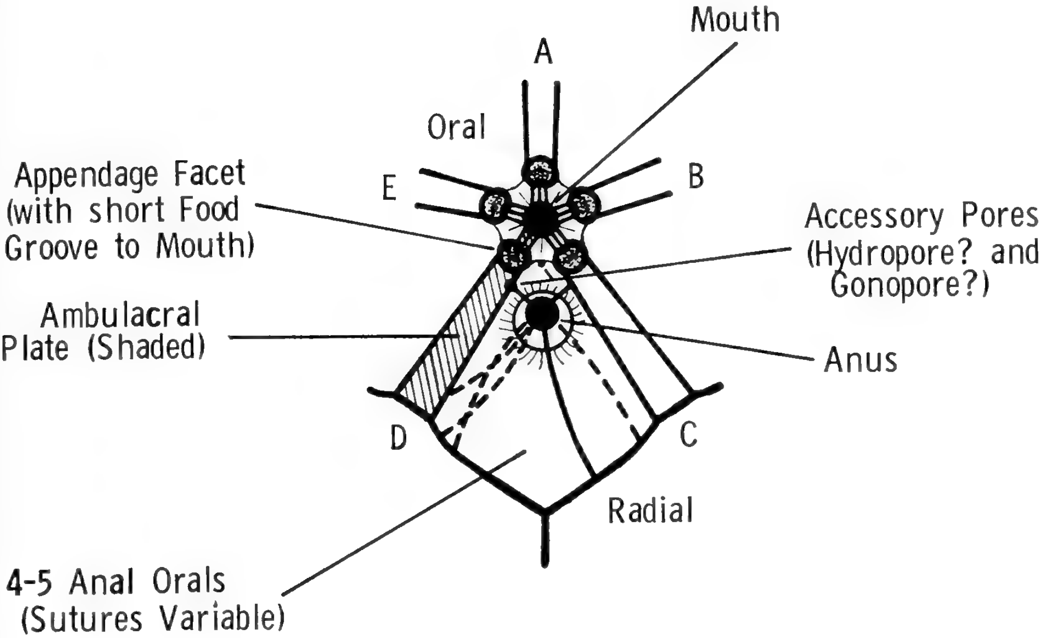
Text-figure 34. Plating arrangement in *Lysocystites sculptus.* Diagram constructed from Springer's plesiotype specimens (USNM S3163a–d) showing major sets of plates; note divided anal oral and previously unfigured ambulacral plates with appendage facets between orals.

large and pentagonal; the third, located in the "AB" interradius, is diamond-shaped and only about half the size of the others (Pl. 33, fig. 3; Text-fig. 34). This arrangement is very similar to that found in most blastoids in which three unequal basals are present in the same positions. The aboral ends of the three basals form a prominent facet, apparently for the insertion of a normal stem, with each basal contributing approximately equal 120° segments.

Five relatively large, equal-sized, rectangular radials form the middle portion of the calyx above the basals. These radial plates make up approximately half the surface area of the calyx. Five rhombic or deltoid-shaped oral plates are located interradially above the radials. These orals surround the central mouth on the peristome and may also make up the edges of the short food grooves (Text-fig. 35). The oral plate containing the anal opening on the "CD" side is divided into at least four pieces by oblique sutures.

In between these five orals are five thin, elongate, radially located plates extending all the way down to the adoral edge of the radials (Text-figs. 34 and 35; Pl. 33, figs. 7–8). These plates, which have not been correctly described before, are here termed ambulacral plates. Each ambulacral plate bears an appendage facet near the mouth, and perhaps a portion of the food groove leading from this facet to the mouth. There is apparently no separate plate around the facet itself, as described and figured by Springer (1926: 143, pl. 33, fig. 22) and Ubaghs (1967b: S488, fig. 317, 2, 3). These ambulacral plates bear a resemblance to the lancet plates of blastoids, although no separate brachiole-bearing ambulacral plates are mounted on them in *Lysocystites.*

Three-cornered, foldlike evaginations, apparently representing respiratory structures, are present at the three-cornered sutures between major rows of interradial (basal and oral) and radial plates. These structures open internally and are covered externally by a thin calcite sheet, forming ornamental triangular ridges radiating from these corners to the centers of the plates (Text-fig. 36; Pl. 33, figs. 1–5). These structures are almost symmetrically

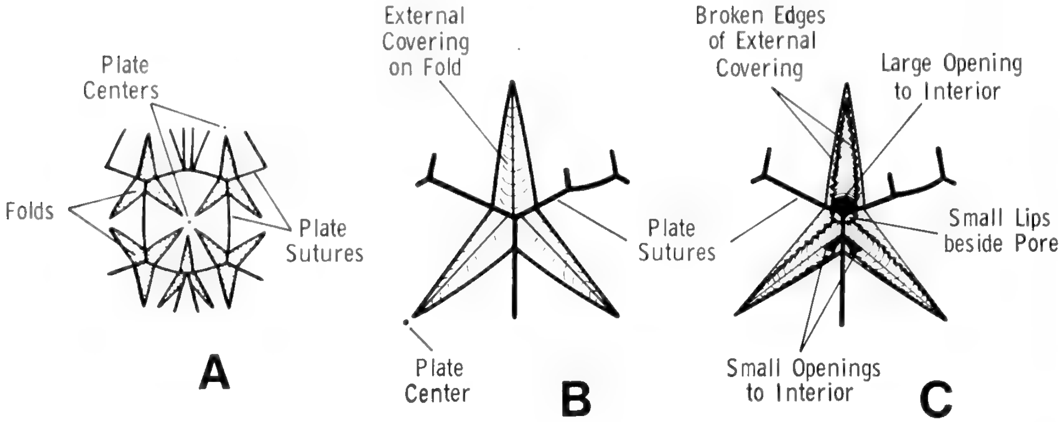


Text-figure 35. Summit morphology in *Lysocystites sculptus.* Composite summit region showing five appendage facets on the adoral edges of the five elongate ambulacral plates, with short food grooves to the central mouth, lateral anus in "CD" interradius surrounded by 4- (or 5-) piece anal oral with somewhat variable sutures, and two additional tiny accessory pores between mouth and anus.

arranged around the axis of the specimen. The single ad- or aboral fold has one relatively large opening to the interior at its base near the sutures (Text-fig. 36C). The two oblique folds are interconnected below the external calcite covering, and each has a smaller opening to the interior near the suture. The ad- or aboral fold may not be connected to the two oblique folds, because there is a high ridge between them to which the external sheetlike calcite covering is attached (Text-fig. 36C). In the interconnected oblique folds, the two pores may represent an incurrent-excurrent combination for the circulation of coelomic fluids, while in the third ad- or aboral fold, both currents may have been present through the single larger opening.

This general type of respiratory structure, covered on the exterior and opening to the interior for the outward closed circulation of coelomic fluids, was termed an exospire by Hudson (1915: 166). Exospire types of calcified respiratory folds are rare in blastozoan echinoderms, but are present in a few paracrinoids and crinoids. Three-cornered respiratory folds are found only in a few crinoids such as *Porocrinus,* except that these folds are reversed and open externally and not internally.

The ambulacral system of *Lysocystites* consists of five appendage facets and short food grooves connecting them to the central mouth (Text-fig. 35). These facets are located on the adoral ends of the five ambulacral plates, are very shallow and symmetrical, and apparently could have had either biserial brachioles or uniserial or biserial arms mounted on them. At present these food-gathering appendages of *Lysocystites* are still unknown, and this is one of the main reasons why this taxon cannot be assigned with certainty to any of the known blastozoan or crinozoan classes. There are no openings through the facets to the calyx interior, the implication being



Text-figure 36. Exospire respiratory folds in *Lysocystites sculptus.* A, location of folds on calyx plates; note that each fold segment grows out from plate center toward three-plate corner. B, complete exospire fold with external calcite covering intact. C, complete exospire fold with broken external covering showing single large and paired small openings to interior, small lips beside openings, and channels beneath each fold segment.

that no radial canal extended out from the calyx interior to the appendage. The food grooves to the mouth are very short, approximately equal to the size of the facets. They slope strongly down into the mouth and are underlain either by the edges of the oral plates or by an adoral continuation of the ambulacral plates. One of the smaller studied specimens (S3163a) shows the former arrangement, while one of the larger ones (S3163d) shows the latter (Pl. 33, figs. 7–8).

The anal opening is located laterally on the "CD" side of the summit in the center of a divided oral plate. It is rounded in shape, and is surrounded by a raised spout-like lip. There are four or more oral segments surrounding it (Text-fig. 35), apparently to allow this opening to increase in size during ontogeny. This anal oral is divided by two somewhat variable oblique sutures aborally into three large elongate segments, and by two relatively symmetrical sutures adorally into a fourth smaller piece. A smaller "third opening," perhaps representing either a hydropore or a hydropore-gonopore combination, is present on the suture between the "D" ambulacral plate and two of the anal oral segments. Another tiny opening is present just below the mouth in the "CD" interradius. No pyramids have been preserved over the central mouth, the anus, or these other openings, although they were probably present in life at least over the mouth and anus.

Most of the calyx plates have fine growth lines on their exterior, the implication being that they probably increased in size by holoperipheral growth. This feature suggests that *Lysocystites* is more likely to have been a blastozoan echinoderm than a crinozoan one.

In conclusion, *Lysocystites* shows a combination of features not found in any of the known echinoderm classes. I have concluded that this taxon is probably not an eocrinoid because of the unusual exospire-type respiratory structures, and also because of its late occurrence in the middle Silurian. However, at present I cannot assign it with certainty to any of the other blastozoan or crinozoan classes, or conclusively eliminate it from the eocrinoids.

Class *PARABLASTOIDEA* Hudson, 1907

Diagnosis. Stemmed blastozoan echinoderms having a blastoid-like calyx with many regularly arranged plates and well-developed pentameral symmetry. Most of the calyx vault is made up of 5 large triangular interradial deltoids bearing slits for the respiratory cataspire system. Five radial ambulacra, composed of biserially arranged flooring plates of only one kind, each bearing a brachiole, lie between the deltoids. Other calyx plates include basals (inferred), radials, and sometime bibrachials, and interbrachials in the pelvis, as well as orals, oral crest plate(s), and sometimes ambulacral wing plates in the vault. A cylindrical or conical oral crest is usually present over the central mouth; ambulacral crests may also be present. The cataspire system consists of multiple pleated folds lying under the deltoids and attached to 3 sets of plates lengthwise: radials (or bibrachials and interbrachials), deltoids, and ambulacral flooring plates. Aboral cataspire openings (probably incurrent) through the deltoids consist either of short aboral slits or else long slits with multiple elongate pores; adoral openings (probably excurrent) consist of relatively large pores between the ambulacral plates at the deltoid margin. Anal opening located between posterior deltoid and oral; no hydropore or gonopore known. Basal cavity usually present. Calyx plates show holoperipheral growth lines sometimes "banded" into larger (perhaps seasonal) groups. Three genera. Early–middle Ordovician, eastern and western North America, and Estonia (U.S.S.R.).

Discussion. Parablastoids form a small but relatively well-defined class of advanced blastozoan echinoderms. They were established as a separate order (of the class Blastoidea) by Hudson (1907: 97), and have recently been raised to class rank by Fay (1967a: S294). They differ from rhombiferan cystoids and blastoids, their closest relatives, in having the following characteristic features: only one type of ambulacral flooring plate (instead of two) with no underlying lancet plate, brachioles articulated with both an ambulacral plate and the edge of the adjacent deltoid, five sets of internal, interradially centered, pleated respiratory structures called cataspires attached lengthwise to three sets of plates with incurrent slits developed only through the large deltoids (and not crossing a plate suture), characteristic calyx plating with strong pentameral symmetry, and a large oral crest sometimes combined with high protective ambulacral crests. When found in the field, the large triangular deltoid plates of parablastoids (see Text-fig. 37) are probably their most distinctive diagnostic feature.

Parablastoids apparently represent a small experimental blastozoan class that adopted a blastoid-like calyx shape and life habitat before true blastoids first appeared. They do not seem to be very closely related to either blastoids or rhombiferan cystoids, and probably had a separate but unknown origin from more primitive eocrinoid ancestors. Since the three genera (one new) and seven species (five new) are known only from the early and middle Ordovician, parablastoids apparently lived only a short time before becoming extinct and never became very widespread. Some forms (including at least two species of *Blastoidocrinus*) seem to have a relatively strong association with algal, sponge, or bryozoan "reefs" (bioherms or biostromes). Their disarticulated remains are often found in dipping beds of calcarenites alongside (but usually not in) massive reef limestones or dolomites, the implication being that these parablastoids may have lived on or alongside these reef buildups in turbulent water. This paleoecologic interpretation is also supported by the prominent development of oral and ambulacral crests in several parablastoids, apparently to protect the short, delicate, retracted brachioles from damage by strong current action. Other genera without ambulacral crests and with long brachioles probaby lived in more quiet-water environments. The three known parablastoid genera are compared in Table 4.

TABLE 4. COMPARISON OF MORPHOLOGY IN THE THREE KNOWN PARABLASTOID GENERA

Genus	Pelvis plating	Aboral cataspire openings	Shape of ambulacra	Oral crest	Ambulacral crest	Brachioles
Blastoidocrinus	many sets of small plates	short slits on aboral margin of deltoid	long and thin	1-piece cylindrical to conical	high crest with wing plates	short and slightly asymmetric
Blastocystis	uncertain, few large plates?	short slits on aboral margin of deltoid	long and thin	unknown	unknown	unknown
Meristoschisma n. gen.	one set of large plates (+ basals)	long slits with multiple pores along deltoid	relatively short and wide	5-piece conical	no crest	long and symmetric, some "abnormal"

Family BLASTOCYSTIDAE Jaekel, 1918

Parablastoids with short cataspire slits confined to the aboral edge of the deltoids. Other features include long, relatively narrow ambulacra, a complexly plated pelvis, a one-piece cylindrical or conical oral crest either with or without protective ambulacral crests, and perhaps short brachioles. Two known genera; early-middle Ordovician.

Genus *Blastoidocrinus* Billings, 1859

Type species, Blastoidocrinus carchariaedens Billings, 1859

Diagnosis. Parablastoids having a wide biconical calyx shape, complex pelvis plating, short aboral cataspire slits on the deltoids, and a 1-piece oral crest usually combined with ambulacral crests. Large vault made up of 5 large triangular deltoids and 5 long ambulacra; smaller pelvis more complex, consisting of 5(?) small hidden basals mounted in a large, very deep, basal cavity, 5 recurved radials, 5 sets of 2 bibrachials, and 5 sets of 13–14 small interbrachials. Ambulacra long and relatively narrow, with only one set of ambulacral flooring plates present. High ambulacral crest often present, made up of 3–4 flaring wing plates mounted on large cover plates protecting main food groove in center of each ambulacrum. Numerous short and slightly asymmetric brachioles mounted along the edges of each ambulacrum; these fit under top of flaring wing plates when folded in against crest. Cylindrical or conical, fluted, oral crest plate covers central mouth and abuts against adoral edges of wing plates (when present). Cataspire system consists of numerous thin-walled closed folds extending under each deltoid from a single set of short slits (incurrent) on its aboral margin to a set of pores (excurrent) opening between the ambulacral flooring plates along the deltoid margin. Stem made up of large rounded columnals with a small lumen. Lower middle Ordovician (Chazian and

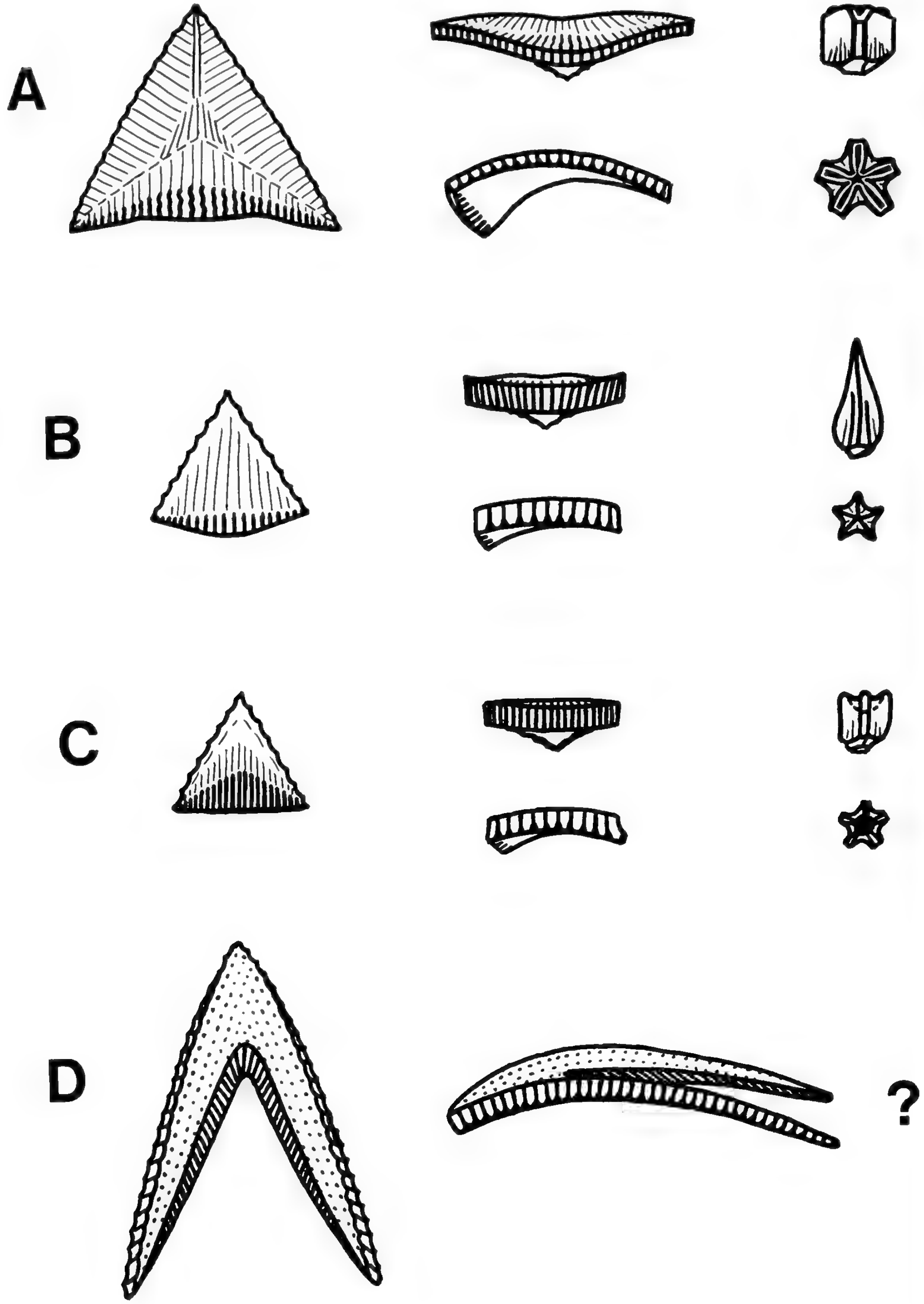
Whiterockian), eastern New York and southern Quebec; northern Utah; central and southwestern Nevada; eastern California; and western Alberta, Canada.

Discussion. Blastoidocrinus is distinguished from other parablastoids by its wide biconical calyx shape, arrangement of numerous small plates in the pelvis below the five large deltoids, cataspires opening as single short slits on the aboral margins of the deltoids, and often by the high, projecting ambulacral crest on each ambulacrum protecting the numerous short, asymmetric brachioles. Other distinctive features include the one-piece oral crest plate that is usually cylindrical in forms with abutting ambulacral crests but may be conical in at least one species, the deep basal cavity housing the stem attachment, and the long thin ambulacra. *Blastocystis* from the Lower Ordovician of Russia is relatively similar to *Blastoidocrinus* in calyx shape, ambulacral development, and cataspire system arrangement, but has a poorly known pelvis that may be quite different and no known oral or ambulacral crests. *Meristoschisma* n. gen., from a slightly younger portion of the middle Ordovician in the central Appalachians, is considerably different in its calyx plating, cataspire slit development, and crest arrangement.

Blastoidocrinus is the most widespread and diverse parablastoid now known, with four assigned or questionably assigned species (Text-fig. 37) in both eastern and western North America. *Blastoidocrinus carchariaedens* from New York and Quebec is still the only species known from more or less complete specimens. Because most of the known specimens are damaged and covered with brachioles, several morphologic features such as the location of the anus and the size, shape, and location of oral plates are still unknown. However, at least one specimen (see Pl. 34, figs. 1–5) is excellently preserved, so except for these minor points, the number, arrangement, and shape of the calyx plates, ambulacral system, and respiratory cataspires are relatively well known. The other three *Blastoidocrinus* species, all new and based on fragmentary plate material from the Rocky Mountains, can only be questionably assigned to this genus because of the incomplete knowledge of their morphology. At least one of these incompletely known species (*B.*(??) *elongatus* n. sp.) is based on deltoid plates very different from all other known species of *Blastoidocrinus* and may belong to another genus.

Several other scattered reports of *Blastoidocrinus* occurrences are probably in error. Phleger (1933: 3) reported the occurrence of *Blastoidocrinus carchariedens* (*sic*) in the Mazourka Formation of eastern California; I examined his studied material in January, 1970, and it represents "*Cheirocrinus*" rhombiferan plates and not *Blastoidocrinus*. Ross (1968: H2 and H11) reported a personal communication from G. A. Cooper that *Blastoidocrinus* plates occur in the Edinburg Formation in central Virginia; since this occurrence is of Black River–Porterfield age and is based only on plates, it very likely represents plates of *Meristoschisma*, which occur in beds of the same age nearby in southwestern Virginia. However, the reported occurrence of "*Blastoidocrinus* sp." plates by Aitken and Norford (1967: 203) in the Outram Formation in southwestern Alberta, Canada, is apparently correct (B. S. Norford, personal communication, 2 July 1968); unfortunately I have not had an opportunity to study this material.

Several of the known *Blastoidocrinus* occurrences are strongly associated with middle Ordovician reefs or banks. Many of the Chazian occurrences of *B. carchariaedens* are associated with small algal or bryozoan reefs. Specimens of *B.*(?) *nevadensis* n. sp. and *B.*(??) *elongatus* n. sp. occur with other echinoderms in the famous "Sponge Beds" at Ikes Canyon, central Nevada; this unit apparently represents a very extensive sponge bank or biostrome. These two species also occur together in dipping beds alongside and just above the top of a very


A
B
C
D
?

large bioherm at Meiklejohn Peak, southwestern Nevada, which was studied by Ross and Cornwall (1962: B231–3). At all of these occurrences, separate plates are very abundant in cross bedded or dipping calcarenite beds, while complete specimens are very rare or nonexistent. These parablastoids probably lived in turbulent water either on or alongside these built-up reefs or banks, and when they died their remains were broken up and swept together into the nearby calcarenite flanking beds. *Blastoidocrinus* seems to have been well adapted for this type of rough water environment, with its protective oral and ambulacral crests, short brachioles, deep stem cavity, and often thick plates. Judging from the abundance of its plates at many of these localities, *Blastoidocrinus* was probably very successful in these favorable environments.

Blastoidocrinus carchariaedens Billings, 1859
Plates 34 and 35; Text-figure 37A

Streptelasma (*Streptoplasma*) *expansa* Hall, 1847: 17, pl. 4, figs. 6a–b; Raymond, 1906: 541; Fay, 1961a: 247–248.

Blastoidocrinus carchariaedens Billings, 1859: 18–22, pl. 1, figs. a–n, text-fig. 6; Miller, 1889: 229, fig. 257; Bather, 1900: 81, text-figs. III–1, 2; Hudson, 1907: 97–120, pls. 1–7, text-figs. 1–3; Hudson, 1911: 203–211, pls. 1–4, text-fig. 1; Jaekel, 1918: 106, text-fig. 99; Wanner, 1933: 496, text-fig. 37; Bassler and Moodey, 1943: 213; Fay, 1956 (unpubl.): 79–80, pl. 36, figs. 1–11; Fay, 1967a: S293–296, text-figs. 175–176.

Nearly all of the known complete specimens of *Blastoidocrinus carchariaedens* were studied for this project. The holotype (GSC 1016; Pl. 35, figs. 1–4), originally described by Billings (1959: 18–22), and the complete and excellently preserved specimen studied by Hudson for his 1907 paper (AMNH 25068) were borrowed for study and comparison. This latter specimen was sectioned by Hudson for information on internal structures (Hudson, 1907: 105; see Pl. 34, figs. 2–4) but unfortunately the polished or thin sections that were made have now been lost. I also borrowed Hudson's collection of figured individual plates from the New York State Museum; a selection of these to show the morphology of the major sets of calyx plates is figured in Plate 34, figures 6–38.

A third partially complete small specimen was found in the University of Cincinnati collection (UC 26022; Pl. 35, fig. 5). Finally, a small collection including three to four small fragmentary pieces and one larger and mostly complete polished specimen (Pl. 35, figs. 6–10) was borrowed from the University of Kansas through Robert O. Fay and Donald B. Macurda, Jr. These specimens have an original Geological Survey of Canada label, and may represent a collection originally made by G. Winston Sinclair that is now missing from the GSC collections (G. W. Sinclair, personal communication, 19 June 1969). No other complete specimens of *Blastoidocrinus carchariaedens* are known to exist except for one that may be in the Wanner Collection, in Bonn, West Germany.

There is a minor systematics dispute involving *Blastoidocrinus carchariaedens* and the taxon *Streptelasma expansa* Hall, 1847, which was originally described as a

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Text-figure 37. Comparison of deltoid and oral crest plates in species of *Blastoidocrinus*. A, *B. carchariaedens* from the Chazy Group and Aylmer Formation, eastern United States and Canada; note large size, thinness, and strong convex profile of deltoids longitudinally, plus squat, cylindrical shaped oral crest plates with shallow summit grooves. B, *B.*(?) *rossi* n. sp. from the Garden City Formation, northern Utah; note bulged aboral margin, great thickness, and slanted lateral cataspire slits in deltoids, as well as high conical oral crest plates. C, *B.*(?) *nevadensis* n. sp. from the Antelope Valley Limestone of Nevada; note long, closely spaced cataspire slits and great thickness of deltoids, as well as elongate cylindrical shape and summit concavity in oral crest plates. D, *B.*(??) *elongatus* n. sp. from the Antelope Valley Limestone of Nevada; note large size of deltoids, extremely elongate limbs with a slight inward "twist," and numerous ambulacral plates and cataspire slits.

coral but may be a *Blastoidocrinus* fragment. This problem was mentioned by Raymond (1906: 541) in a footnote, and reviewed in a short paper by Fay (1961a: 247–248); however, neither of these authors examined Hall's original material. Until the type specimen of S. *expansa* is found and studied (it is supposed to be in the American Museum of Natural History), no action can be taken concerning this possible synonymy.

Specific description. The calyx in this species has a wide biconical shape and is slightly wider than long (L/W ratio = 0.95). The vault with its ambulacral crest is much longer than the pelvis (V/P ratio = 3.9). Hudson's specimen has a large and moderately deep basal cavity, 8.0 mm in diameter and at least 3.0 mm deep, occupied by 5–6 articulated round disklike columnals, each 3 mm in diameter and 0.7 mm thick with a small lumen (Pl. 34, fig. 1). The basals, located deep in the basal cavity, are hidden by the attached stem in all except Billings' type specimen (Pl. 35, fig. 1), where they appear on the broken vertical surface through the center of the specimen. Both Hudson and Fay have inferred that the most likely number of basals is 5 and that they are interradial in position. The 5 thick radial plates are strongly recurved to form the lip of the basal cavity and the lower part of the calyx (Pl. 34, figs. 1 and 22–27). They are surmounted by 5 pairs of radially located bibrachial plates, notched at their adoral ends to receive the aboral tips of the ambulacra (Pl. 34, figs. 1 and 4–5). The 2 bibrachials in each set are approximate mirror images of each other, and are joined together by a relatively deep, strong suture (Pl. 34, figs. 28–32). Between the bibrachial sets and above the radial circlet in an interradial position are 5 groups of small interbrachial plates in 2 configurations: A) 3 larger plates surmounted by 10± smaller ones (Pl. 34, fig. 4, left), or B) 2 larger plates surmounted by 11± smaller ones (Pl. 34, fig. 4, right). These 2 interbrachial configurations alternate in the following pattern: "-B-A-B-A-B-," and not the "all-A" configuration indicated by Fay (1967a: S294, fig. 175, 2). This arrangement defines a vertical plane of symmetry through the specimen that may extend through the "CD" interradius (central B area with A's on both sides?) where the still unknown anal opening was located. At present, this slight variation in the interbrachial plating represents the only externally visible departure from strict pentameral symmetry that has been seen in these complete specimens of *Blastoidocrinus*.

The 5 large and distinctive deltoids of *Blastoidocrinus carchariaedens* are one of the most characteristic features of this species, and allow its identification even from isolated plates. Each deltoid is almost an equilateral triangle in side view, although it is folded into a moderately concave profile transversely, and a moderately convex profile longitudinally (Pl. 34, figs. 3–14; Text-fig. 37A). These deltoids are relatively thin for their size, and are often found broken in the field. In Hudson's studied specimen, the deltoids are 13 mm wide at the base, 14 mm long on a side, and 11.5 mm high. Each deltoid is bordered by an ambulacrum bearing brachioles along its lateral margins. The aboral margin of each deltoid contains the incurrent openings to the internal cataspire system. These aboral openings are moderately short thin slits separated by relatively prominent ridges. Hudson's specimen has between 32–34 cataspire slits at the base of each deltoid, ranging in length from 1.7 mm long near the center of the deltoid down to 0.2–0.3 mm near the corners. Each of the cataspire slits is about 0.08–0.1 mm wide. The central 9–12 longest slits above the interbrachial plates have a sinuous or wavy opening; most of the shorter slits on either side are nearly straight (Pl. 34, fig. 5). These aboral cataspire slits usually match up either with the interbrachial sutures or with groovelike ornament on the bibrachial plates (Pl. 34, figs. 4–5); however, the slits into the calyx interior are present only on the deltoids and do not extend any further aborally onto these bordering plates.

The cataspire folds extend under the deltoid up to the edges of the bordering ambulacra, where they apparently open in a line of pores near the attachment bases of the brachioles. Billings' type specimen shows that these pores lie between the ambulacral flooring plates at the edge of the deltoid (Pl. 35, fig. 3). However, the number of pores bordering the side of each deltoid (25–27 in Hudson's specimen) is considerably larger than half the number of aboral cataspire slits (16–17 in this specimen); therefore, each cataspire fold must open adorally into 1 or more pores.

The 5 ambulacra in *Blastoidocrinus carchariaedens* are relatively long and narrow, extending from the oral surface down over the calyx to the adoral edges of the bibrachial sets. In Hudson's specimen, the ambulacra are approximately 14.0 mm long and 5.5–6.0 mm wide near the top (Pl. 34, figs. 3–4). Billings' type specimen shows that the ambulacra are made up of alternating flooring plates of only one type, and lie just below the edge of the adjacent deltoid (Pl. 35, fig. 3). There is no underlying lancet plate present. The main food groove runs down the center of the ambulacrum, sending off short side food grooves to each of the brachioles. There is a biserial set of relatively large and thick ambulacral cover plates protecting this main food groove (Pl. 35, figs. 8–10) with 3–4 long, vertical, flaring, rail-shaped wing plates mounted on top of them in an ambulacral crest (Pl. 34, figs. 3–5 and 33–38). The brachioles are mounted on facets at the abmedial edge of the ambulacral flooring plates up against the edge of the deltoid; it seems likely that the lowest brachiolar plate is articulated with the deltoid also (Pl. 34, fig. 5). There are 25–27 brachioles mounted on each side of the ambulacrum in Hudson's specimen, giving a total brachiole count of approximately 250–270 in this specimen. The brachioles are relatively short, ranging from 10.0 mm long at the aboral end down to 7.5 mm at the adoral end of the ambulacrum (Pl. 34, figs. 3–5). When infolded against the ambulacral crest, probably their normal resting position, they reach almost to the flared top portion of the wing plates. Thus, these wing plates probably served to protect the infolded resting brachioles from damage by current action or predators. As is true in the rhombiferan cystoid *Caryocrinites,* which also has a protective ambulacral crest on its arms (see Sprinkle, 1968: 210), the brachioles in *Blastoidocrinus* are slightly asymmetrical, with one set of brachiolar plates slightly larger than the other. This probably results from the need to fold tightly against the crest with no brachiolar sutures exposed, and to have a more massive column of brachiolar plates facing the outside. Except for this slight asymmetry, the brachioles in *Blastoidocrinus carchariaedens* appear to be normal with a regular biserial arrangement of brachiolar plates, and probably only one set of very small, biserial, brachiolar cover plates.

On the basis of his own figures of the sections (now missing) that Hudson made in the side of his specimen, the cataspire folds appear to extend up under the deltoids to the edge of the ambulacra as thin-walled closed tubes. The presence of thin slits aborally and larger round pores adorally indicates that the flow is most probably in an adoral direction (see p. 33), opposite to that proposed by Hudson (1915: 165).

The mouth in *Blastoidocrinus* appears to have been located in a central position on the summit at the junction of the 5 ambulacra. It probably lay directly beneath the large capping, cylindrical and fluted, oral crest plate (Pl. 34, figs. 2–3 and 15–21; Text-fig. 37A), which abuts the adoral ends of the 5 ambulacral crests. The anus

Table 5. Measurements for the deltoid growth series of *Blastoidocrinus*(?) *rossi* n. sp.

Deltoid	Length (mm)	Width (mm)	DAmb suture (mm)	# Amb. facets	# Cataspire slits	Slit length (mm)
D1	2.7	2.9	2.5	3–4	6	0.46
D2	2.9	3.7	3.0	4	6	0.42
D3	3.7	3.8	3.2	4	6	0.50
D4	4.3	4.7	3.8	5	8	0.69
D5	4.7	5.4	4.8	5–6	9	0.77
D6	5.2	5.8	5.2	7	12	0.78
D7	5.8	7.3	5.8	7	12	0.88
D8	6.3	7.3	6.4	7–8	12(?)	0.92
D9	6.9	9.4	7.5	7–8	15(?)	1.00
D10	7.1	9.4	9.0	10	16	0.96
D11	8.5	10.3	9.3	10–11	17	0.85
D12	9.6	10.2	10.6	11	19	1.80
D13*	10.9	13.7	10.8	11	21	2.00
D14	11.8	12.7	12.8	12	19	2.40

* Holotype

has not yet been found, probably because of the complete brachiole cover or incompleteness of most of the known specimens. No hydropore or gonopore has been observed in these specimens, and oral plates surrounding the mouth, similar to those in *Blastoidocrinus*(?) *rossi* n. sp. and *Meristoschisma hudsoni* n. gen., n. sp., are also unknown at present.

Discussion. Based on the studied specimens, both the New York and Quebec occurrences seem to belong to the same species. Most of the known complete specimens come from the area around Montreal; however, none of these is as well preserved as Hudson's single specimen from Valcour Island, New York. At both localities this parablastoid is associated with small algal, stromatoporoid, and bryozoan reefs (see p. 143). The absence of oral plates from Hudson's plate material is puzzling; since no orals are exposed in his complete specimen, he probably didn't recognize any orals in his washed residue as coming from *Blastoidocrinus* or pick them out. Unfortunately, all the remaining unfigured plate material mentioned in his 1907 article is now missing from Hudson's collections in New York City and Albany.

Stratigraphic and geographic range. Chazy Group, lower Middle Ordovician, Lake Champlain region of New York and Vermont; Aylmer Formation of same age, Montreal region, Quebec, Canada.

Studied specimens. Holotype GSC 1016, figured plesiotypes UC 26022, as well as a large unnumbered specimen apparently belonging to the Geological Survey of Canada, all from near Montreal, Canada; figured plesiotypes AMNH 25068 and plates NYSM 7390–7450, from Valcour Island, Lake Champlain, New York.

Blastoidocrinus(?) *rossi* new species

Plate 36; Text-figure 37B

Blastoidocrinus cf. *B. carchariaedens* (Billings), Ross, 1949: 480; 1951: 27, 30, 31; 1968: H10–11, pl. 4, fig. 24.

R. J. Ross, Jr. (1949, 1951, 1968) reported the occurrence of deltoid plates referable to the genus *Blastoidocrinus* from zones K and L of the Garden City Formation in northern Utah. A large collection of *Blastoidocrinus* plates accumulated by Ross was borrowed from the U. S. Geological Survey in Denver, and additional material was collected in the field in 1967. The material is preserved only as separate silicified plates recovered from acid residues of thin-bedded fossiliferous limestones. This taxon, representing a new species, is provisionally referred to *Blastoidocrinus* because of the incomplete nature of the preserved material and differences from *B. carchariaedens* shown by some of the separate plates. Deltoid plate USNM 165478 is here designated as holotype and figured with 13 additional deltoids and seven other calyx plates on Plate 36. Measurements for the deltoid growth series are listed in Table 5.

Specific description. Deltoid plates, oral crests, two bibrachials, and several possible oral plates are present in the borrowed and collected material. The characteristic deltoid plates are the most abundant plates in this silicified material. They are triangular and often nearly equilateral in shape with a slightly bulged aboral margin. The plate width is slightly greater than the length, and the plates are relatively thick for their size (Pl. 36, figs. 2–4), much thicker than in *B. carchariaedens.* These deltoids have a slightly convex shape longitudinally and a flat to slightly concave shape transversely. The cataspire slits are developed as single, relatively short slits only at the aboral margin of the plate. The longest slits in the center of the plate are only 2.0 mm long in the holotype specimen, which has a total length of about 11 mm. Besides being longer, these central slits are spaced somewhat further apart in the exterior than the slits nearer the margins of the plate, and an aboral edge view of the deltoid shows that these central slits "flare" towards the exterior, with the lateral slits on either side slanting slightly (Pl. 36, fig. 2). This increased spacing of the central slits may also be present in *B. carchariaedens,* but there is apparently no slanting of the lateral slits in this latter form. Several of these deltoids, especially the smaller ones, have relatively coarse vertical ridges located between the cataspire slits and extending up most of the length of the plate (see Pl. 36, figs. 23–29). The growth series has a relatively large size range, from extremely small to medium size. A few larger incomplete specimens were also present in the acid residues, but were not well enough preserved to be included in this series. The total number of ambulacral facets on both lateral margins of the deltoid, indicating the number of ambulacral flooring plates and cataspire pores, is somewhat greater than the total number of cataspire slits on the deltoid (24 vs. 19 in deltoid D14—see Table 5), the indication being that some cataspire folds must exit through more than one ambulacral pore.

The distinctive oral crests represent the second most abundant plates of *B.*(?) *rossi.* These oral crests are one-piece, elongate, conical to cylindrical plates with ridgelike fluting running up their sides (Pl. 36, figs. 6–10; Text-fig. 37B). They have a rounded, faceted adoral end where they were attached to the peristome, sometimes with an opening on one larger face ("CD"?) where the anal pyramid may have been located. These oral crest plates are about twice as long as they are wide and only the few partially cylindrical ones have any vertical faceted edges. The oral crest plates in *B.*(?) *rossi* have a much different shape from those of *B. carchariaedens* (compare Text-figs. 37A and B). In addition, the conical shape of most of the plates implies that no ambulacral crest with abutting wing plates was present as in *B. carchariaedens.*

Two plates that appear to be bibrachials of *B.* (?) *rossi* were found in one of the residue collections (Pl. 36, figs. 11–16). They have an elongate, asymmetrical, hexagonal shape and are moderately concave in edge view. These plates are relatively thick (the same is true in *B. carchariaedens*), and have a straight interbibrachial suture, and a slightly curved bibrachial-deltoid suture with fine vertical marking, perhaps indicating the location of the cataspire slits on the adjacent deltoid. The exterior of these plates (especially the lower half) is ornamented with relatively coarse ridges running from the center of the plate to each edge (Pl. 36, fig. 12).

Several possible oral plates that may

belong to *B.*(?) *rossi* have also been picked out of the acid residues. However, since the orals are still unknown in *B. carchariaedens,* identification of these plates remains especially difficult. They are small plates having a rounded pentagonal shape and bilateral symmetry (Pl. 36, figs. 17–22). The two sloping lateral margins and adoral end have bevelled edges above the vertical sutures (Pl. 36, figs. 19–20) that could represent the locations of the main food grooves leading to the mouth. These plates have relatively smooth and unornamented exterior surfaces, with only a thin shallow furrow running down the center of the plate. The aboral edge has a small central projection near the top of the vertical suture (Pl. 36, figs. 17–18), perhaps analogous to the small "nick" and projections noted on the orals in *Meristoschisma hudsoni* (see p. 163). Until a complete specimen of *B.*(?) *rossi* is found, it can only be inferred that these oral plates belong to this taxon.

Discussion. Blastoidocrinus(?) *rossi* seems to be relatively closely related to *B. carchariaedens* from the Chazy Group and to *B. nevadensis* n. sp. from the Antelope Valley Limestone. It differs from both in having small, thick, slightly bulged, deltoid plates with slanted lateral cataspire slits, and in having a long conical oral crest instead of a squat cylindrical one. Since most of the pelvis plating is still unknown, and ambulacral crests may have been absent (inferred from the conical shape of most of the oral crests), this new form can only be provisionally referred to the genus *Blastoidocrinus.* The determination of these unknown features will probably have to await the discovery of a complete specimen of *B.*(?) *rossi* from the Garden City Formation. *B.*(?) *rossi* occurs with cystoid plates belonging to the genus "*Cheirocrinus,*" crinoid plates belonging to *Palaeocrinus* and other genera, many brachiopods, and relatively few trilobites.

Etymology. This species is named after Reuben J. Ross, Jr. of the U. S. Geological Survey, Denver, who originally collected and figured this taxon, and who greatly assisted me in my search for Ordovician blastozoan echinoderms in the Rocky Mountains.

Stratigraphic and geographic range. Trilobite zones K and L (*Orthidiella* zone), Garden City Formation, lower Middle Ordovician (Whiterockian), northern Utah (USGS localities D190d CO and D190e CO [both Ross], and my localities LO-1. and MU-1.).

Studied specimens. Holotype USNM 165378 (deltoid D13), figured paratypes USNM 165379–91, (deltoid growth series D1–12 and D14), USNM 165392–4 (oral crests), USNM 165395–6 (bibrachial), and USNM 165397–8 (possible orals). The remainder of this acid residue material is deposited in USGS collections D190d CO and D190e CO (Denver), and MCZ 612.

Blastoidocrinus(?) *nevadensis* new species
Plate 37, figures 1–18; Text-figure 37C

This species, known from only two localities in Nevada, is not as well preserved or distinctive as the other Rocky Mountain species of *Blastoidocrinus.* Deltoid MCZ 613 is here chosen as holotype and described along with eight other deltoid plates and one oral crest designated as paratypes. Measurements for the nine specimens in the deltoid growth series are listed in Table 6.

Specific description. Deltoids and a few oral crests are the only plates that have been found. The deltoids are triangular, somewhat wider than long, and relatively thick (Pl. 37, figs. 1–5). They have a moderately convex profile longitudinally and a slightly concave profile transversely. The aboral margin bearing the cataspire slits is straight to slightly concave, unlike *B.*(?) *rossi* in which this margin is slightly convex or bulged (Text-figs. 37B and C). A relatively large number of cataspire slits is present on each deltoid, and the slits are very narrow and closely spaced. These

TABLE 6. MEASUREMENTS FOR THE DELTOID GROWTH SERIES OF *BLASTOIDOCRINUS*(?) *NEVADENSIS* N. SP.

Deltoid	Length (mm)	Width (mm)	DAmb (mm)	# Amb. facets	# Cataspire slits	Slit length (mm)
D1	3.2	3.8	3.4	6	8–9	0.3
D2	3.9	4.1	4.5	8	12?	0.3
D3	5.2	5.7	5.7	9^{+}	13^{+}	0.5
D4	5.6	5.9	6.3	10	17	0.4^{++}
D5	6.3	7.2	7.2	11	20^{+}	–
D6	7.8	7.7	8.5	12–13	22	0.5^{++}
D7*	7.6	8.8$^{\pm}$	8.5	12–13^{+}	21^{++}	2.1
D8	9.3	10.0$^{\pm}$	10.0$^{\pm}$	13^{++}	24^{++}	0.9^{++}
D9	10.9	–	–	17^{+}	24^{++}	3.5

* Holotype

slits are also relatively long in relation to the plate size (3.5 mm long in the 11-mm long largest paratype). There is no slanting of the lateral slits, and the center slits have only a slightly greater interslit spacing than the lateral ones (Pl. 37, figs. 1, 2, and 4). In most of these features, *B.*(?) *nevadensis* more closely resembles *B. carchariaedens* from the eastern United States and Canada than either of the other Rocky Mountain species.

Most of the oral crest plates of *B.*(?) *nevadensis* are relatively short and cylindrical in shape (Pl. 37, figs. 6–9; Text-fig. 37C), but a few are taller and partially conical. They have deeply fluted, vertical sides and a convex attachment base at the bottom. The length and width are nearly the same in most of the larger plates, but smaller plates are relatively taller. In top view they are strongly star-shaped, with a relatively deep, hemispherical cavity in the center of the upper surface (Pl. 37, figs. 7 and 9), unlike *B. carchariaedens*, which has 5 radiating shallow grooves here (Text-figs. 37A and C). The cylindrical shape and vertical sutured sides of these oral crest plates imply that *B.*(?) *nevadensis* probably had ambulacral crests with vertical wing plates that abutted against the oral crest. No other calyx plates of *B.*(?) *nevadensis* are known.

Discussion. *B.*(?) *nevadensis* from the Antelope Valley Limestone of Nevada appears to be more closely related to *B. carchariaedens* from the Chazy Group of the eastern United States and Canada than to the other Rocky Mountain species. It differs from this eastern species in having a much thicker deltoid with a less convex longitudinal section and straight, closely-spaced slits, and a somewhat more elongate oral crest with a large hemispherical cavity on the upper surface. Since the pelvis plating is still completely unknown in *B.*(?) *nevadensis*, it can only be questionably assigned to this genus at the present time. *B.*(?) *nevadensis* differs from *B.*(?) *rossi* in having somewhat differently shaped deltoids with longer, more numerous, nonslanted cataspire slits, and in having cylindrical instead of elongate-conical oral crests. *B.*(??) *elongatus*, which occurs with *B.*(?) *nevadensis* at both of the known localities in Nevada, has a much different deltoid shape with many more cataspire slits and ambulacral facets. If the pelvis plating of *B.*(?) *nevadensis* is found to be similar to that in *B. carchariaedens*, then this Whiterockian species from the Rockies could either be ancestral to, or a contemporary of, the similar-appearing Chazian species, depending on how these middle Ordovician stages are correlated.

Stratigraphic and geographic range. Antelope Valley Limestone (*Orthidiella*(?) zone), early Middle Ordovician (Whiterockian), flanking beds near the top of the large reef at Meiklejohn Peak (locality MJ-1.), southwestern Nevada, and in the

Table 7. Measurements for the two figured deltoids of *Blastoidocrinus*(??) *elongatus* n. sp.

Measurement	Holotype MCZ 610	Paratype MCZ 611a
Length of Limb (mm)	26.7 (incompl.)	20.6 (incompl.)
Total Width (mm)	14.9 (incompl.)	14.8 (incompl.)
# Cataspire Slits	68–69$^+$	58–59$^+$
# Amb. Facets/Side	35$^+$	30$^+$
Max. Width of Limb (mm)	3.8	3.7
Angle between Limbs	35–40°	~45°
Max. Slit Length (mm)	2.5	2.5

"Sponge Beds" at Ikes Canyon (locality IK-3.), central Nevada.

Studied specimens. Holotype MCZ 613 (deltoid D7); paratypes MCZ 614 (deltoids D1–6, D8–9) and MCZ 615 (oral crest), all from MJ-1.; additional material, MCZ 643, approximately 20–30 additional poorly preserved silicified deltoids and oral crests from MJ-1., and MCZ 644, several additional deltoid plates from IK-3.

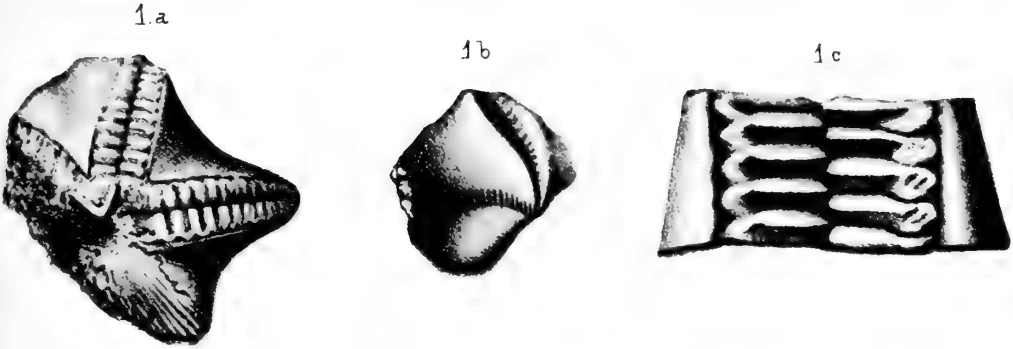
Blastoidocrinus(??) *elongatus* new species

Plate 37, figures 19–23; Text-figure 37D

This striking new form, very questionably referred to the genus *Blastoidocrinus*, is known only from a few deltoid plates from central and western Nevada. Deltoid MCZ 610 is here designated as holotype and described along with 16 additional paratypes under numbers MCZ 611a–c. Measurements for the holotype and figured paratype are listed in Table 7.

Specific description. The deltoid plates in this new species are very large, equalling or surpassing in size the largest deltoid plates of *B. carchariaedens* that I have observed. They have a strongly elongate, inverted parabola- or V-shape in side view, with a moderately convex profile longitudinally (Pl. 37, figs. 19–23; Text-fig. 37D). The inverted "limbs" of these deltoid plates are very thick and strongly calcified along the adjacent ambulacra, but the aboral central portion of the plate where the cataspire slits opened was apparently more weakly calcified. These long deltoid limbs are slightly curved inward, and show a gradual "twist" that serves to raise the ambulacra on the exterior margins slightly and depress the central cataspire slit area (Text-fig. 37D). The cataspire openings appear to have been single, relatively short slits acting as inlets to the short cataspire folds running obliquely under the limbs of the deltoid to porelike openings along the margin of the ambulacrum between each 2 flooring plates (Pl. 37, fig. 23), as in other species of *Blastoidocrinus*. The original shape of the aboral margin of these deltoids probably was relatively similar to the preserved shape, with the large parabola-shaped interior region filled in with many interbrachial (or accessory) plates. The long limbs and large number of ambulacral facets (Pl. 37, figs. 22–23) indicate that this species must have had very long narrow ambulacra with many flooring plates and brachioles. The total number of ambulacral facets on both margins is very close to the total number of cataspire slits (70+ vs. 68 to 69+ in holotype MCZ 610), the implication being that there was probably only 1 outlet pore per inlet slit, without any branching or coalescing in the cataspire folds. This is unlike most species of *Blastoidocrinus*, in which these numbers are unequal. Deltoid plates preserved in calcite (see Pl. 37, fig. 21) have rows of strong pustular ornament paralleling the ambulacral margins. No other calyx plates of *B.*(??) *elongatus* are known.

Discussion. Blastoidocrinus(??) *elongatus* differs strongly from all other species of this genus by having: 1) very large, parabola-shaped deltoid plates with extremely long marginal limbs, 2) very numerous short cataspire slits along the entire inside edge of the deltoids, 3) extremely long ambulacra with many flooring plates (and brachioles), and 4) apparently equal num-



Text-figure 38. Original figures of *Blastocystis rossica*. Summit view (left) of only known complete specimen showing long narrow ambulacra, large concave deltoids, and possible oral plate (top center); side view (center) of same specimen showing short aboral cataspire slits in deltoid and lack of plates in pelvis; enlarged view of an ambulacrum (right) showing only one type of flooring plate with brachiole facets. From Schmidt (1874: pl. 3, figs. 1a–c).

bers of inlet slits and outlet pores for the cataspire system. *B.*(??) *elongatus* appears to have had longer ambulacra and more cataspire slits than any other known parablastoid. It seems likely that when more complete material is eventually collected, this unusual species will be found to belong to a new parablastoid genus, and not to *Blastoidocrinus*. However, because only a few deltoid plates are now known, I have decided for the present to refer this species provisionally to *Blastoidocrinus*.

Stratigraphic and geographic range. Antelope Valley Limestone, *Orthidiella*(?) zone, early Middle Ordovician (Whiterockian), flanking beds near the top of the large reef at Meiklejohn Peak (locality MJ-1.), western Nevada, and in the "Sponge Beds" at Ikes Canyon (locality IK-3.), central Nevada.

Studied specimens. Holotype MCZ 610; figured paratype MCZ 611a; additional paratypes MCZ 611b–c (15 specimens).

Genus *Blastocystis* Jaekel, 1918

Type species, Blastocystis rossica Jaekel, 1918

Diagnosis. Poorly known parablastoids having a biconical calyx shape. Calyx vault composed of 5 large triangular deltoids and 5 long ambulacra; pelvis incomplete, poorly known, perhaps composed of few large plates. Ambulacra relatively long and narrow, made up of only 1 biserial set of ambulacral flooring plates. Brachioles unknown, probably 1 per ambulacral plate; ambulacral (and oral) crests absent? Mouth central, surrounded by 5(?) small orals; anus probably lateral, at adoral edge of deltoid. Cataspire system consists of closed internal folds opening aborally as short slits at the aboral edge of the deltoids and adorally as pores between the ambulacral plates at the deltoid margins. Stem, internal structures, and other features unknown. Kunda Formation (B_3), upper Lower Ordovician, near Leningrad, U.S.S.R.

Blastocystis rossica Jaekel, 1918
Text-figure 38

Blastoidocrinus carchariaedens (Billings) aff., Schmidt, 1874: 27–28, pl. 3, figs. 1a–c; Jaekel, 1899: 389, pl. 7, figs. 12–13.

Blastocystis rossica Jaekel, 1918: 106–107; Bassler and Moodey, 1943: 213; Fay, 1967a: S296.

Discussion. Only one incomplete specimen of this genus and species is known to exist (Text-fig. 38), and this specimen was not available for study during this project. From the described and figured morphology, *Blastocystis* seems to be most closely related to *Blastoidocrinus* in having a similar calyx shape, long narrow ambulacra, and cataspires opening in a set of short slits at the aboral edge of the deltoids. It differs from *Blastoidocrinus* in having poorly known pelvis plating (perhaps only a few large plates) and possibly in lacking ambulacral and oral crests. However, some of these differences, especially in regard to the loosely articulated crests, may result from the incompleteness of the only known specimen. If Schmidt's drawing of the poorly preserved pelvis is incorrect (Text-fig. 38, 1b), *Blastocystis* could be very closely related to *Blastoidocrinus* and perhaps even synonymous. Because of the very different aboral cataspire openings and the differently shaped ambulacra, *Blastocystis* does not seem to be very closely related to *Meristoschisma*. Although poorly known, *Blastocystis* now represents the earliest recorded parablastoid (late early Ordovician).

Family MERISTOSCHISMATIDAE new family

Diagnosis. Parablastoids with long cataspire slits on the deltoids divided internally into multiple pores. Other features include relatively short, wide ambulacra, a simple pelvis with only 2 sets of plates, relatively large oral plates, a 5-piece conical oral crest with no ambulacral crests, and long brachioles. One genus; middle Ordovician.

Discussion. This new family is based on the new genus *Meristoschisma*, which differs considerably from the other two parablastoid genera included in the family Blastocystidae. The most important differences involve the aboral cataspire openings, the pelvis plating, and the oral crest and brachiole arrangement.

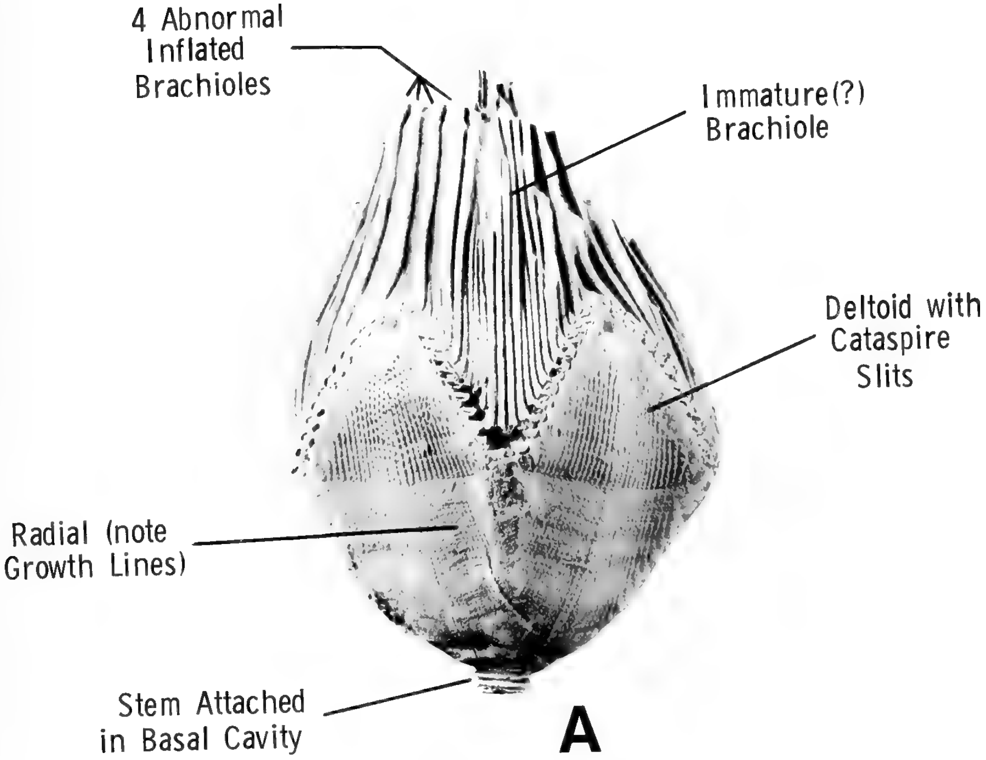
Genus *Meristoschisma* new genus

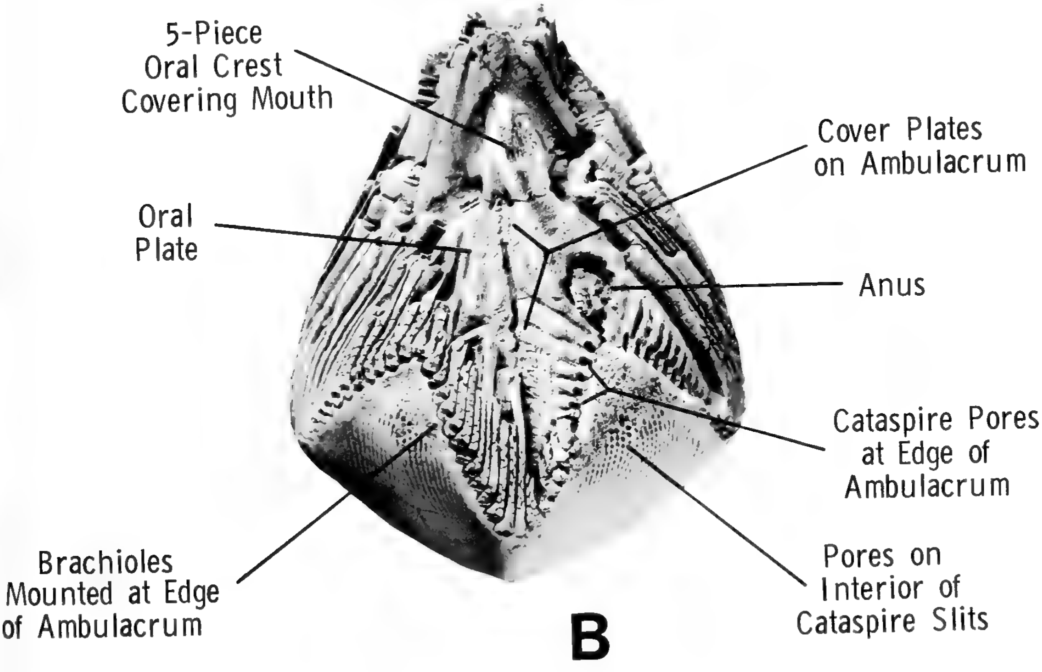
Type species, Meristoschisma hudsoni new species

Diagnosis. Parablastoids having a rounded biconical calyx with simplified plating and well-developed pentameral symmetry. Calyx vault made up of 5 large triangular deltoids, 5 smaller orals around mouth, and 5 relatively short, wide ambulacra. Pelvis consists of 5 large radials and 5(?) small hidden basals located in a moderately deep basal cavity. Ambulacra relatively short and wide, bearing only 1 set of ambulacral flooring plates. Brachioles long and symmetrical, mounted at the edge of the ambulacra next to the deltoids. Every fourth or fifth brachiole slightly abnormal; inflated to about twice normal size with irregular brachiolar plating. Anus located near aboral edge of "CD" oral, which is divided into several segments. Central mouth covered by sharply pointed and fluted conical oral crest made up of 5 small plates; covered food grooves from ambulacra enter under edge of crest. Cataspire system consists of numerous thin-walled internal folds extending under each deltoid, opening aborally as long (inlet?) slits with multiple elongate pores along most of deltoid length, and adorally as larger (outlet?) pores between the ambulacral flooring plates along the deltoid margin. Cataspire folds show sharp outward bend near ambulacra, and several folds may coalesce to open into a single outlet pore. Larger calyx plates show holoperipheral growth lines and possible seasonal banding. Stem made up of thin flanged columnals with a small lumen. Benbolt Formation, Middle Ordovician (Black River–Porterfield), southwestern Virginia and northeastern Tennessee.

→

Text-figure 39. Calyx and brachiole morphology of *Meristoschisma hudsoni* n. gen., n. sp. A, side view of holotype specimen MCZ 594 showing calyx proportions, large deltoid and radial plates, short stem segment attached in basal cavity, and normal and abnormal brachioles attached to edge of wide ambulacra. B, oblique summit view of same showing 5-piece oral crest, oral plates, anal opening, ambulacra with tiny cover plates, and excurrent cataspire openings.


4 Abnormal Inflated Brachioles
Immature(?) Brachiole
Deltoid with Cataspire Slits
Radial (note Growth Lines)
Stem Attached in Basal Cavity
A


5-Piece Oral Crest Covering Mouth
Cover Plates on Ambulacrum
Oral Plate
Anus
Cataspire Pores at Edge of Ambulacrum
Brachioles Mounted at Edge of Ambulacrum
Pores on Interior of Cataspire Slits
B

Etymology. The generic name is derived from *meristos* (Gr.)—divided, and *schisma* (Gr.)—slit, referring to the multiple openings through the cataspire slits on the deltoids.

Discussion. Meristoschisma appears to be somewhat more advanced than the other two known parablastoid genera. The pelvis plating has been considerably simplified by the apparent combination of the radial-bibrachial-interbrachial sets found in *Blastoidocrinus* into a single series of radials that are now larger than the characteristic deltoids. The aboral cataspire openings are developed as long slits with multiple pores instead of the short slits found in other parablastoids; however, the rest of the cataspire system is probably very similar. Ambulacral crests are absent and the oral crest is conical and consists of five plates. The brachioles are also long and symmetrical. These last two features suggest that *Meristoschisma* was not a rough-water, near-reef inhabitant like many of the species of *Blastoidocrinus*. This may imply that although *Meristoschisma* was more advanced in its calyx structures, it was less specialized or restricted than some other parablastoids in its environmental requirements.

As far as I have been able to determine, this is the first described report of parablastoids in the southern Appalachians. This is somewhat surprising considering how abundant separate *Meristoschisma* plates, including the characteristic deltoids, are at some localities in the Benbolt Formation. No material belonging to *Meristoschisma* was found in the extensive Bassler or Springer collections at the U. S. National Museum or in other collections. I suspect that some occurrences of *Meristoschisma* plates have been referred to as "cystoid plates" in various stratigraphic publications or county and quadrangle reports. The only published report that may represent a *Meristoschisma* occurrence is the note by Ross (1968: H2, H11) of a personal communication from G. A. Cooper concerning *Blastoidocrinus* plates in the Edinburg Formation of central Virginia. The age of this occurrence (Black River–Porterfield) and the proximity to the Benbolt outcrop belt suggests to me that this material most likely belongs to *Meristoschisma*.

Another probable reason why *Meristoschisma* has not been reported before is the relative scarcity of complete specimens. Although separate plates are abundant at several localities, I was able to collect only two complete specimens in approximately seven weeks of field work. Since the calyx is made up of two major sets of plates joined by a suture that extends all the way around the equator, it probably tended to fall apart quite easily soon after death. This has resulted in a wealth of plates, but relatively few complete specimens ever being preserved intact. Fortunately, the holotype specimen is so well preserved (Text-fig. 39) and fortuitously weathered on one side to show the ambulacra, oral region, and anal opening, that almost all the morphologic features of this new genus can be described.

Meristoschisma hudsoni new species

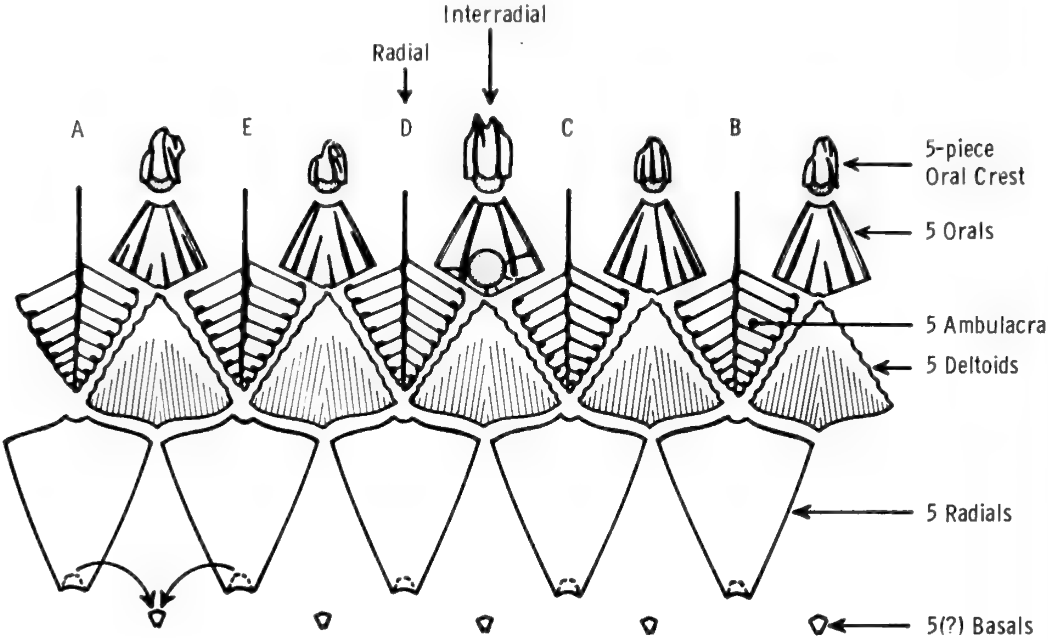
Plates 38–39; Plate 40, figures 1–10; Plate 41, figures 1–20; Text-figures 5G, 18, and 39–42

Only two complete specimens of this parablastoid are known to exist (Pl. 38, figs. 1–8). The small paratype (MCZ 595) and the large, excellently preserved holotype (MCZ 594) were both collected during the summer of 1967; measurements for these two specimens are listed in Table 8. In addition, approximately 300 well-preserved separate plates of this species have also been found at several localities in the Valley and Ridge Province of southwestern Virginia and northeastern Tennessee. These have been used to construct growth series for each of the major calyx plates (Pl. 41, figs. 1–20). These complete specimens and separate plates are described in the sections below.

Specific description. The calyx has a

TABLE 8. MEASUREMENTS FOR THE TWO COMPLETE SPECIMENS OF *MERISTOSCHISMA HUDSONI* N. GEN., N. SP.

Measurement	Holotype MCZ 594	Paratype MCZ 595
Calyx—total length	29.3 mm	~11.7 mm
length minus oral crest	24.2 mm	9.7 mm
width	23.2 mm (av.)	10.9 mm
L/W ratio	1.26	1.07
vault (total)	19.2 mm	~8.4 mm
pelvis	10.3 mm	3.3 mm
V/P ratio	1.90	~2.5
Basal Cavity—diameter	3.9 mm	2.2 mm
depth	—	1.5 mm (incompl.)
Stem—diameter	2.9 mm	1.9 mm
columnal height	0.4 mm	—
Radials—length	14.3 mm	5.4 mm
width	10.4 mm	4.8 mm
RR suture	11.1 mm	4.8 mm
RD suture	6.2 mm	2.6 mm
basal cavity lip	2.3 mm	1.4 mm
# ridges	13–15	—
Deltoids—length	9.7 mm	3.8 mm
width	12.0 mm	5.3 mm
DAmb suture	10.8 mm	4.0 mm
DR suture	6.2 mm	2.6 mm
# ambulacral facets/side	13–14	6–7
# cataspire slits	32–34	13–14
max. cataspire slit length	6.4 mm	1.6 mm
max. # pores/slit	16	5
Ambulacra—length	12.6 mm	~5.3 mm
maximum width	9.3 mm	4.6 mm
# ambulacral plates/amb.	27–28	13–14
length of amb. plates	0.7–1.2 mm	0.4–0.5 mm
width of amb. plates	0.9–4.7 mm	0.4–2.2 mm
Brachioles—# brachioles/amb.	27–28	13–14
# brachioles total	135–140	65–70
brachiole length	20.0 mm (incompl.)	4.5 mm (incompl.)
brachiolar height	0.9–1.2 mm	—
brachiole width	0.5–0.7 mm	0.3 mm
BCP/BP ratio	~4.0	—
Orals—length	8.3 mm	—
width	6.2 mm (reg.) 6.8 mm (anal)	—
OO suture	4.8 mm	—
Oral Crest—diagonal length	5.4 mm	—
width	4.6 mm	—
OOCr suture	1.4 mm (reg.) 2.6 mm (anal)	—
Anus—diameter	3.0 × 2.5 mm	—



Text-figure 40. Plating arrangement in *Meristoschisma hudsoni* n. gen., n. sp. Diagram of calyx plates in holotype MCZ 594 showing five(?) basals located above stem in basal cavity, divided anal oral, and unequal segments of five-piece oral crest covering mouth.

rounded biconical shape in side view, and a pentagonal shape with flat to slightly concave sides in top and bottom views (Pl. 38, figs. 1–5). In the holotype, the length (including the oral crest) is slightly greater than the width (L/W ratio = 1.26), while the vault (including the oral crest) is almost twice as long as the pelvis (V/P ratio = 1.9). Five major sets of plates (as well as the 5 ambulacra) make up the calyx in *Meristoschisma hudsoni* (Text-fig. 40). These include very small interradial basals of unknown number in the basal cavity, 5 large recurved radials making up the remainder of the calyx pelvis, 5 large triangular interradial deltoids bearing slits for the cataspire system in the vault, separated by 5 large wide brachiole-bearing ambulacra in a radial position, 5 rhomboid-shaped interradial orals surrounding the mouth on the summit, and a conical, 5-piece oral crest.

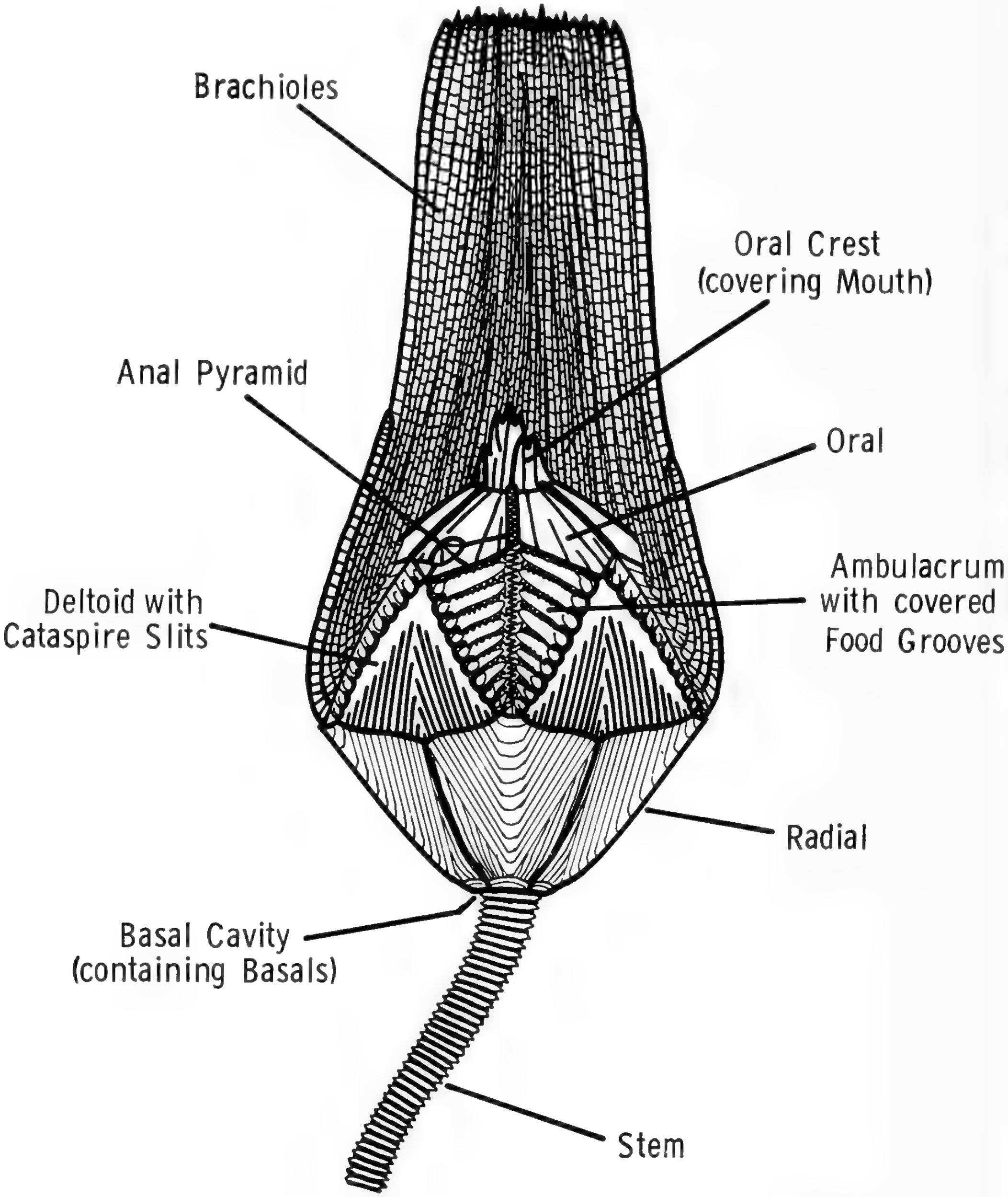
The moderately shallow basal cavity is best shown in the smaller paratype MCZ 595 (Pl. 38, fig. 8); it is a steep-walled cavity somewhat wider than deep (2.2 mm vs. 1.5+ mm). At least one columnal, approximately 1.9 mm in diameter and bearing a small rounded flange, is present in the bottom of this basal cavity, obscuring the view of the basals. Apparently the basal cavity and stem diameter do not increase in size as fast as the rest of the calyx, since in holotype MCZ 594 (Pl. 38, figs. 1–3), which is almost 3 times as large, they have not quite doubled in size. At least 5 slightly flanged columnals are present in the holotype stem segment.

Basals are apparently present in this species, because many of the isolated radials have facets on their aboral edges (Pl. 40, figs. 8–10), indicating the presence of another set of small interradial plates between them and the stem in the basal cavity. The number of basals is not known, but the most likely number is 5. These basals would be very small rhomboid-shaped plates about 1.5 by 1.0 mm in size, and probably form a relatively flat surface to which the stem is attached.

The 5 large radials of *M. hudsoni* comprise the entire pelvis outside the basal cavity, and form a strongly expanding saucer-shaped base for the calyx (Pl. 38, fig. 3). Each of these radial plates has a small strongly recurved lip that extends into the basal cavity, and a larger external portion that gradually increases in size adorally until it reaches its maximum width at the base of the deltoids and ambulacra (Pl. 40, figs. 6 and 10). These radial plates have a strongly convex profile transversely, with a prominent central ridge extending vertically up the length of the plate. This ridge extends into a small lip that separates the two overlying deltoids and bears the 1–2 newest ambulacral plates and brachioles at the tip of the ambulacrum (Text-fig. 39A; Pl. 40, figs. 6, 9, and 10). Each of these radial plates has relatively subdued ridgelike ornament subparallel to the interradial sutures, faint growth lines grouped into larger bands parallel to the radiodeltoid and interradial sutures, and overgrowths of secondary calcite around the edge of the basal cavity (Pl. 40, fig. 6).

The 5 large interradial deltoids make up about half of the calyx vault in *M. hudsoni*, considerably less than in *Blastoidocrinus carchariaedens*. They are approximately equilateral in shape, with a slightly concave to nearly flat transverse section near the base, and a slightly convex longitudinal profile (Pl. 40, figs. 1–5). The lateral edges are slightly raised along the margins of the adjacent ambulacra, and have prominent notches where the ambulacral plates and brachioles were located. The most prominent feature on the deltoids is the series of cataspire openings that appear in completely unweathered specimens as long parallel slits separated by low ridges extending much of the length of the plate (Pl. 40, fig. 1). In the holotype these slits range in total length from 6.4 mm near the center of the deltoid down to only 0.2 mm near each of the bottom corners. On weathered exterior surfaces and on the interior of the deltoids, each of these slits shows up as a column of slightly elongate pores (a maximum of 16 in holotype MCZ 594) separated by thin bridges of deltoid plate material (Pl. 40, fig. 5). The external appearance of low ridges between these slits is quite similar to the ornament present on the radial plates and the two match up along the radiodeltoid sutures (Pl. 38, figs. 3–4), but there are no openings present through any part of the radials. Tiny growth lines extend across much of the deltoid width parallel to the radiodeltoid suture, and a small amount of lateral growth toward the ambulacra may also be present (see Pl. 39, fig. 2). As in the radials, these tiny growth lines are grouped into larger periodic bands. The adoral tip and lateral edges of the deltoid exterior are relatively smooth, probably from thin overgrowths of secondary calcite. Evidence of deltoid thickening in these regions can also be seen in along the ambulacral margins in some specimens (Pl. 40, figs. 3–4).

The 5 ambulacra with their flooring plates are relatively short and quite wide in *Meristoschisma hudsoni*. Each one extends from the adoral tip of the radial plate up between the two adjacent deltoids to the aboral margins of the relatively large orals. Only one type of ambulacral flooring plate is present (Pl. 39, figs. 2–6; Text-fig. 40), unlike the ambulacra in rhombiferan cystoids and blastoids, and there is apparently no lancet or other calyx plate present beneath the ambulacrum either. The main food groove runs down the center of each ambulacrum, alternately sending off branches to each side leading to the brachioles. Each of these side food grooves runs out to a brachiole facet at the lateral edge of the ambulacrum; this groove is slightly oblique to (and crosses) the suture between the flooring plates (Pl. 39, fig. 5). Both the main and side food grooves are



Text-figure 41. Reconstruction of *Meristoschisma hudsoni* n. gen., n. sp. Side view with brachioles stripped off half of calyx to show plates; note proportions of calyx, wide ambulacra with brachioles attached to edges, and slowly tapering long stem. Total brachiole length estimated.

covered by a biserial set of tiny ambulacral cover plates, which become somewhat larger on the orals and near the oral crest (Text-fig. 39B). There is a cataspire pore between each two flooring plates at the deltoid margin.

The brachioles in *M. hudsoni* are long and symmetrical. Paratype MCZ 595 probably had about 70 brachioles at least 4.5 mm long; holotype MCZ 594, a much larger specimen, has 135 incomplete brachioles at least 20.0 mm long, and probably much longer (Text-fig. 41; Pl. 38, figs. 2–5). The brachioles are attached, 1 per ambulacral flooring plate, to a small facet at the abmedial edge of the plate (Pl. 39, figs. 1 and 5). The lowest adoral brachiolar plate of each brachiole fits into a concave facet on the vertical edge of the adjacent deltoid plate (see Pl. 39, figs. 1–4); it appears that the brachiole was articulated with the deltoid as well as with its flooring plate (this possibility was also noted in *Blastoidocrinus carchariaedens*—see p. 149). There is a prominent, horizontal, wedge-shaped gap near the base of the brachiole between brachiolar plates 1–2 and plates 3–4 (Text-fig. 39B), which may have contained muscles or ligaments to allow the brachiole to fold down over the ambulacrum and peristomal regions of the calyx from its upright position. The remaining distal portions of most brachioles are normally plated, with two equal-sized, alternating, brachiolar plates (BP), forming most of the hemielliptical brachiole and bearing a small shallow food groove covered by tiny brachiolar cover plates (BCP) on the adoral surface (see Text-fig. 5G and Pl. 39, figs. 21–23). There are approximately 4.0 BCP/BP in brachioles on the holotype specimen. The brachiolar food groove empties into a small pore at the abmedial end of the side food groove; food particles were apparently carried down the brachiole, across the ambulacrum to the main food groove, and up this main groove to the mouth.

Approximately 15–20 percent of the brachioles in the large holotype specimen (MCZ 594) appear to be somewhat "abnormal," both in their shape and plating arrangement. These abnormal brachioles are located primarily in the "older" parts of the ambulacrum near the tips of the deltoids, where they appear to occur about every fourth or fifth brachiole (Text-fig. 39A). They show a marked change in shape as they are traced distally from their attachment point; they gradually become inflated to about 1.5 times the normal width and length of the other brachioles, and some are slightly asymmetric. Also, the brachiolar plating is slightly to strongly irregular at various points along these abnormal brachioles (see Text-fig. 5G), a feature very unusual in any blastozoan echinoderm. There is no evidence of parasitic activity along these brachioles, and they appear to have been functional like the remainder of the brachioles. These "abnormal" brachioles appear to be draped over the exterior surface of the other brachioles in a protective fashion (Text-fig. 39A; Pl. 39, fig. 22). *M. hudsoni* completely lacks protective ambulacral crests, as in *Blastoidocrinus carchariaedens,* and these larger abnormal brachioles may have served a similar purpose of protecting the other smaller and more delicate brachioles from current or predator damage when they were in their infolded, resting position. This type of protective mechanism was apparently also evolved by some calceocrinid crinoids, where the more massive main axil of an arm folds over and protects the more delicate secondary and tertiary ramules when in their resting position (Brower, 1966: 618).

There are 5 rhomboid-shaped, interradial oral plates surrounding the mouth in *M. hudsoni* (Text-fig. 40). These plates have prominent vertical fluting on their exterior surface, and bear the 5 main food grooves leading to the mouth on their interoral sutures (Pl. 39, figs. 7–15). There is a prominent "nick" with small adjacent projections in the center of the interior aboral

TABLE 9. MEASUREMENTS FOR THE DELTOID AND RADIAL GROWTH SERIES IN *MERISTOSCHISMA HUDSONI* N. GEN., N. SP.

Deltoid	Length (mm)	Width (mm)	DAmb suture (mm)	DR suture (mm)	# Amb. facets	# Slits	Slit length (mm)	# Pores per slit
* D1	3.5	4.7	3.9	2.3	6	13^{+}	0.9	2–3
D2	3.9	5.4	4.5	2.8	7	16	1.4	4
D3	5.0	6.7	5.5	3.4	8	18	2.7	5–6
D4	5.8	8.0	6.9	3.9	9	22	3.0	7
D5	6.8	8.6	7.6	4.5	10	22	3.5	7–8
D6	7.2	9.6	8.5	4.9	12	27	4.1	10
** D7	8.7	10.9	10.1	5.5	13	32	4.9	10–11
D8	9.8	12.0	10.7	6.1	13	31	6.4	11
D9	10.6	12.9	11.7	6.6	13	34	6.8	11–12
D10	12.2	14.6	13.9	7.9	17	38^{+}	7.8	14

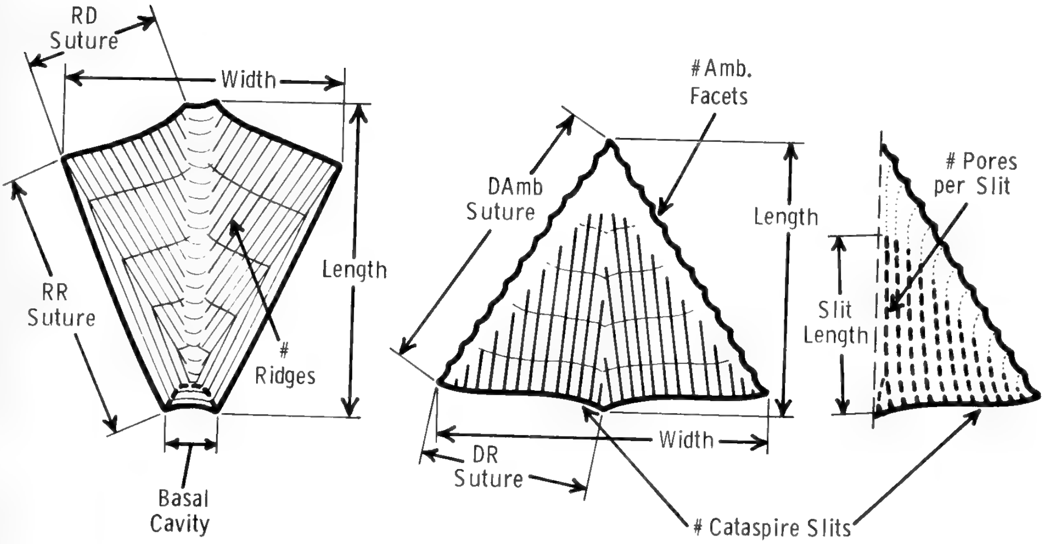
Radial	Length (mm)	Width (mm)	RR suture (mm)	RD suture (mm)	Basal cavity (mm)	# Ridges
* R1	5.1	4.4	2.9	2.8	1.1	15
R2	6.1	5.3	4.1	3.6	1.6	17
R3	7.3	5.8	5.1	3.2	1.6	19
R4	8.3	7.0	6.2	4.5	1.5	22
R5	9.5	7.5	6.5	5.0	1.7	23
R6	11.0	8.2	7.7	5.9	1.8	28
R7	11.1	9.1	8.7	5.5	2.0	31
R8	12.2	9.3	8.2	6.3	2.1	32
** R9	12.8	10.3	10.0	6.5	2.1	35
R10	13.7	9.9	10.6	7.5	2.5	31

* Relative positions of deltoids and radials in small paratype MCZ 595.
** Relative positions of deltoids and radials in large holotype MCZ 594.

margin (Pl. 39, figs. 8, 12, and 14). The anal opening is located near the aboral margin of the posterior oral (Text-figs. 39B and 40), which appears to be slightly larger than the other orals and is apparently divided into several segments laterally and below the anus (Text-fig. 40). No anal pyramid is now preserved over the anal opening in the holotype, although one may have been present in life.

The adoral tips of the orals abut against the lower edges of the conical, fluted, 5-plate, oral crest that covers the mouth (Text-fig. 39; Pl. 39, figs. 16–19). The 5 main food grooves enter the peristome under the edge of this oral crest, and paratype MCZ 598 shows that the cover plates over the main food grooves apparently continue under the crest right to the mouth (Pl. 39, fig. 19). The posterior oral crest plate is slightly larger than the others, which are approximately equal in size and arranged in a bilaterally symmetric pattern around the "A"–"CD" axis (Text-fig. 40). The oral crest is probably conical rather than cylindrical because there are no wing-plated ambulacral crests abutting it as in several species of *Blastoidocrinus.* The orals and oral crest plates do not show any exterior growth lines or banding, and little can be inferred about their growth.

The cataspire system of *Meristoschisma hudsoni* appears to have been a highly developed respiratory system. Thin-walled parallel cataspire folds extended under the deltoids for the closed circulation of sea water into the coelomic cavity with exchange of dissolved gasses. These folds appear to have been attached aborally to the adoralmost edge of the radials (Pl. 39, fig. 20), medially to the underside of the deltoid, and adorally to the two ambulacral flooring plates surrounding each pore (Pl. 39, fig. 2). Thus, 3 sets of plates (and 4



Text-figure 42. Location of measurements taken on the radials (left) and deltoids (external and internal views—right) of *Meristoschisma hudsoni* n. gen., n. sp. and *M. fayi* n. sp. (see Tables 8–10).

plates) are attached to each cataspire fold, unlike the 2 plates involved in rhombiferan cystoids and blastoids. The arrangement of openings strongly suggests that the flow internally was in an adoral direction, with the thin multiple slits on the deltoid serving as inlets, and the larger ambulacral pores as outlets (see Paul, 1968b: 714). The number of cataspire folds and entrance slits is somewhat larger than the number of exit pores (as derived from the total number of ambulacral plates on both margins—see Table 9), and there appears to be some branching of folds to give one or more rows of entrance slits (mostly near the center of the deltoid) a single exit pore. Many of the folds show a sharp outward bend near the lateral margin of the deltoid (Pl. 39, fig. 2); this may imply slight lateral growth of the deltoid and extension of the folds in this direction. The attachment of the aboral ends of the cataspire folds to the adoral edge of the radials apparently required continual readjustment during radial growth along this suture. The growth pattern for the cataspire system is discussed below.

The pattern of calyx plate growth in *M. hudsoni* is shown by 2 10-plate growth series for the radials and deltoids, figured in Plate 41, figures 1–20. Measurements for the specimens in these growth series are tabulated in Table 9; Text-figure 42 shows the measurements used in this table. The relative positions of the large complete holotype (MCZ 594) and the small paratype (MCZ 595) are marked in Table 9 with reference to members of these deltoid and radial growth series.

The major calyx plates of *M. hudsoni* (and probably *M. fayi* also) appear to have increased in size by holoperipheral growth. Tiny growth lines parallel to one or more plate margins are preserved on the exterior plate surfaces of both the deltoids and radials in holotype MCZ 594 (Pl. 38, figs. 3–4) and in several of the better preserved separate radials and deltoids (see Pl. 40, fig. 6 for example). No growth lines are present on the interior of these plates (see Pl. 40, figs. 5 and 10), probably because they are hidden by thin overlayerings of secondary calcite secreted by the echinoderm to thicken the plate during lateral growth. Each of these tiny growth lines or increments is approximately 0.12–0.16 mm wide, and appears to extend along the entire growth front. In the radials, most of the growth was toward the radiodeltoid (RD) suture, and growth lines are well exposed along this front; growth toward the RR and RB sutures is apparently much slower, and minute growth lines along these fronts have not been observed. In the deltoids, most of the growth was toward the corresponding radiodeltoid (DR) suture and growth lines are often present here; slow growth toward the two lateral DAmb sutures is also suspected, but is apparently hidden by thin overlayerings of secondary calcite covering the exterior of the deltoids along these ambulacral margins (see Pl. 40, figs. 3–4 for evidence of this). Thus, most of the growth in the deltoids and radials of *M. hudsoni* was concentrated along the suture between these 2 rows of plates in the middle of the calyx. Because of this rapid "lengthwise" growth, the L/W ratio for both the deltoids and radials gradually increases with increasing size. No growth lines have been observed in the orals, oral crest plates, or ambulacral plates although these may also have increased in size by holoperipheral growth. *Meristoschisma hudsoni* now represents the only parablastoid in which holoperipheral plate growth is known to occur for certain, but I would infer that all parablastoids probably had this type of primary plate growth.

In several specimens, these minute growth lines are grouped into larger growth "bands" separated by prominent ridgelike markings, apparently representing periodic slowing or cessation of growth (see Text-fig. 18). These "bands" show up both as markings on the exterior of well-preserved plates and as grabenlike depressions in slightly weathered plates. Five and a half "bands" are preserved in large radial MCZ 600–R10 (Text-fig. 18A); each band contains approximately 10–16 smaller growth lines, and has approximately the same width (about 2.0 mm). This may indicate a relatively constant rate of growth from band to band.

These growth bands in *M. hudsoni* most probably represent yearly increments of growth. The implication is that radial MCZ 600–R10 belonged to a parablastoid that was at least 5½ years old when it died, and that holotype MCZ 594 (Pl. 38, figs. 1–5) was probably more than 6 years old when it died. At present, it is impossible to tell which of the climatic or physiological factors is responsible for this observed banding of growth lines in *M. hudsoni* (see p. 49).

The calyx growth of *Meristoschisma* appears to have been highly coordinated. The plates all fit together tightly, and several of the important systems in this parablastoid, especially the ambulacral system with its brachioles and the cataspire system with its respiratory folds, are apparently closely tied in with the growth of the major calyx plates. The ambulacra appear to have increased in size by the formation of new ambulacral plates in two rows at the aboral end of the ambulacrum. Older plates apparently continued to grow laterally to fill out the remainder of the increasingly wide ambulacrum as they "migrated" adorally (Text-fig. 39B). The addition of new ambulacral plates was strongly controlled by the relative growth of the deltoids, because deltoid growth provided nearly all the "room" in the calyx vault for the addition of new ambulacral plates. After formation, the ambulacrum plates apparently did not move in relation to the adjacent deltoid, because ambulacral facets and markings for cataspire pores are present on the edge of the deltoid. Provided there was no relative motion between these two sets of plates, the brachioles, mounted on the abmedial edge of the ambulacral plates, could also have been articulated with the edge of the adjacent deltoid. As each new ambulacral plate was added, the single brachiole mounted on it apparently grew relatively rapidly at an early stage of ambulacral plate development. Even the newest ambulacral plates in the holotype of *Meristoschisma* have well-developed brachioles (Pl. 39, fig. 23), although they are not as long as the brachioles on older ambulacral plates. The formation of the "abnormal" brachioles, which are concentrated in the "older," more interradial parts of the ambulacra, may have been a relatively late-stage feature of brachiole growth. Since they are inflated and considerably larger than their adjacent normal brachioles, it seems likely that growth continued longer in these abnormal brachioles or was resumed at a later stage.

The cataspire system was also highly coordinated with calyx plate growth. The cataspire folds are attached internally to three sets of calyx plates, and therefore cross two plate sutures along which growth of the folds could have taken place. One of these was the actively growing radiodeltoid suture, where both the radials and deltoids were growing toward each other at a relatively high rate. Older cataspire slits and their internal folds were elongated aborally along the radiodeltoid suture during growth of the overlying deltoid. Short new cataspire slits were added laterally along this suture as the deltoid increased in width. A few new slits were also added medially along this suture as the adjacent cataspire slits on either side slowly diverged during growth along their respective radiodeltoid margins (see Pl. 40, fig. 1). Internally, folds for these new short slits in the center of the deltoid branched off from the adjacent long folds (Pl. 40, fig. 5). Thus, new exit pores in the ambulacrum were not needed for these new central folds. The new slits on the lateral margins of the deltoid have their own new folds internally and their own exit pores along the margins of the adjacent ambulacra. The addition of each new lateral cataspire slit thus required the addition of a new ambulacral plate to the adjacent ambulacrum to provide a place for a new exit pore to form. Therefore, the addition of new lateral cataspire slits and folds was strongly correlated with the growth of the two ambulacra bordering the deltoid. On the interior where the cataspire folds are attached, the radiodeltoid suture must extend through each of the folds. Lengthening of the folds apparently took place along the deltoid half of this suture to match the growth of the overlying deltoid. The aboral attachment of the cataspire fold to the radial apparently did not grow, but constantly shifted with the margin of the overlying radial as it grew toward the deltoid.

Growth of the cataspire folds was apparently much slower along the deltoid-ambulacrum suture. There is some evidence of growth of the deltoids toward the ambulacra, and the ambulacral plates may also have grown very slightly in an abmedial direction toward the deltoid. The strong outward bending of the cataspire folds at this place (Text-fig. 42; Pl. 39, fig. 2) suggests that some growth of the folds took place along this suture as the overlying deltoid slowly grew laterally.

Discussion. Most of the separate plates of *M. hudsoni* and the small paratype were found in thin-bedded shaly limestones with abundant bryozoans, receptaculitids, brachiopods, and echinoderm plates. This probably represents a relatively turbulent shallow-water environment. The holotype was collected from a fine-grained, thin-bedded, nodular, limy shale with scattered bryozans and other complete echinoderms, probably representing more quiet water conditions. For additional ecologic information, see the discussion section for the following species (p. 169).

Etymology. This species is named after the late George H. Hudson of Plattsburg, New York, who published the first complete description of *Blastoidocrinus* and who proposed the order (now class) Parablastoidea for these echinoderms.

Stratigraphic and geographic range. Benbolt Formation and its equivalents (Ottosee Group), lower Middle Ordovician (Black River–Porterfield), localities CS-2., GV-1., HO-1A., LB-1., LV-2., RC-7., RC-8., RC-9., and SG-1., all from the

TABLE 10. MEASUREMENTS FOR THE DELTOID AND RADIAL GROWTH SERIES IN *MERISTOSCHISMA FAYI* N. SP.

Deltoid	Length (mm)	Width (mm)	DAmb suture (mm)	DR suture (mm)	# Amb. facets	# Slits	Slit length (mm)	# Pores per slit
D1*	9.2	12.0	10.9	5.9	15	29	5.5	7–8
D2	10.8	13.0	11.1	6.7	13	28	6.0	8–9
D3	10.8	14.3	11.8	6.9	16	28	5.8	8
Radial	Length (mm)	Width (mm)	RR suture (mm)	RD suture (mm)	Basal cavity (mm)	# Ridges		
R1	10.3	8.6	8.2	6.4	3.3	25		
R2	12.1	9.9	10.0	5.6	3.1	24		
R3	14.0	10.5	10.4	6.0	3.2	24		
R4	15.2	12.4	12.2	7.4	3.3	27		

* Holotype

Valley and Ridge Province of southwestern Virginia and northeastern Tennessee.

Studied specimens. Holotype MCZ 594, found at locality LV-2. by my field assistant Gary Stuckey; complete paratype MCZ 595, collected from locality RC-8.; figured plate paratypes MCZ 596–601 and MCZ 644; and nearly 300 additional separate plates in collection MCZ 645 primarily from locality RC-9.

Meristoschisma fayi new species

Plate 40, figures 11–20; Plate 41, figures 21–27

A second species of *Meristoschisma*, known only from a few scattered radial and deltoid plates that closely resemble those of *M. hudsoni*, also appears to be present in the Benbolt Formation. *Meristoschisma fayi* differs most notably from *M. hudsoni* in having much thicker radial and deltoid plates with pronounced rugose ornamentation on their exterior surfaces (Pl. 40, figs. 11–20). Deltoid MCZ 602–D1 is here selected as holotype and described below along with eight additional paratype specimens. Most of these plates, making up incomplete radial and deltoid growth series, are illustrated in Plate 41, figures 21–27, and their measurements are listed in Table 10.

Specific description. The radials are elongate pentagonal in shape and much longer than wide. The L/W ratio in the radials of *M. fayi* is only slightly larger than in *M. hudsoni.* These radials are strongly refolded at their aboral ends to form the edge and sides of the basal cavity. In *M. fayi* the edge of the basal cavity is considerably larger than in *M. hudsoni,* perhaps implying a larger stem. Basals are inferred to have been present, as in *M. hudsoni,* from the occurrences of sutures on the recurved end of the radials. Adorally, the radials expand slowly from the edge of the basal cavity until the maximum width is reached along the radiodeltoid margin. A central ridge extends up the center of the plate, but is usually much less prominent than in *M. hudsoni* (compare Pl. 40, figs. 8–9 and 18–19). Therefore, the radials are somewhat less angular and convex in adoral view and transverse section. The adoral margin of the radial has a small central projection where the aboral end of the ambulacrum was located, and faint marks laterally along both radiodeltoid sutures where the cataspire folds were apparently attached. The radials in *M. fayi* are almost twice as thick as those in *M. hudsoni* (compare Pl. 40, figs. 7–9 and 17–19). The external ornament in *M. fayi* is very coarse and consists of prominent ridges that are 1) perpendicular to the two RD sutures and form a set of large nested chevrons in the center of the plate, similar to but much stronger than *M. hudsoni*, and 2) perpendicular to the RR sutures in small triangular areas at the lateral margins of the plate, differing greatly from *M. hudsoni*, which has no ornament here. Secondary deposits of calcite are present around the edge of the basal cavity, but because of the coarse ornament there is little trace of growth lines.

The deltoids are triangular in shape, with the base somewhat longer than the sides. The L/W ratio for the deltoids in *M. fayi* is almost identical to that in *M. hudsoni*. The deltoids are slightly convex longitudinally and flat to very slightly concave transversely. The cataspire slits extend up approximately 60 percent of the deltoid length from the aboral margin; there are somewhat fewer slits than in *M. hudsoni* and each slit is slightly shorter (compare Table 10 with Table 9). These cataspire slits open to the interior as a series of elongate pores separated by bridges of plate material. In *M. fayi*, these pores are more elongate and fewer in number than in *M. hudsoni*. The lateral edges of the deltoids bear facets where the ambulacral flooring plates and brachioles were located. The exterior of the deltoids in *M. fayi* has coarse ornament in the form of parallel nodular ridges that lie between the cataspire slits and are perpendicular to the DR sutures. No growth lines have been observed on the deltoids, probably because of the coarse ornament. Thin secondary deposits of calcite appear to be present near the adoral tip and along the lateral edges of the deltoid (Pl. 40, fig. 11). The deltoids in *M. fayi* are somewhat thicker, especially along the DR sutures, than in *M. hudsoni*.

A single poorly preserved oral plate was also found at one of the localities where *M. fayi* occurs, and may belong to this taxon. It is very similar to the orals in *M. hudsoni*, and also has coarse ridgelike ornamentation on the exterior surface. No other calyx plates of *M. fayi* are known.

Discussion. Meristoschisma fayi appears to differ from *M. hudsoni* in several consistent features. Most notably, both the deltoids and radials are considerably thicker and much more coarsely ornamented in *M. fayi*. The radials of *M. fayi* also have a slightly greater L/W ratio, a somewhat less convex shape in transverse section, a basal cavity edge more than one and a half times as large as that found in *M. hudsoni*, and different ornamentation along the lateral margins of the plate. In addition, the deltoids of *M. fayi* have considerably fewer and somewhat shorter cataspire slits, and fewer and more elongate cataspire pores opening into the interior.

Many of these differences, especially the coarse ornament, greater plate thickness, larger basal cavity, and cataspires with more elongate and restricted pores, could reasonably be explained if *M. fayi* lived in more turbulent and perhaps shallower waters in which sediment was often stirred up. Using this interpretation, I have considered the possibility that *M. fayi* might have been an ecologic variant of *M. hudsoni* and not a separate species. This remains a slight possibility, because the two species have not been found occurring together even though they both occur in the same formation over the entire area studied. However, no specimens have been found with intermediate features; taking ornament as an example, all of the collected plates either have very low ridges crossed by faint growth lines (*M. hudsoni*), or else very coarse pustular ridges showing no growth lines at all (*M. fayi*) (see Pl. 41). In addition, the two species occur in very similar sediment types, usually a shaly, nodular, thin-bedded, fossiliferous limestone, and not in widely different sediment types, which might be expected if they lived under different ecologic conditions. The two species apparently also occur with somewhat different echinoderm faunas; *M. hudsoni* has been found most often with the paracrinoids *Platycystites* and *Columbocystis* and the crinoid *Hybocrinus*, while *M. fayi* seems to occur with the paracrinoid *Canadocystis*, the rhombiferan cystoid *Pleurocystites*, and the crinoid *Palaeocrinus*. This difference in the echinoderm faunas suggests that these two species of *Meristoschisma* occur at different stratigraphic levels in the Benbolt Formation, but not enough work has been done on the limited exposures of this formation to piece together a complete section having both species present. Thus, I have decided to describe these two forms as separate species, while noting the relatively unlikely possibility that they could conceivably represent variants of a single species.

Etymology. The species is named after Robert O. Fay of the Oklahoma Geological Survey, who revised the known parablastoids for Treatise Volume S, and who greatly encouraged me with his advice and interest during my work on this new parablastoid genus with its two species.

Stratigraphic and geographic range. Benbolt Formation and its equivalents (Ottosee Group), lower Middle Ordovician (Black River–Porterfield), Valley and Ridge Province of southwestern Virginia (localities MC-3. and SL-1.) and northeastern Tennessee (DT-3. and DT-3A.).

Studied specimens. Holotype MCZ 602–D1; paratypes MCZ 602–D2–3 (deltoids), MCZ 602–RO–5 (radials), and MCZ 602a (oral plate); plus about ten additional unfigured deltoid and radial plates included under MCZ 602b.

Class *RHOMBIFERA* Zittel, 1879

Diagnosis. Blastozoan echinoderms with a globular or flattened calyx usually having 5 major rows of alternating plates (basals, infralaterals, laterals, radials, and orals) arranged in fairly good pentameral symmetry. Respiratory structures either widely scattered over the calyx or occupying 3 fixed positions; composed of sets of slits or pores called pore rhombs (pectinirhombs, cryptorhombs, etc.) crossing the suture between 2 plates and connected internally by a set of calcified pleated folds (dichopores) for the closed circulation of seawater. Pore rhombs always cross 1 suture only, have equal internal development on the 2 plates (external openings often modified), and the longest opening (and fold) is always central on the plates. Ambulacral system consists of 2-plate sets of flooring plates arranged in a biserial series either extending down over the calyx plates (sometimes between them or in a sinus within 1 plate) or extending out from the summit as erect arms. Each set of flooring plates bears a single relatively short erect brachiole. Stem present in nearly all rhombiferans, modified proximally in 1 large group of genera to a much enlarged flexible portion with a large lumen. Holoperipheral calyx plate growth thought to be present in nearly all rhombiferans. Anus lateral on side of calyx; hydropore and gonopore openings usually present below mouth in "CD" interradius. Approximately 50 genera; early Ordovician–late Devonian, world-wide distribution.

Discussion. Until 1967 or 1968 the Rhombifera was considered one of the two orders of cystoids in the Class Cystoidea von Buch, 1844 (see Kesling, 1963: 107–116; 1967a: S166–169). However, Paul, in a series of recent articles, has suggested that the two ordinal groupings of cystoids are completely unrelated and have an independent origin (making "cystoids" as a class polyphyletic), and has proposed that the name Cystoidea be dropped and the two ordinal names, Rhombifera and Diploporita, be raised to class rank (Paul *in* Jefferies et al., 1967: 566; 1968a: 594; 1968b: 726–727). I agree with this proposal and have here considered the Rhombifera and Diploporita as separate classes. However, it should be noted that the Rhombifera as presently constituted may still be polyphyletic, since the superfamilies

Polycosmitida and Caryocystitida with eight genera having irregularly plated calyces and unusual pore structures may not be related to other rhombiferans. Rhombiferan cystoids are definitely blastozoan echinoderms, but at present diploporan cystoids cannot be assigned with certainty to either of the known subphyla of attached echinoderms (see p. 186).

Rhombiferans are relatively advanced blastozoan echinoderms. They have true brachioles, foldlike respiratory structures, a true stem, relatively well-developed pentameral symmetry, and apparently holoperipheral plate growth. The pore-rhomb respiratory structures are relatively simple in their arrangement and structure (see Text-fig. 12), and are usually not arranged into a strong five-sided pattern as in parablastoids and blastoids. The ambulacra are also relatively simple (see Text-fig. 6), although they have the very succesful brachiole-supporting arrangement that uses two-plate sets as in blastoids. Some rhombiferans with a normal stem were probably attached "high-rise" filter feeders, but Paul (1968a: 596–8) has suggested that the many forms having an enlarged proximal stem and no evidence of distal attachment were free-living, with the calyx held upright while much of the stem lay trailing behind on the sea floor. These rhombiferans may have been able to swim by flexing the stem.

I consider that many or all rhombiferans evolved through the genus *Macrocystella* in the early Ordovician from a thin-plated, nonrhomb-bearing eocrinoid ancestor. The exact systematic position of *Macrocystella* is discussed elsewhere (see p. 122), but when it first appeared this genus had already developed the characteristic calyx plating and stem structures found in many other early rhombiferans. The only rhombiferan feature missing in *Macrocystella* was the characteristic respiratory pore rhombs, which apparently developed as sutural invaginations between pairs of calyx plates. Once developed, this successful respiratory system was never drastically changed in later rhombiferans, although certain parts are modified for better flow control and particle exclusion (see Paul, 1968b) and the system was apparently lost in at least one genus (see p. 122). I consider the acquisition of pore rhombs as the most basic and important defining characteristic of rhombiferans.

Rhombiferan cystoids were most common and widespread during the Ordovician and Silurian (see Kesling, 1967a: S130, table 3). By the middle Devonian, they were considerably reduced and apparently became extinct at the end of this period. This reduction may have been at least partially caused by competition with more advanced blastoids (see Text-fig. 20), which greatly increased in diversity at this time. Newell (1952: 379) has considered this a possible case of replacement within a single environmental niche, and this seems to be a very likely explanation.

I did not study any rhombiferan cystoids in detail during this project because of time limitations and active work by several other authors on this class. However, information from a separate paper in preparation on the arm structures of *Caryocrinites* (see Sprinkle, 1968: 210) was used in several places. For additional information about rhombiferans, readers are referred to the major review article by Kesling (1967a) in Treatise Volume S and to a recent series of excellent general and detailed papers by Paul (1967a, 1967b, 1967c, 1968a, 1968b).

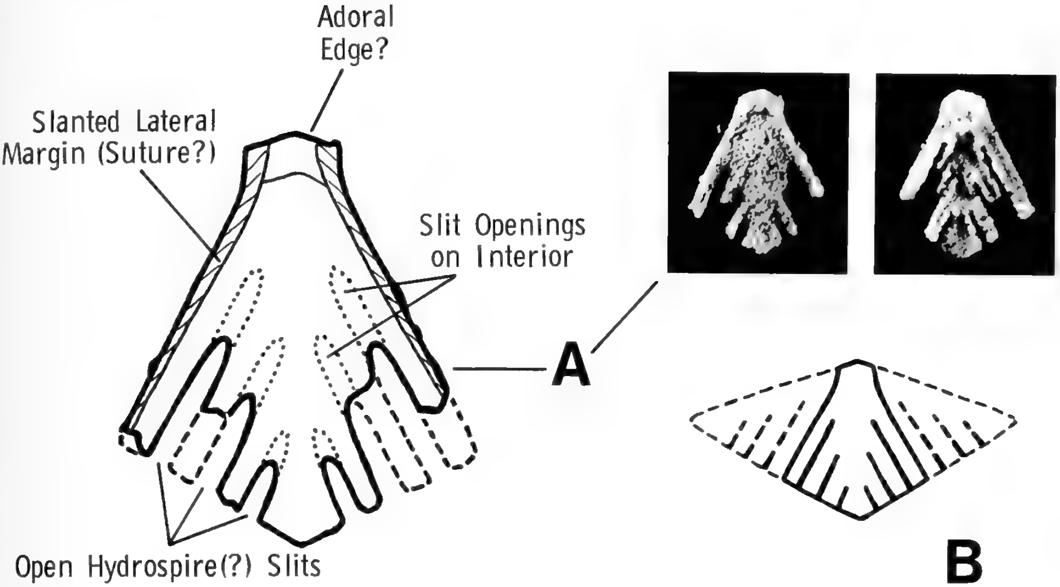
Class *BLASTOIDEA* Say, 1825

Diagnosis. Hydrospire-bearing, stemmed, blastozoan echinoderms having advanced calyx plating and ambulacral structures. Calyx bud-shaped with reduced and standardized plating that includes 3 unequal basals, 5 large forked radials, 5 elongate lancets in the radial sinuses, and 4 regular deltoids, as well as 2–6 anal deltoids in the "CD" interradius. Ambulacral system highly developed, with 5 elongate ambulacra each made up of a central covered or exposed lancet plate and many biserially arranged sets of 2 (rarely 3) types of side (flooring) plates, each set supporting a long, normally plated brachiole. Foldlike hydrospire respiratory structures located alongside ambulacra and only crossing radiodeltoid suture; consisting either of open hydrospires having 1 or more long slits or closed hydrospires having a series of small ambulacral pores and a large excurrent spiracle adorally. Longest hydrospire folds central on radials, but lateral on deltoids; tubelike enlargements usually present at bottom of closed hydrospire folds. Pentameral symmetry usually strongly marked in calyx plating, ambulacra, and hydrospire arrangement. Most calyx plates show holoperipheral growth with well-developed tiny growth lines on exterior, plus secondary deposits on interior and scattered parts of exterior. Long, columnal-bearing stem usually present. Approximately 87 genera. Middle Ordovician(?), middle Silurian–late Permian, world-wide distribution.

Discussion. Blastoids appear to be the most advanced and specialized class of blastozoan echinoderms. They are characterized by a nearly constant and highly symmetrical calyx plating arrangement, highly developed ambulacra bearing numerous long brachioles, respiratory hydrospires occupying a fixed position and having relatively strong current control, and a long, highly developed stem. Several features are present only in this class: 1) the standardized plating arrangement combined with long ambulacra extending into V-shaped radial sinuses, 2) a specialized lancet plate underlying each ambulacrum, 3) a respiratory system in which the longest folds are lateral and not central on one set of plates (deltoids), and 4) respiratory folds shared by only two sets of calyx plates (radials and deltoids) along two adjacent sutures. Blastoids also represent the most diverse, most successful, and longest-lived of the known blastozoan classes. All of these factors (as well as their probable independent origin from eocrinoids) indicate that blastoids represent a separate and distinct group of blastozoan echinoderms at the class level. Attempts to combine them with the other "cystoids" or "hydroporoids" (Regnell, 1945: 27; 1960: 73–74) are here rejected both because of the many morphological differences pointed out above and because any combined grouping, in my opinion, would probably be polyphyletic. Blastoids seem to represent a very successful "quantum jump" over other blastozoan classes in terms of their advanced morphologic features (plating, symmetry, ambulacra, and respiratory structures).

Previous classifications of the blastoids have been summarized by Fay (1961b: 16–20) and Beaver et al. (1967: S388–S392). The Blastoidea was first established by Say (1825: 293) as a new family that would "constitute the link between the Crinoidea and Echinoidea" (then also classed as "families"). Blastoids were raised to class rank by Etheridge and Carpenter (1886: 117), and have remained at or just below this level ever since. Blastoids are now divided into two orders, Fissiculata and Spiraculata, a division proposed by Jaekel (1918: 107–108). This system seems to have become stabilized during the past several years, but may have to be modified or even rejected because of evidence from investigations now in progress (D. B. Macurda, Jr., personal communication, 11 November 1969).

In several recent papers, Fay (1962: 205; *in* Beaver et al, 1967: S393) has proposed that blastoids evolved from the middle Ordovician class Edrioblastoidea, which is at present based on the single genus *Astrocystites.* I have strongly objected to this proposed origin as discussed on page 188. My major objection involves the absence of brachioles in *Astrocystites;* normal brachioles are present in blastozoan echinoderms dating back as far as the early Cambrian,



Text-figure 43. Possible blastoid(?) plate from the middle Ordovician of Nevada. A, reconstructed drawing (left) and exterior and interior photographs (right) of described specimen (USNM 165409); note slanted lateral margins which appear to be sutures and slits opening into folds (mostly lost) on interior with longest slits marginal. B, hypothetical reconstruction of normal rhombiferan-like plate if lateral margins were fractures and not sutures; note that longest slits would now be central in each plate segment.

and a new and separate development of almost identical food-gathering appendages in the evolution of blastoids seems very unlikely. I feel that blastoids evolved from an unknown brachiole-bearing eocrinoid ancestor between the late Cambrian and the middle Ordovician (see next section). Their sudden reappearance in the middle Silurian with already standardized morphology and considerable diversity implies a long period of previous evolution that is practically unknown at present.

Except for the single plate described below, no other blastoids were studied in detail for this project.

Order **FISSICULATA**(?) Jaekel, 1918
Family INDETERMINATE
Possible Ordovician Blastoid(?) Plate from Nevada
Text-figure 43

In July, 1967, I discovered a single silicified plate, which may represent a deltoid plate from a primitive blastoid(?), in a collection of acid residues made by Reuben J. Ross, Jr. at the U. S. Geological Survey, Denver. This plate (USNM 165409) comes from the upper part of the Antelope Valley Limestone (Middle Ordovician) at USGS locality D1634 CO in southwestern Nevada. If this plate is truly of blastoid origin, then it represents the earliest record of the class Blastoidea now known, since the oldest previous occurrences (at least three genera represented by numerous complete specimens), are middle Silurian in age. There is some question, however, whether this plate is complete as preserved, and whether it represents an early blastoid instead of some other type of blastozoan echinoderm, such as a rhombiferan cystoid. At least one additional plate of similar appearance was found during field work in the Antelope Valley Formation at locality IK-3. in central Nevada, but was so poorly silicified that it was almost completely destroyed when I tried to extract it by acid etching. The USGS specimen is briefly described below.

This plate is relatively small (approximately 3.5 mm long and 3.0 mm wide), relatively thick for its size, bilaterally symmetrical, and deltoid-shaped with five sutured(?) margins (Text-fig. 43A). The top edge of the plate is relatively thick, but the thickness decreases gradually toward the bottom of the plate. The plate apparently lacks ornamentation and is relatively smooth on both the exterior and interior. The two lateral margins are slightly oblique with a slight upward slant that increases toward the top; the top margin is flat and has a downward slant. Two symmetrical groups of three slits each are present on the lower margins of the exterior surface, opening on the interior into apparent thin pleatlike folds that have now been mostly eroded away (Text-fig. 43A). These slitlike openings are considerably longer on the interior than on the exterior, and range from about 1.0 mm long on the exterior (1.9 mm on the interior) down to about 0.4 mm long on the exterior (0.8 mm on the interior). All of the slits are about 0.15–0.2 mm wide.

Besides having a general deltoid shape, the most blastoid-like feature is that the longest slits (and folds) are marginal and not central (Text-fig. 43A). This is a characteristic feature of blastoid deltoid plates and is not known to occur in any other group of blastozoan or crinozoan echinoderms. This feature might be explained if the lateral margins of the plate were fractures and not sutures; the implication is that this plate as preserved is incomplete and represents only part of a larger plate on which the longest slits were originally centrally located (see Text-fig. 43B), as in some other blastozoan groups. However, the lateral margins are completely symmetrical, very straight, smooth and suture-like, and both show the same upward slant. Therefore, these lateral edges are almost certainly sutures and not fractures. The small upper edge (adoral?) may also be a suture, either bordering the mouth or attached to oral plates covering the mouth. G. Winston Sinclair (personal communication, 17 September 1967) suggested the possibility that this plate might represent a basal plate of some early crinoid-like *Carabocrinus*. However, there is no evidence of a stem facet, lumen canal, or secondary deposits on this small upper edge, and the problem of long marginal slits with internal folds still remains. Therefore, this possible origin seems unlikely.

The only known specimen is USNM 165409 from the upper member of the Antelope Valley Limestone (*Anomalorthis*? zone), lower Middle Ordovician (Whiterockian), locality USGS D1634 CO, Ranger Mountains just south of Frenchman Flat on the Nevada Test Site, Frenchman Lake Quadrangle, southwestern Nevada. Unfortunately, I was unable to revisit this locality to try and collect additional material.

Discussion. Because only a single deltoid plate of this possible blastoid is known, no name is proposed for it here. At present the evidence suggests that this single plate is most likely of blastoid origin; the plate shape and arrangement of slits with internal folds do not fit any other echinoderm group. The open slits imply that this plate probably comes from a fissiculate blastoid, but it differs from most Silurian fissiculates in that the plate surface bearing the slits is flat and does not slope steeply into the ambulacral sinuses (on the lateral margins?). The possible implications of this difference will have to await the discovery of more complete material from the Antelope Valley Limestone.

Subphylum **CRINOZOA** Matsumoto, 1929 (restricted herein)

Diagnosis. Living and extinct "pelmatozoan" echinoderms having a highly organized and differentiated calyx usually bearing large erect arms and often attached to the substrate by a columnal-bearing stem. The arms are relatively large, erect, food-gathering appendages usually continuing the calyx plating and containing extensions of the coelomic systems and the water vascular system with its tube feet. Arms are heavily plated, uniserial or less commonly biserial, often branch, and usually bear smaller uniserial appendages called pinnules. The calyx is well organized and usually shows a high degree of pentameral symmetry. In most crinozoans the calyx is differentiated into a dorsal cup with several rows of large plates and covered by a plated or unplated tegmen. However, some early crinoids and most paracrinoids have a more irregular calyx. Calyx respiratory structures are usually not present, except in some of the earlier forms having large globular calyces and short arms. The calyx plates probably increased in size by overlayering plate growth, with growth on the lateral margins and exterior of the plate. Nearly all crinozoans except the earliest members have a columnal-bearing attachment stem at some stage in their ontogeny. As restricted here, the subphylum contains only 2 classes, Crinoidea and Paracrinoidea, with approximately 820 genera ranging from the middle Cambrian to the Recent. Crinozoans (especially crinoids) were the dominant group of attached echinoderms during most of the Paleozoic, and contain the only living "pelmatozoan" echinoderms.

Discussion. The subphylum Crinozoa contains only two classes of attached arm-bearing echinoderms, crinoids and paracrinoids; a third class, the Diploporita, is left unassigned at present but may not belong here (p. 186). Also, paracrinoids do not seem to be especially close to crinoids in their known morphology (see p. 184), and are included here only with some reservations.

The major morphologic features of crinozoans, erect arms with tube feet, well-organized calyx, and long attachment stem, have remained relatively stable throughout much of their history. Crinozoans have probably not evolved into any other major group of echinoderms (for an alternate view, see Fell, 1963: 481–489), and their major achievement seems to have been their extremely successful domination, especially during the Paleozoic, of the niche or adaptive zone for attached, "high-rise," filter feeders. Crinozoan forms do not seem to converge toward blastozoans in their morphology even back to the beginning of the fossil record for these two groups (early to middle Cambrian), and it appears that they represent independent but parallel attempts to colonize the same major adaptive zone. No common ancestor for these two groups can be inferred at present, and it is not known why the very different types of food-gathering appendages and water vascular systems were developed. With only a single Cambrian record at present (see p. 177), additional information is sorely needed concerning the early evolution and diversification of crinozoans in the Cambrian.

Class *CRINOIDEA* Miller, 1821

Diagnosis. Arm-bearing, stemmed or stemless, crinozoan echinoderms with a differentiated calyx and well-developed pentameral symmetry. Calyx globular or cup-shaped, differentiated into a heavily plated dorsal cup supporting the arms and a plated or unplated tegmen covering the oral surface. Calyx plates usually show strong pentameral symmetry and are divided into 4–5 types arranged as alternating rows (infrabasals, basals, radials, orals, etc.). Plates may grow by primary overlayering growth with scattered secondary deposits on the exterior. Calyx respiratory structures usually absent. Large, erect, food-gathering arms attached to the radial plates and continue calyx plating. Usually 5 or some multiple of 5 arms present. Arms composed of uniserial (primitive) or biserial (specialized) arrangement of relatively large brachial plates, may be branched or unbranched, and often bear smaller uniserial appendages called pinnules. Arms and pinnules contain ambulacral grooves extending out from the mouth, and also extensions of the coelom, nervous system, and water vascular system with its tube feet; these latter systems enter the calyx interior through a large opening at the radial facet. Stem long and well developed in most fossil and some living crinoids, composed of 1-piece disklike columnals. Five-piece columnals or a multiplated holdfast present in the earliest crinoids. Stem often has smaller cirri present along its length and a rootlike structure or cemented disk at the base. Approximately 800 genera and 6000 species (630 living). Middle Cambrian(?), early Ordovician–Recent, worldwide distribution.

Discussion. Crinoids are by far the most successful attached echinoderms in the fossil record, and represent the only crinozoan or blastozoan class that is still living today. Therefore, they are the group to which all other extinct attached echinoderms must be compared for information on morphologic features, growth, and paleoecology. Unfortunately, many aspects of the functional morphology and ecology of modern crinoids are still poorly known (Fell, 1966: 49).

Crinoids dominate the Paleozoic record of all echinoderms from the middle Ordovician on. During this time they were usually two to five times more diverse in terms of number of genera than any of the blastozoan groups (see Text-fig. 1). Their great success can be ascribed to at least two factors: 1) their very efficient design for a filter-feeding way of life, with a long stem, symmetrical and well-organized calyx, and long pinnulate branching arms, and 2) the presence of tube feet on the arms to aid in feeding, respiration, movement, and sensory perception, in contrast to other attached echinoderms that may have lacked tube feet. Although other factors may also have been present, these two seem to be the most likely features that were lacking in other less successful groups of attached echinoderms.

Crinoids are characterized by several well-defined (but not exclusive) morphologic features. The large highly developed symmetrical arms that are heavily plated, either uniserial or biserial, often pinnulate and branching, and carrying extensions of the coelomic, nervous, and water vascular systems with tube feet are probably the most distinctive feature. Paracrinoid "arms" are somewhat similar, but are asymmetrical and may or may not have had tube feet. Most blastozoan food-gathering appendages (brachioles) are considerably different, except when the entire ambulacral system is developed as an "arm," such as is found in *Caryocrinites* (see p. 20). In these cases, the "arm" (= ambulacrum) is always biserially plated and bears biserial "pinnules" (= brachioles), a condition unknown in crinoids. Another characteristic crinoid feature is the differentiation of the calyx into a dorsal cup covered by a tegmen; however, a similar arrangement is found in several eocrinoids and rhombiferan cystoids. Except for a few early crinoids with large globular calyces, crinoids have rarely developed specialized calyx respiratory structures such as are commonly found in blastozoan echinoderms. This is probably because the tube feet on the highly developed arms were sufficient to carry out the respiratory needs of most crinoids. A few fossil crinoids are known to have had an overlayering type of primary plate growth in contrast to the holoperipheral plate growth found in most blastozoan echinoderms; however, little work has been done on the growth of living crinoids, and it is not known for certain whether this feature is a characteristic of the entire class (or subphylum). Finally, the long, columnal-bearing stem of crinoids is matched by very similar structures of independent origin in several other blastozoan (and perhaps crinozoan) classes.

Unquestioned crinoids first appeared in

the fossil record in the early Ordovician, and by early middle Ordovician times all three Paleozoic subclasses of crinoids were present. This early diversity implies a considerable previous record in the Cambrian and earliest Ordovician. The new middle Cambrian crinoid(?) from the Burgess Shale described in the following sections may fill in a portion of this gap. This new genus, *Echmatocrinus,* has numerous large uniserial arms, perhaps with tube feet, but irregularly plated calyx with little organization, and an attachment holdfast instead of a columnal-bearing stem. *Echmatocrinus* is definitely a very early crinozoan, and probably qualified as a true crinoid because of the characteristic arms. This early crinozoan had already developed many of the characteristic features of the subphylum by middle Cambrian times, and does not seem to converge in several of these critical features on known Cambrian blastozoan eocrinoids. Because of these facts, it appears that crinozoan and blastozoan echinoderms have been distinct groupings since at least the early Cambrian and probably the late Precambrian, and that crinoids could not have evolved from any known groups of Cambrian eocrinoids, as proposed by Moore (1954: 131, 144) and Regnell (1960: 71, 76).

The three Paleozoic subclasses of crinoids, Inadunata, Camerata, and Flexibilia, flourished during most of this era, but were reduced almost to extinction at the Permo-Triassic boundary. A few crinoids, apparently mostly inadunates, survived into the Triassic (Moore, 1952: 350; Rhodes, 1967: 63) and crinoids slowly recovered some of their previous abundance. A fourth subclass, Articulata, is defined for all post-Paleozoic crinoids, but it may be a polyphyletic grouping (see comments by Moore *in* Rhodes, 1967: 63). Articulate crinoids were relatively abundant in the Jurassic and Cretaceous, but their dominant position in terms of echinoderm diversity had been taken over by the echinoids. Today, crinoids are relatively common and widespread, but are still somewhat of a relict group in comparison to their past diversity and importance.

Subclass *INDETERMINATE*
Order **INDETERMINATE**
Family ECHMATOCRINIDAE new family

Diagnosis. Primitive crinoids(?) having a conical calyx made up of numerous irregularly arranged plates, 8 or more large uniserial arms possibly bearing soft tube feet(?), and an irregularly multiplated attachment holdfast instead of a stem. Middle Cambrian.

Genus *Echmatocrinus* new genus

Type species, Echmatocrinus brachiatus new species

Diagnosis. Early crinoids(?) having a large conical to bowl-shaped calyx with a flattened summit. The adjacent calyx plates appear to be irregularly arranged, except for wide plates beneath each of the arms that may be primitive radials. The calyx is attached to objects lying on the sea bottom by a long or short, tapering, irregularly plated holdfast. At least 8 (and possibly as many as 10) large, uniserially plated arms are attached to the edge of the calyx summit. Each arm tapers slowly in a distal direction and is made up of 8–12 uniserial brachial plates. The lowest 2–3 plates appear to have large triangular areas aborally, perhaps for the insertion of muscles or ligaments. At least 1 specimen has secondary soft appendages attached alternately(?) to the brachial plates of the arms. These could either be tube feet or, less likely, uncalcified pinnules; they are now preserved as an organic film that is nearly invisible unless the specimen is immersed in a liquid. The holdfast, calyx, and arms (but not the soft appendages attached to them) have a coarse granular ornament preserved in pyrite, apparently representing the original echinoderm calcite microstructure. Middle Cambrian (*Bathyuriscus-Elrathina* zone), Burgess Shale, western Canada.

Etymology. The generic name is derived from *echmatos* (Gr.)—holdfast, stalk, referring to the large attachment holdfast appendage found in this early crinoid.

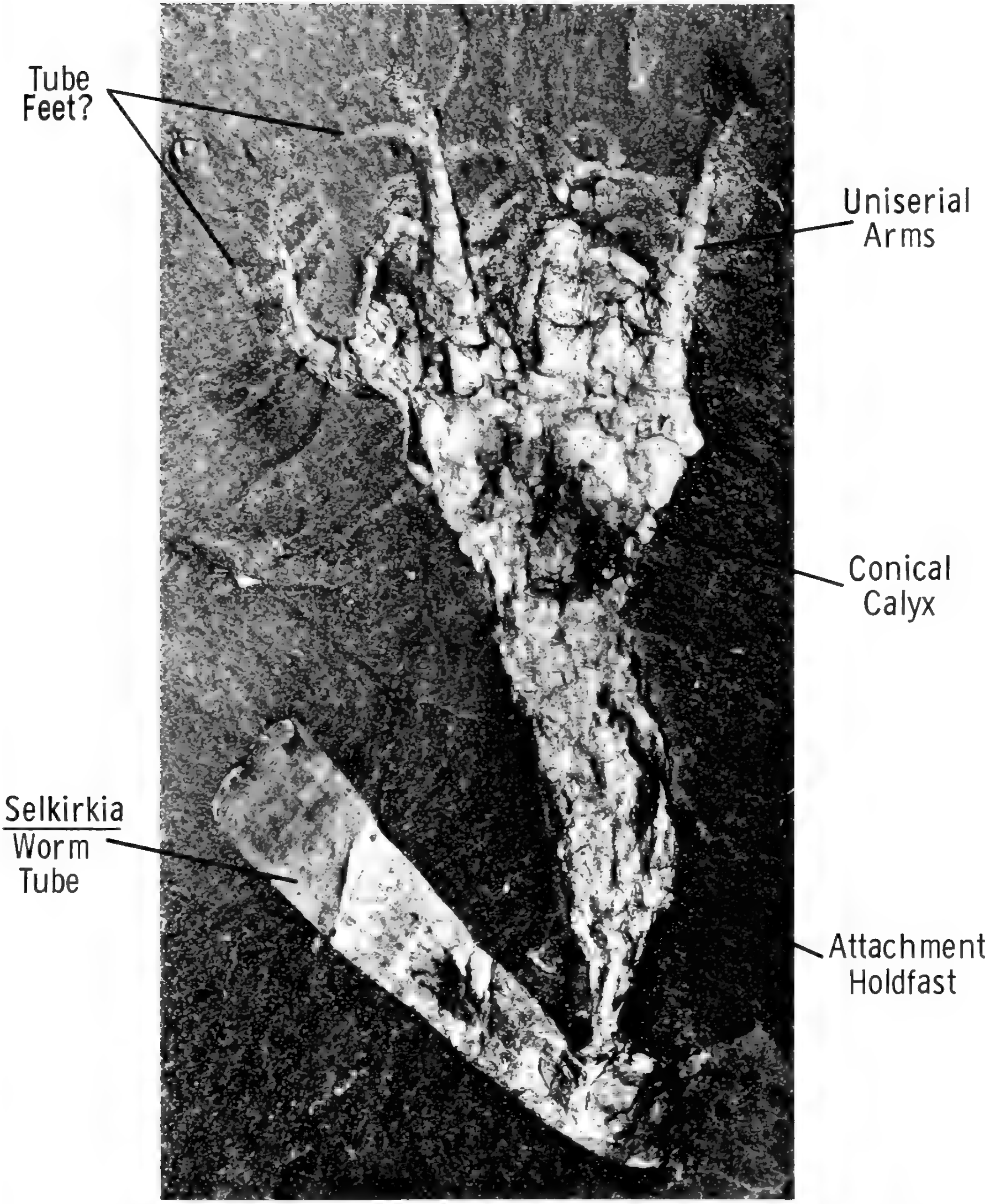
Discussion. *Echmatocrinus* is now the earliest crinoid-like form (and certainly the earliest crinozoan) known from the fossil record. Whether or not it is accepted as a true crinoid depends on one's interpretation of 1) the apparently irregular calyx plating, and 2) the presence of an irregularly plated holdfast instead of a columnal-bearing stem, both features unknown in later crinoids, in comparison to 3) the well-developed, uniserial, erect arms (perhaps bearing tube feet). Because of this last important feature, I can see no alternative but to regard *Echmatocrinus* as a true crinoid belonging to the previously unknown Cambrian stock from which later crinoids probably evolved.

The oldest previously described crinoids, the inadunates *Aethocrinus moorei* Ubaghs and *Ramseyocrinus cambriensis* (Hicks) from late Tremadocian or early Arenigan strata at the base of the Ordovician, are somewhat intermediate between *Echmatocrinus* and later crinoids. The primitive stem in these two genera is regularly organized into four- or five-piece "columnals" surrounding a large central lumen (Bates, 1968: 400; Ubaghs, 1969: 7). This stem grades proximally into the lower part of the calyx, while at the distal end there is an enlarged attachment(?) area with irregular tiny plates (Ubaghs, 1969: 3). The calyx in these two genera shows relatively well-developed rows of plates, although in *Ramseyocrinus* the plates show quadrate symmetry and in *Aethocrinus* the plates have a slightly irregular pentameral symmetry. In the latter genus, the radial plates may alternate with the first brachials (Ubaghs, 1969: 13), a very unusual feature; however, this interpretation has been challenged by Philip and Strimple (1971: 491–493). Finally, both genera have long and heavily plated uniserial arms that branch isotomously and lack pinnules.

If *Echmatocrinus* is regarded as an ancestral crinoid, several important changes would have to have taken place between its occurrence in the middle Cambrian and the first known appearance of other crinoids in the early Ordovician. The calyx plating would have to have been considerably reduced and modified to an imperfect pentameral (or quadrate) symmetry, the holdfast would have had to become better organized, more symmetrical, and greatly increased in length, and the arms would have to have been somewhat modified, reduced in number, and branched. *Echmatocrinus* could have been on the main evolutionary line leading to many or all later crinoids or it may have been a very early, and perhaps somewhat specialized, offshoot from this line.

The nature of the soft appendages attached to the arms of the holotype specimen is one of the most critical features found in *Echmatocrinus.* Although I am certain they were soft and not calcified like the rest of the echinoderm skeleton (see p. 182), these small appendages attached to the arms could either be tube feet from the water vascular system or possibly unplated pinnules (with or without accompanying tube feet). If they are interpreted as tube feet, then there is already a record of a definite crinozoan (and probably a true crinoid) in the middle Cambrian having uniserial arms with the water vascular system and tube feet well developed. With these characteristic features, this crinozoan is already quite distinct from the attached blastozoans (eocrinoids) living at the same time, the implication being a long separate history for these two groups before the middle Cambrian.

Echmatocrinus also has some bearing on the origin of other major echinoderm groups. Fell (1963: 483) has postulated that the earliest and most primitive asterozoan group, the Somasteroidea, may have evolved from a crinoid ancestor before their first appearance in the early Ordovician. *Echmatocrinus* is now the only Cambrian crinoid(?) known, but it does not seem to



Text-figure 44. Morphology of *Echmatocrinus brachiatus* n. gen., n. sp. Holotype specimen GSC 25962B (immersed in water) showing calyx, long attachment holdfast, and arms with possible tube feet(?); note irregular but poorly preserved plating in calyx and holdfast, globular pyritic concretion(?) where holdfast is attached to *Selkirkia* worm tube, strongly plated uniserial arms, and alternate arrangement of soft tube feet(?) on several arms.

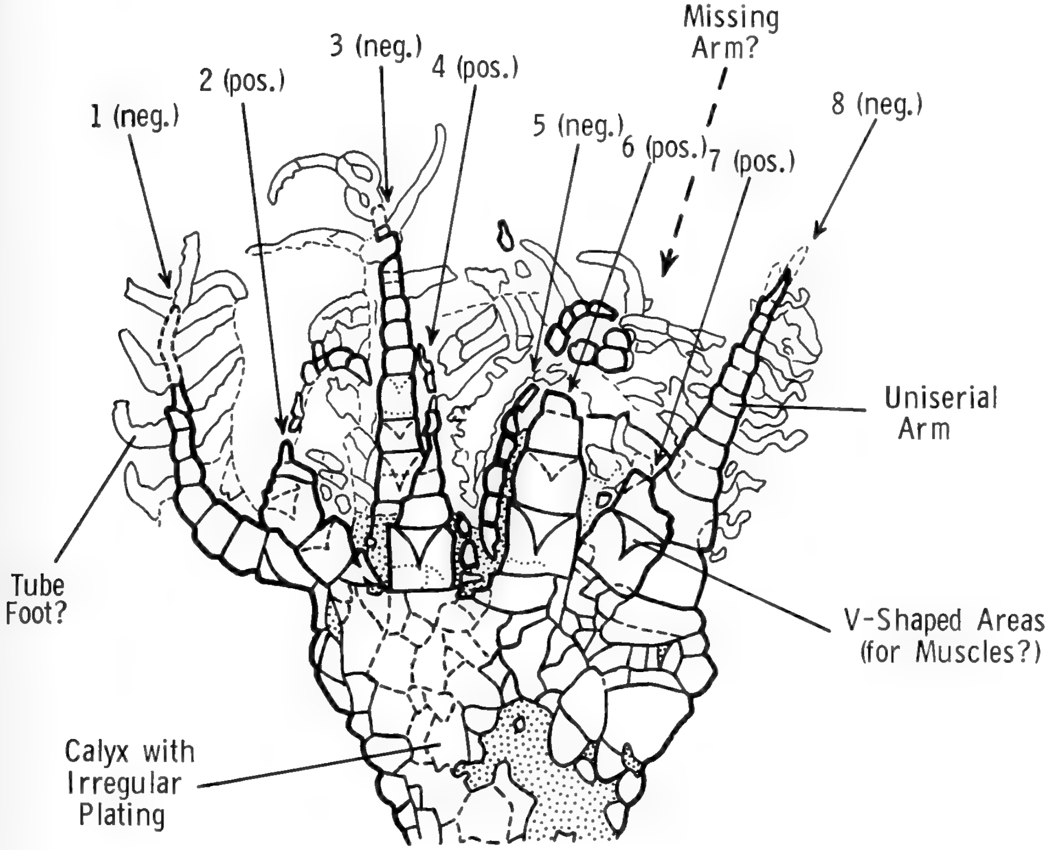
have any of the characteristics necessary for this proposed crinoid-somasteriod transition. It has a large instead of a reduced calyx, uniserial versus biserial arms, and no plated pinnules. This negative evidence, however, does not refute the proposed derivation (although it does make it somewhat less likely), because other very different crinozoans may also have been living in the Cambrian seas along with *Echmatocrinus*.

Echmatocrinus brachiatus new species

Plates 42 and 43; Text-figures 44–45

Only five partially complete specimens of this primitive crinoid are known to exist. Four of these specimens (paratypes USNM 165405–8), ranging in preservation and completeness from poor to relatively good, were originally collected by Walcott between 1911 and 1917 during his quarrying work in the Burgess Shale. However, they were never described by Walcott or later workers, and remained unstudied in the U. S. National Museum collections until they were shown to me by J. Wyatt Durham during a visit to Washington in May, 1966. The fifth specimen (holotype GSC 25962), which is the largest, best preserved, and the only specimen having any of the soft parts preserved, was found on 25 July 1967, during re-excavation work at the Burgess Shale Quarry by members of the Geological Survey of Canada and Harry B. Whittington and students. I was visiting the quarry that day during field work in the Rockies and was present when this new specimen was found. It came from a thick but relatively unfossiliferous bed between eight feet and eight feet, seven inches above the floor of the quarry, and fortunately both counterparts were recovered intact. This specimen is much larger than any of the others, has small soft appendages (tube feet?) attached to the arms, and is the only one of these specimens to come from one of the bluish, silty, conchoidally fracturing beds in which most of the soft-bodied arthropods, worms, etc. have been found. No calcite is preserved in any of these specimens, and the plating shows up only as a thin film of pyrite with coarse reticulate ornamentation, apparently representing the original echinoderm calcite microstructure. Plate sutures are not well shown, and additional cracks are present from diagenetic crushing. In the three specimens with matched counterparts, only one side of the crinoid is preserved, and is represented by a positive counterpart (containing the rest of the specimen) and a negative counterpart. Because of these problems, our knowledge of this crinoid is still imperfect and additional specimens, especially ones preserving the original calcite, would be very desirable.

Specific description. The complete specimens of *Echmatocrinus* range in size from about 29 mm up to 79 mm for the holotype. They are composed of 3 major parts, the calyx, holdfast, and arms (Text-Fig. 44). The calyx is rounded-conical to bowl-shaped in the 4 specimens in which it is preserved. It expands rapidly from its narrowest point where it is attached to the holdfast and reaches its maximum width just below the arms. The maximum width at this point is somewhat greater than the total length of the calyx, and the calyx L/W ratio ranges from 0.53 to 0.85. Although the plating is not especially well preserved, there appear to be about 65–70 irregular polygonal plates on each side of the calyx (Text-fig. 45). These plates appear to be relatively thin and adjacently sutured, and do not show any pore- or foldlike openings into the calyx interior. Unlike nearly all later crinoids, there does not seem to be any rowlike regularity or symmetry in the calyx plating. In holotype GSC 25962, the larger plates, located in the middle and upper parts of the calyx, range up to about 5–6 mm in size. Just below several (and perhaps all) of the arms, there are short wide rectangular plates, which may represent primitive radials or first primibrachials (Text-fig. 45). Some parts of the calyx are obscured by matrix



Text-figure 45. Calyx, arm, and tube foot(?) morphology in *Echmatocrinus brachiatus* n. gen., n. sp. Drawing of calyx and arms in holotype specimen GSC 25962B (compare with Text-fig. 44); arms numbered and labelled with type of relief (positive or negative). Note irregular but imperfectly preserved calyx plating, elongate calyx plates (radials?) beneath several arms, V-shaped areas (for muscles?) on lower brachial plates, alternate branching of the tube feet(?) (one per brachial plate) on arms #1 and 3, and alternating arm relief except between arms #6 and 7, where an additional arm (now missing) from the rear of the calyx may have been located.

material and other parts are badly crushed in the holotype and some of the paratypes.

The holdfast is a long or short, tapering, irregularly plated, attachment appendage. It tapers from a maximum diameter in the upper 1/3 of its length to almost a point (1–2 mm) where it is attached distally (Text-fig. 44). The three preserved complete holdfasts show considerable variation in length; the holdfast L/W ratio ranges from 5.0 to 1.3, while the HF/C ratio varies from 0.8 to 1.9. The plate sutures are not well exposed on the holdfast, and cracks from diagenetic crushing further complicate analysis of the plating. Most of the holdfast plates appear to be roughly rectangular in shape and somewhat wider than long. They may be arranged in irregular (perhaps alternating) columns considerably less organized than the primitive 5-part stem of the early Ordovician crinoid *Aethocrinus* (Ubaghs, 1969: 7). All 3 of the specimens with complete holdfasts (holotype GSC 25962, and paratypes USNM 165405 and USNM 165408) are attached to objects that apparently were lying on the sea bottom. The holotype specimen is attached to a conical worm tube belonging to the genus *Selkirkia* (H. B. Whittington, personal communication, 4 September 1969). There is a circular pyritic concretion(?) near this point of attachment, but it does not appear to be part of the crinoid specimen because it lacks the granular surface texture shown by the pyritized echinoderm plates. Paratype USNM 165405 has its considerably shorter holdfast attached to another of these pyrite concretions(?); again, because of the lack of surface texture it does not seem likely that the concretion is part of the echinoderm. Isolated holdfast USNM 165408 is apparently attached to a small hyolithid. The large variation in holdfast length, especially between the holotype and paratype USNM 165405, is somewhat unusual. However, because of the apparent adjacent plating, the holdfast was probably not expandable lengthwise, in contrast to the imbricately plated expandable holdfast in the early Cambrian eocrinoid *Lepidocystis* (see p. 67). There is little change in plating where the holdfast is attached to the calyx, only a gradual increase in width.

The heavily plated uniserial arms of *Echmatocrinus* represent the most crinoid-like morphologic structure of this genus. These arms are relatively short, unbranched, uniserially plated, and attached around the margin of the summit. Holotype GSC 25962 has 8 arms exposed; a ninth arm is very likely present (but broken) on the unexposed side of the calyx (Text-fig. 45), and originally there may have been as many as 10. Paratypes USNM 165405 and 165406 have 7–8 and 6+ arms, respectively. These arms, particularly on the holotype and best paratype specimens, show strong positive and negative relief (see Pl. 43, figs. 1–2 and 6), indicating to which side of the body they are attached. On the counterpart still containing the calyx, the arms on the exposed side of the calyx have positive relief while the arms on the opposite unexposed side have negative relief; this arrangement is reversed on the other counterpart. In the holotype the arms are between 22–24 mm long when complete and just over 4 mm wide (and high?) at the base. There are 10–12 uniserially arranged brachial plates making up each arm in this specimen. The smaller paratype specimens have shorter arms with fewer brachial plates (Plate 43), as might be expected if the arms increased in length during ontogeny. The brachial plates on the arms of the holotype are slightly longer than wide near the base but appear to be wider than long distally. The two most proximal brachial plates have a prominent triangular area of darker material on their aboral side near the distal edge (Text-fig. 45; Pl. 43, fig. 8). These areas may have contained ligaments or muscles used by the crinoid to flex its arms outward to a horizontal position (perhaps for feeding). The more distal brachial plates lack this triangular marking and have flush sutures.

The most outstanding feature shown by holotype specimen GSC 25962 is the numerous soft secondary appendages attached to the brachial plates of the arms (Text-fig. 45). These soft appendages show up only when the specimen is immersed in a liquid (water, xylene, etc.); they are almost invisible when the specimen is dry (compare Pl. 42, figs. 1–2 with Pl. 43, fig. 6). Paratype USNM 165405 also has possible traces of these secondary appendages in 1 or 2 places on its arms, but they appear to be completely lacking from all of the other paratypes. These tiny appendages are usually 4–6 mm long and about 1.0 mm wide near their base. In several places (especially the leftmost arm in Text-figs. 44 and 45), these secondary appendages appear to be attached 1 to each brachial plate on alternate sides of the arm. However, the true arrangement may be more complicated than this. These secondary appendages attached to the arms are known for the following reasons to have been soft-bodied and unplated: 1) they show no plate sutures like the brachial or calyx plates; 2) since they show up very poorly when the specimen is dry, they apparently have a different composition from the strongly pyritized portions of the echinoderm where calcite plates were originally present; 3) they do not show the characteristic reticulate pattern present on the remainder of the specimen, probably representing the original calcite plate microstructure; 4) they show no relief at all, unlike the plated arms; and 5) several of these secondary appendages are severely folded and bent over on themselves (Text-fig. 45), implying a soft structure. The actual composition of the preserved material in these secondary soft appendages has not been analyzed, but under high magnification it appears to be composed of an extremely thin sheet of pyrite-like material containing organic carbonaceous specks. The pyritic(?) phase of this material appears to have grown or been precipitated in circular patches that have pushed the organic carbonaceous phase into tiny triangular specks between them.

I feel that these secondary soft appendages attached to the arms are probably tube feet from the water vascular system, but it is also possible that they represent uncalcified pinnules unrelated to the water vascular system. The soft nature, relative size compared to other fossil tube feet, location along the entire arm length, and others factors (such as the known later history of crinoids), support an interpretation of these appendages as tube feet. The apparent alternate attachment to each brachial plate and the relative size compared with the tube feet in modern crinoids may support a noncalcified pinnule interpretation. Pinnules are not known in later crinoids until the middle or late Ordovician and seem to develop as reduced branches of the arm itself (Moore and Laudon, 1943: 10). In particular, pinnules are completely absent from the simple uniserial arms of the early Ordovician crinoid genera *Aethocrinus* and *Ramseyocrinus,* which are the next crinoids to appear in the fossil record. If *Echmatocrinus* is in fact a primitive but true crinoid, then tube feet would be expected on the arms as the external projections of the water vascular system.

There is no information about calyx structure such as the mouth, ambulacral system to the arms, or the location of an anal pyramid or tube from the presently available specimens. The location and description of these structures and a complete interpretation of the calyx and holdfast plating will have to await the discovery of additional new material, most likely preserved differently from the specimens of *Echmatocrinus* studied here. Natural molds, or calcite specimens in a noncalcareous shale from which molds and then latex castings could be made, would be the most desirable type of preservation.

Etymology. The specific name *brachiatus* (Gr.)—arm-bearing, refers to the characteristic large uniserial arms found in this early crinoid.

Stratigraphic and geographic range. Burgess Shale Member of the Stephen Formation, Middle Cambrian (*Bathyuriscus-Elrathina* zone), Walcott's Quarry (USNM loc. 35k) and the smaller quarry about 75 feet above (USNM loc. 35k/10), ridge on the south side of Mt. Wapta, near Field, British Columbia.

Studied specimens. Holotype GSC 25962; complete paratypes USNM 165405–165408; one additional separate brachial plate (paratype USNM 165426); and one poorly preserved possible additional specimen (USNM 165427). All specimens are from Walcott's main Burgess Shale Quarry (loc. 35k) except for USNM 165408, which is from the small accessory quarry (loc. 35k/10).

Class, Order, and Family INDETERMINATE

Cystidea nugatula Barrande, 1887

This taxon was briefly described by Barrande (1887: 180; pl. 31, figs. 3–5 and explanation) as a stem fragment attached to the base of a calyx belonging to an indeterminate cystoid. Barrande figured a natural mold, but did not cast it or show the surrounding matrix. I have figured a latex cast of this specimen (S 31, Caster Collection, University of Cincinnati) on Plate 33, figure 11. It represents a very striking distal attachment structure connected to a five- to seven-part primitive stem and mounted on the flat central glabella of a very large trilobite cephalon. Two specimens are present, only one of which has the stem partially preserved. Because of the age (D_4—middle Ordovician) and the partial resemblance of these structures to the five-part stem and enlarged irregularly plated distal structure in *Aethocrinus* (Ubaghs, 1969: 7), *Cystidea nugatula* probably comes from a primitive crinoid and not a blastozoan echinoderm.

The stem is relatively large and has five to seven rows of alternating columnal plates enclosing a large central lumen. The distal attachment structure is dome-shaped with a flat base (Pl. 33, fig. 11). The upper portion is made up of large polygonal plates with apparent concentric growth lines(?). Near the lower edge the plating becomes much smaller, like that found around the rim of most edrioasteroids. There is a deep conical cavity in this structure at the top where the stem is attached. This cavity has deeply indented vertical fluting and an enlarged groove just inside the structure (see Barrande, 1887: pl. 31, fig. 4). This cavity probably housed muscles for attachment and perhaps other structures such as glands for secreting mucus or cement.

This attachment structure is very similar to the distal attachment ends of many eocrinoid holdfasts. The presence of this type of structure attached to the primitive stem of an apparently early crinoid shows that early stems like this almost certainly evolved from an irregularly multiplated holdfast. Apparently the change to a true stem with advanced attachment structures took place gradually in early crinoids and in some forms was not completed until at least the middle or late Ordovician.

Class *PARACRINOIDEA* Regnell, 1945

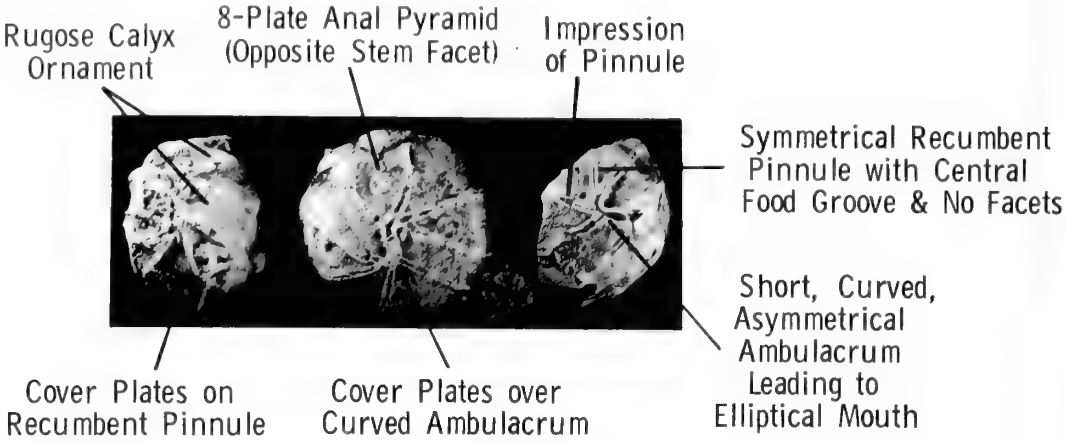
Diagnosis. Stemmed echinoderms with a globular or lens-shaped calyx having numerous thick or thin plates without pentameral symmetry; anus usually opposite stem facet and mouth lateral in position. Ambulacral system consists of 2–5 branches radiating from mouth developed either as recumbent, asymmetrical ambulacra bearing smaller uniserial armlike appendages (= pinnules), or else erect, asymmetrical, uniserial "arms" (= ambulacra) with smaller uniserial pinnules. Ambulacra or arms usually show left-lateral asymmetry looking aborally, with pinnules branching off the left side and food groove on the right. Arms have asymmetrical facets where attached to calyx, while ambulacra often curve, sometimes branch, and may reach to stem facet. Hydropore and/or gonopore usually present near mouth. Thin-plated forms lack respiratory structures, but thick-plated ones usually have incomplete pore- or foldlike structures on or near the plate sutures. These structures are usually covered on the exterior or do not completely penetrate the plate internally. Stem strongly curved near calyx attachment and perhaps vestigial in some forms; calyx may have sat directly on sea floor with the recumbent stem holding it upright or anchoring it in place. Sixteen genera; middle Ordovician, North America and Europe.

Discussion. Paracrinoids form a relatively compact group of genera that share several unusual characteristics. They were set up as a separate class by Regnell (1945: 37–40), who noted that they could not reasonably be assigned to the eocrinoids, cystoids, or crinoids. His diagnosis (p. 37) considered some of the main features, and others were noted by Kesling (1967b: S273, S277), who has recently reviewed the class and redescribed many of the genera. Other genera, however, were provisionally included in the eocrinoid chapter for the Treatise (Ubaghs, 1967b) and are here transferred to the paracrinoids (see p. 138).

No other class of echinoderms has asymmetrical ambulacra or the anus opposite the stem facet with the mouth lateral. These seem to be exclusively paracrinoid features, and many have evolved because of the possible bottom-living habitat of paracrinoids bearing a reduced or strongly curved anchoring stem. The ambulacral system seems to be the most characteristic feature of paracrinoids. The two to five main branches from the mouth are developed either as recumbent ambulacra bearing smaller uniserial armlike appendages, or as erect "arms" with the smaller uniserial appendages developed as pinnules. In both cases these main ambulacral branches are asymmetrical with a "left-lateral" pattern of pinnule attachment; looking in an aboral direction, the food groove runs down the right side of the ambulacrum and pinnules branch off the left side, one per ambulacral plate. When developed as erect uniserial arms, the attachment facets on the peristome show a strong asymmetry like the arms (see Text-fig. 33); this asymmetry can be used to identify paracrinoids even when the armlike appendages are lacking, as in the case of *Columbocystis*. When these ambulacral branches are recumbent, the shorter ambulacrum (or both if they are equally short) curves strongly to the right (looking aborally), apparently to allow the maximum room for the erect pinnules branching off the outer left side. The longer ambulacrum (if present) usually curves only slightly and sometimes extends down over the entire calyx to the stem facet. The implication may be that the calyx sat on the sea floor on the side opposite this long ambulacrum (J. Wyatt Durham, personal communication, 2 August 1967), or was held in an upright but tipped position by the strongly curved stem (R. L. Parsley, personal communication, 12 November 1968).

The genus *Malocystites* has an even more unusual arrangement of its ambulacral system. The two main ambulacra are very short and strongly curved in an "S" or sigma-shaped pattern with three to five long recumbent "branches" extending from each ambulacrum down over much of the calyx. This unusual branching pattern is different from that in all other paracrinoids but a careful examination of several well-preserved specimens (MCZ 718a–c) from a locality near Ville de Laval, just north of Montreal, shows that each of these "branches" is symmetrical, has a covered food groove but no appendage facets, and comes from a single asymmetrical ambulacral plate (Text-fig. 46). Therefore, it appears that these "branches" are in fact recumbent pinnules, and that *Malocystites* has gone to the extreme of putting all portions of its food-collecting system directly on the calyx surface. From the manner in which it occurs and its association with the crested parablastoid *Blastoidocrinus* (see p. 145), I suspect that *Malocystites* lived in a relatively turbulent environment where any erect food-gathering appendages would have been easily damaged or torn off if the calyx was tipped over or rolled around on the bottom. Few other "pelmatozoan" echinoderms are known to have a completely recumbent ambulacral system like this.

Pore- or foldlike respiratory structures are present only in paracrinoids having relatively thick calyx plates; thin-plated forms were probably able to respire directly through the plate surface and did not need specialized structures. This is similar to the situation found in some Cambrian and Ordovician eocrinoids (see p. 35). Specialized respiratory structures in paracrinoids are usually sutural and are nearly always covered externally or divided medially so that there is no direct connection between the exterior and interior as in



Text-figure 46. Recumbent "arms" and "pinnules" in *Malocystites murchisoni.* Summit views of three well-preserved plesiotypes (MCZ 718a–c) showing elongate mouth with two strongly curved ambulacra radiating in opposite directions from it, and uniserial recumbent "pinnules" which branch off the ambulacra one per ambulacral plate, bear a central food groove protected by tiny cover plates, and lack additional appendage facets. (× 1.2)

eocrinoid epispires or diploporan diplopores.

Paracrinoids include at least 16 genera and are known only from the middle Ordovician of North America and Europe. They are most common in limy shales of Chazy, Black River, and Trenton age in eastern and central North America. At present, only one genus is known from Europe. Besides the genera considered by Kesling (1967b: S277–S288), I have also assigned the following genera to the Paracrinoidea: *Columbocystis, Springerocystis,* and *Foerstecystis.* The Ordovician genera *Ulrichocystis* and *Palaeocystites* and the poorly known middle Silurian genus *Allocystites* Miller, 1889, may also belong here, but need to be restudied.

Unassigned Blastozoan or Crinozoan Class
Class *DIPLOPORITA* Müller, 1854

Diagnosis. Globular unstemmed or stemmed echinoderms having numerous plates bearing diplopores and usually primitive ambulacra with poorly known appendages. Calyx globular or elongate, often either attenuated or strongly flattened on base. Plates numerous, irregularly arranged in most forms; some or all plates bear numerous small diplopore pore-pairs, usually oriented with long axis through pores perpendicular to suture of the plate segment they occupy. Three to five very short to long ambulacra usually consist only of food grooves on calyx plates leading to appendage facets; some advanced forms have specialized ambulacral plates. Appendages small, poorly known: either uniserial "pinnules" or biserial brachioles. Stem usually poorly developed or absent; some forms have a primitive stem with multi-piece columnals. Pentameral symmetry usually developed only in ambulacral system. Type of plate growth unknown. Thirty-five genera; early Ordovician–early Devonian, world-wide distribution.

Discussion. Diploporan cystoids have recently been raised from their original ordinal ranking (Müller, 1854: 249) to class status by Paul (*in* Jefferies et al., 1967: 566, 1968b: 727). Their major defining characteristic as a class is the unique diplopore respiratory pores passing through the calyx plates. Unfortunately, the ambulacral appendages are so poorly known at present that I have been unable to assign the Diploporita either to the amended subphylum Crinozoa or to the new subphylum

Blastozoa. Previous authors have figured diploporan specimens both with biserial brachioles (*Protocrinites, Dactylocystis*) (see Kesling, 1967a: S326, figs. 2f, 4a), and with uniserial "pinnules" (*Asteroblastus*) (*ibid.*: S259, fig. 1g). However, some of these original appendage reconstructions may have been inaccurate or imaginary. I have examined the holotype specimen of the apparent diploporan *Regnellicystis typicalis* (USNM 113308), and found traces of small uniserial pinnule-like appendages near the ambulacral grooves (but not attached in place). If this type of appendage is a characteristic feature of diploporans, then their phylogenetic assignment would depend on whether these appendages were derived from normal blastozoan (probably eocrinoid) brachioles by modification of the brachiole plating (for a similar example, see p. 20), or whether these appendages represent reduced crinozoan arms. At present, I cannot answer this question conclusively. Other morphologic features of diploporans seem to favor a possible blastozoan origin. The ambulacra are similar in development to those of many eocrinoids, and my own observations and those of others (C. R. C. Paul, personal communication, 6 April 1968) suggest that diploporan ambulacra probably lacked radial water vessels and tube feet. Diplopores could easily have been derived from eocrinoid epispires by modifying an elongate epispire into separate incurrent and excurrent openings and then "trapping" it within one of the plates shared by the suture. The characteristic orientation found in most diplopores suggests this type of origin. A similar origin from epispire-like pores in some crinoids, however, is also possible. If diploporans are blastozoan echinoderms, then they represent a somewhat aberrant branch of mostly bottom-living forms having poorly developed symmetry, modified brachioles, specialized porelike respiratory structures, and often no stem.

I did not study any diploporan cystoids in detail for this project. Several other authors (C. R. C. Paul, R. L. Parsley) are currently working on members of this class.

Class Removed from the Blastozoa and Crinozoa

Class *EDRIOBLASTOIDEA* Fay, 1962

Diagnosis. Echinoderms having a bud-shaped calyx made up of numerous large and small plates that show a fair degree of pentameral symmetry. Plates arranged into circlets consisting of 5 large basals, 5 large radials, 5 large inverted V-shaped deltoids forming the ambulacra, 5 small oral plates, and small accessory plates located interradially below the deltoids and between the basals. Most of the larger plates have elongate irregular sutural indentations apparently penetrating to the calyx interior. The 5 long ambulacra extend down over much of the calyx exterior; they are composed of halves representing the long deltoid limbs. The large and deep central food groove is flanked by raised rows of pores extending to the calyx interior, apparently for tube feet. Brachioles are absent, and the entire ambulacrum is protected by a biserial set of elongate cover plates. The anal pyramid, surrounded by numerous accessory plates, is located on the side of the calyx in the "CD" interradius along with a slitlike hydropore and 2 or more possible gonopores in the same interradius. The primitive stem is made up of 5-piece columnals surrounding a large lumen. One genus; middle Ordovician, eastern North American and Australia.

Discussion. Edrioblastoids have represented an enigmatic group of echinoderms ever since the only known genus *Astrocystites* was first described from the middle Ordovician of the Ottawa region by Whiteaves in 1897. Although specimens of *Astrocystites* are very rare, the morphology is well enough known to indicate that a puzzling combination of features, not known in any other group of echinoderms, is present. Because of this, previous authors have assigned edrioblastoids to at least four classes and two echinoderm subphyla.

Most earlier authors classified *Astrocystites* either as an edrioasteroid (Bather, Bassler, Bassler and Moodey) or as a blastoid (Hudson) (see Mintz, 1970: 872–873 for a complete review). However, after restudying the lectotype of *Astrocystites ottawaensis*, Fay (1962: 201–205) erected the new class Edrioblastoidea for it and discussed the possibility that an edrioblastoid may have been ancestral to true blastoids, a point which I have disputed (see p. 172 and below). Webby (1968: 514–515 and 522–523) described a new species of *Astrocystites* from Australia, and proposed that edrioblastoids be removed from the subphylum Crinozoa and reassigned to the Echinozoa either as a separate class or as an order of the edrioasteroids. Most recently, Mintz (1970: 872–880), after studying a new specimen of the type species from Ontario, has concluded that edrioblastoids are probably an offshoot of the eocrinoids, and has placed them in the present subphylum Blastozoa (Mintz's Crinozoa s. l.). I agree with most of the morphologic interpretations made by Mintz, but disagree with his conclusions.

Both Mintz and Fay have shown that *Astrocystites* definitely lacks brachioles or other plated food-gathering appendages, since no structures of this type are present under the undisturbed cover plates protecting the entire ambulacrum (Mintz, 1970: 877, 879). The puzzling "facets" on the sides of the ambulacra may have served for articulation of the cover plates or may have been associated with the adjacent tube feet or the radial canal system. Mintz has associated the "deep furrows" crossing the plate sutures in *Astrocystites* with epispires in eocrinoids (1970: 874, 878). However, these structures have an irregular branching shape and lack an external raised rim, and thus are quite unlike true epispires in eocrinoids (see Text-fig. 11A) and may not have housed the same type of soft external respiratory structure. It should also be noted that sutural pores are not confined to eocrinoids but are found in several other classes, including the early edrioasteroids. The 5-part stem in *Astrocystites* is another unusual feature. All eocrinoids after the early late Cambrian have a true stem with one-piece disklike columnals. If the middle Ordovician *Astrocystites* were derived from an eocrinoid ancestor, it should also have a true stem. Since it does not, this implies that this stemlike attachment structure is probably of independent origin within the class itself. Finally, the presence of pores through the ambulacra apparently for tube feet (Mintz, 1970: 879) in a "closed" water vascular system indicates probable echinozoan affinities.

I have therefore concluded that *Astrocystites* can neither have been derived from the eocrinoids nor belong in the subphylum Blastozoa (or Crinozoa) as proposed by Mintz. I agree with Mintz (also B. M. Bell, personal communication, 11 November 1970) that *Astrocystites* probably does not belong within the edrioasteroids either, and therefore I am here assigning it to the subphylum Echinozoa as the separate class Edrioblastoidea. *Astrocystites* is apparently an echinozoan that has adopted a "high-rise" filter-feeding way of life, and evolved several blastoid-like calyx and stem features, thus putting it in the "blastoid-spectrum" of Brower (1969: 846–847). However, these similar features have arisen by convergence after the adoption of a similar way of life, and not by evolutionary descent.

I have seen an additional complete but poorly preserved specimen of *Astrocystites*(?) from the Curdsville Limestone of Kentucky in the Springer Collection at the U. S. National Museum. In addition, both C. R. C. Paul and I have collected characteristic V-shaped pore-bearing deltoid plates apparently belonging to an unknown edrioblastoid from the Benbolt Formation of Black Riveran age in southwestern Virginia; several of these plates are in the MCZ collections. Thus, edrioblastoid remains should be expected to occur at other early and middle Ordovician localities.

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APPENDIX 1
Locality Index

The 46 collection localities listed here are ones at which I personally collected blastozoan and crinozoan echinoderms described in this report. Each locality is designated by a two-letter symbol, indicating the geographic area of the locality, combined with a number indicating the specific locality in this area (for example, PI-2. refers to the second collecting locality at Pioche, Nevada). Localities are listed below in alphabetical order based on their two-letter designations.

AS-1. (Antelope Springs, W. Utah) Top 100 ft. of the Wheeler Shale (*Bolaspidella* zone), upper Middle Cambrian, N-S ridge just E of old Antelope Springs "Camp" and hole in two-in. aqueduct pipe, near middle of sect. 2, T. 17 S, R. 13 W, House Range, W of Delta, W. Utah. (Delta, Utah 1:250,000 topo. sheet) *Gogia spiralis.*

AS-2. (Same stratigraphic interval, area, and fossils as above) S nose of N-S ridge and W side of Wheeler Amphitheater, near boundary between sect. 1 and 2, T. 17 S, R. 13 W, same as above.

CF-1. (Calls Fort, N. Utah) Spence Shale Member, Langston Fm. (*Glossopleura* to *Bathyuriscus-Elrathina* zones), Middle Cambrian, talus slope and shale exposures on W side of Wellsville Mtn., near center of sect. 14, T. 10 N, R. 2 W, about 6.3 mi. N of Brigham City, Box Elder Co., N. Utah (Brigham City 7½′ Quad.) *Gogia granulosa, G. guntheri, Ctenocystis utahensis,* and an unidentified stylophoran carpoid.

CL-1. (Clayton, central Idaho) Basal 6 ft. of red shaly siltstone above top of Cash Creek Quartzite (*Albertella*? zone), Middle Cambrian, summit of 6897 ft. quartzite ridge, W side of Squaw Creek, T. 12 N, R. 17 E (unsurveyed), about 7½ mi. NW of Clayton, central Idaho. (Clayton 7½′ Quad.) *Gogia hobbsi.*

CS-2. (Cedar Springs Church, NE Tenn.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), large exposed hill with dipping slabby beds behind farm house, N side of state rt. 131 at entrance to Cedar Springs Church, about 3 mi. NE of Thorn Hill junction, Grainger Co., NE Tenn. (Swan Island 7½′ Quad.) *Meristoschisma hudsoni* plates and *Batherocystis* plates.

DT-3. (Dotson, NE Tenn.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), 3 ft. shale band with limestone beds above and below, sharp curve in state rt. 131 about ½ mi. NE of Dotson General Store, 7 mi. NE of Washburn, Grainger Co., NE Tenn. (Avondale 7½′ Quad.) *Meristoschisma fayi* plates, *Canadocystis, Palaeocrinus,* and other echinoderm plates.

DT-3A. Cedar grove on slope 30 ft. above DT-3., same formation, area, and fossils as above.

EC-1. (Emigration Canyon, SE Idaho) "Spence Shale equivalent" (*Glossopleura* to *Bathyuriscus-Elrathina* zones), Middle Cambrian, small hillside quarry about 300 ft. above N side of rt. 36, Emigration Canyon, SE¼, sect. 15, T. 12 S, R.

41 E (unsurveyed), about 9.5 mi. W of Ovid, Bear Lake Co., SE Idaho. (Preston, Idaho 1:250,000 topo. sheet) *Gogia palmeri* and ctenocystoid plates.

EM-1. (Emigsville, SE Pa.) Kinzers Fm. (*Olenellus* zone), upper Lower Cambrian, shales near middle of long railroad cut about ¾ mi. SE of Emigsville RR station, north of York, York Co., SE Pa. (York Haven 7½′ Quad.) *Lepidocystis wanneri* and *Camptostroma roddyi.*

FC-1. (Furnace Creek, E. Calif.) Carrara Fm. (*Plagiura-Poliella* zone), lower Middle Cambrian, about 100 ft. below base of middle limestone member, large shale and limestone ridge above S side of jeep trail in Echo Canyon, E½, NW¼, sect. 15, T. 27 N, R. 2 E, Funeral Mts., Death Valley National Park, E. Calif. (Furnace Creek 15′ Quad.) *Gogia* sp. 1(?) plates.

GG-1. (Gog Lake, Brit. Col.) Mt. Whyte Fm. (*Plagiura-Poliella* zone), lower Middle Cambrian, talus slopes on both sides of small snow glacier at 7500 ft. elevation, just S of the S end of Gog Lake and about 0.4 mi. E of Naiset Pt., E end of Mt. Assiniboine Prov. Park, SE Br. Col., Canada. (Mt. Assiniboine Prov. Park Map – P.S.–A–2) *Gogia prolifica.*

GR-1. (Graveston, NE Tenn.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), small roadcut at curve on state rt. 131, ¼ mi. SW of Knox-Union Co. line and ¾ mi. NE of Graveston, NE Tenn. (Graveston 7½′ Quad.) *Meristoschisma hudsoni* plates, *Canadocystis, Hybocrinus.*

HL-1. (Hill, SW Va.) Nolichucky Fm. (*Cedaria* zone), lower Upper Cambrian, roadcut above house and between Bench Mark SN 256 and sharp curve on Copper Ridge road, ¾ mi. SSW of Hill, Scott Co., SE Va. (Clinchport 7½′ Quad.) *Nolichuckia casteri* plates.

HO-1A. (Hogskin Valley, NE Tenn.) Benbolt(?) Fm., Middle Ordovician (Black River-Porterfield), on hillside just E of old barn, about 0.7 mi. SW of Mount Eager Church, Grainger Co., NE Tenn. (Powder Springs 7½′ Quad.) *Meristoschisma fayi* plates, *Canadocystis, Ulrichocystis*(?) and *Hybocrinus.*

IK-2. (Ikes Canyon, central Nev.) Antelope Valley Fm. (*Orthidiella* zone), Middle Ordovician (Whiterock), about 75–100 ft. below the "Sponge Beds" on ridge near road just W of large gulley, S side of Ikes Canyon, about ½ mi. from mouth, Toquima Range, central Nev. (Dianas Punch Bowl 15′ Quad.) *Petalocystites ikecanensis,* rhipidocystid plates, *"Pleurocystites"* plates, and *Palaeocrinus* plates.

IK-3. (Same area as above) Antelope Valley Fm. (*Orthidiella*(?) zone), Middle Ordovician (Whiterock), "Sponge Beds" running diagonally up ridge on N side of Ikes Canyon opposite and above IK-2. *Blastoidocrinus*(?) *nevadensis* plates, *B.*(??) *elongatus* plates, *"Pleurocystites," "Cheirocrinus," Petalocystites*(?), and crinoid plates.

KT-1. (Mt. Kitchner, Jasper Park, Alberta) "Stephen Formation" (*Bathyuriscus-Elrathina* zone), Middle Cambrian, steeply dipping beds about 100–150 ft. above massive dolomite, dip slope and talus piles just below at summer snowline near 8000 ft. level on W side of Mt. Kitchner, N of Dome Glacier and above Sunwapta River and Banff-Jasper Hwy., 5.6 mi. WNW of Sunwapta Pass near 52° 14′ 30″ N, 117° 17′ W, Jasper Park, Alberta, W. Can. (Jasper Park south map sheet) *Gogia kitchnerensis.*

LB-1. (Lebanon, SW Va.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), small roadcuts near nose of sharp curve on state rt. 82 about 0.6 mi. NW of its intersection with U.S. rt. 19, just NW of Lebanon, Russell Co., SW Va. (Lebanon 7½′ Quad.) *Meristoschisma hudsoni* plates.

LO-1. (Logan, N. Utah) Garden City Fm. (*Orthidiella* zone), Middle Ordovician (Whiterock), hillside above Meadowville road following Right Fork of Logan River, W½, NW¼, sect. 17, T. 12 N, R. 3 E, about 9.5 mi. NE of Logan, N. Utah. (old Logan, Utah-Idaho 30′ map) *Blastoidocrinus*(?) *rossi* plates, *"Cheirocrinus"*(?), and *Palaeocrinus* plates.

LV-2. (Lee Valley, NE Tenn.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), small shale bank near NE end of roadcut at curve on N side of state rt. 131, 2.3 mi. NE of road intersection at Lee Valley, Hawkins Co., NE Tenn. (Pressmens Home 7½′ Quad.) *Meristoschisma hudsoni, Columbocystis, Platycystites,* and crinoids.

MC-3. (Moccasin Creek, SW Va.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), small shale bank on N side of state rt. 613 near turnoff for dirt road to S, 0.9 mi. W of Mt. Hagen School and about 4.5 mi. E of intersection of rts. 71 and 613, Scott Co., SW Va.

(Hilton revised 7½′ Quad.) *Meristoschisma fayi* plates, *Palaeocrinus* plates, and other echinoderms.

MJ-1. (Meiklejohn Peak, W. Nevada) Antelope Valley Fm. (*Orthidiella*(?) zone), Middle Ordovician (Whiterock), dipping dark limestone beds just above and beside top of large reef on the SW side of Meiklejohn Peak, NE¼, sect. 24, T. 12 S, R. 47 E, about 7 mi. E of Beatty, Nye Co., W. Nev. (Bare Mountain 15′ Quad. (U.S.G.S. map GQ-157)) *Blastoidocrinus*(?) *nevadensis* plates, *B.*(??) *elongatus* plates, and "crinoid plates."

MU-1. (Mantua, N. Utah) Garden City Fm. (*Orthidiella* zone), Middle Ordovician (Whiterock), N side of Round Hill and small ridge just to N, SE¼, sect. 10, T. 9 N, R. 1 W, just north of Mantua, Box Elder Co., N. Utah (old Logan 1:125,000 topo. map). *Blastoidocrinus*(?) *rossi* plates, and *Palaeocrinus* plates.

PI-1. (Pioche, E. Nevada) Chisholm Shale (*Glossopleura* zone), Middle Cambrian, three talus piles in front of Half Moon Mine about 1200 ft. SW of Mt. Ely in Half Moon Gulch, E½, sect. 20, T. 1 N, R. 67 E, W side of Ely Range, about 2.0 mi. W of Pioche, Lincoln Co., E. Nev. (Pioche 7½′ Quad.) *Gogia longidactylus* and an unidentified edrioasteroid.

PI-2. (Same area, formation, and fossils as above) Six talus piles in front of Chisholm Mines, about 1200 ft. W of Mt. Ely in Half Moon Gulch, same as above.

PI-3. (Same as above) Talus piles in front of Blue Eagle Mine, 2000 ft. WSW of Mt. Ely in Half Moon Gulch, same as above.

PI-4. (Same as above) Unnamed small prospect pits near horizontal access road, 3500 ft. SW of Mt. Ely in Half Moon Gulch, same as above.

PI-5. (Same as above) Unnamed small prospect pit on nose of ridge about 2500 ft. WSW of Mt. Ely in Half Moon Gulch, same as above.

PI-6. (Same as above) Three talus piles in front of Alliance Mine on NE side of ridge, about 2000 ft. NW of Mt. Ely, E side of Ely Range, same as above.

PI-7. (Same as above) Two talus piles in front of Abe Lincoln Mine, about 1750 ft. SSW of Mt. Ely, W side of Ely Range, same as above.

RC-7. (Rye Cove, SW Va.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), small shale bank beside county road 647, about 0.6 mi. SW of Rye Cove main intersection (Bench Mark SN 262), Scott Co., SW Va. (Clinchport 7½′ Quad.) *Meristoschisma hudsoni* plates and crinoid plates.

RC-8. (Same area and formation as above) Hillside and valley below power line just NE of old Brick Church, N of county road 650, about 1.2 mi. W of Rye Cove main intersection. *Meristoschisma hudsoni, Platycystites,* and crinoid plates.

RC-9. (Same area and formation as above) Large roadside shale quarry on county road 652 just north of turnoff, about 0.7 mi. N of Rye Cove main intersection. *Meristoschisma hudsoni* plates, *Batherocystis* plates, and crinoid plates.

RP-1. (Republic Creek, Mont.–Wyo.) Snowy Range Fm. (*Conaspis* to *Prosaukia* zones), Upper Cambrian, thin-bedded limestones with green shale partings just above waterfall (top of Pilgrim Fm.?) near Irma Mines, Republic Creek, 1.3 mi. S of Cooke City, SW Mont. (locality is in NW Wyo.) (Cooke City, Mont.–Wyo. 15′ Quad.) *Trachelocrinus resseri* plates and columnals.

SA-1. (Sacajawea Peak, SW Mont.) Snowy Range Fm. (*Conaspis* to *Prosaukia* zones), Upper Cambrian, stromatolite-bearing beds above Pilgrim Fm. in large saddle between Sacajawea Peak and next peak to north, above Fairy Lake Campground, Bridger Range, N of Bozeman, SW Montana (Belgrade(?) 15′ Quad.) *Trachelocrinus*(?) columnals and plates.

SC-1. (Secret Canyon, central Nev.) Top of the Secret Canyon Fm. (*Bolaspidella* zone), Middle Cambrian, talus pile of small prospect pit in fault slice on S side of Adams Hill about 800 ft. N of main dirt road, NW¼, SW¼, NE¼, NW¼, sect. 22, T. 19 N, R. 53 E, about 1.5 mi. WSW of Eureka, central Nev. (Nolan, 1962: Plate 1—Geologic Map of the Eureka Mining District, Nevada) *Eustypocystis minor* and an unidentified carpoid(?).

SC-3. (Same formation, area, map, and fossils as above) Steeply dipping and overturned beds at head of New York Canyon, just SW of Eureka Nevada tunnels, NE¼, SE¼, SE¼, sect. 34, T. 19 N, R. 53 E, about 2.5 mi. SSW of Eureka, central Nev.

SC-4. (Same formation, area, and fossils as above) Small spur ridge beneath Hamburg Dolomite on E side of Secret Canyon about ¼ mi. N of outlet to E through Hamburg Ridge, 5½–6 mi. S of Eureka, central Nev. (unmapped below 1:200,000 (1968)).

SC-4A. (Same as above) Side of ridge about 200–400 ft. above road on E side of Secret Canyon about ¼ mi. N of SC-4.

SD-1. (Sourdough Creek, SW Mont.) Snowy Range Fm. (*Conaspis* to *Prosaukia* zones), Upper Cambrian, thin-bedded limestones associated with "pillar" stromatolites in forest service roadcut just S of Mystic Lake Ranger Station, NW¼, SE¼, sect. 36, T. 3 S, R. 6 E, along Sourdough Creek, about 10 mi. SE of Bozeman, SW Mont. (Bozeman Pass 15′ Quad.) *Trachelocrinus*(?) columnals and plates.

SG-1. (Striggersville, NE Tenn.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), roadcut at big curve on state rt. 70 about 0.3 mi. S of Rock Hill School near Striggersville, Hawkins Co., NE Tenn. (Burem(?) 7½′ Quad.) *Meristoschisma hudsoni* plates, *Platycystites*, crinoids.

SH-1. (Shiloh, SE Pa.) Kinzers Fm. (*Olenellus* zone), Lower Cambrian, overgrown roadcut on NE side of state rt. 74 approximately 300 ft. SE of the intersection with rt. 238, about 2.0 mi. WNW of York, SE Pa. (West York 7½′ Quad.) *Kinzercystis durhami*, *Lepidocystis wanneri*, *Camptostroma roddyi*, and an unidentified edrioasteroid.

SH-2. (Same area, formation, and map as above) W end of corn field about 500–600 ft. NE of SH-1. *Lepidocystis wanneri*, *Camptostroma roddyi*, and an unidentified edrioasteroid.

SL-1. (Slabtown, SW Va.) Benbolt Fm., Middle Ordovician (Black River-Porterfield), flat vacant lot between houses on N side of rt. 71 near Slabtown gas station, 2¼ mi. NE of Gate City, Scott Co., SW Va. (Gate City 7½′ Quad.) *Meristoschisma fayi* plates, *Pleurocystites* plates, and crinoid plates.

TH-1. (Thorn Hill, NE Tenn.) Nolichucky Fm. (*Cedaria* zone), Upper Cambrian, small overgrown roadcut on U.S. rt. 25E about 200 ft. N of gas station and 1.8 mi. N of intersection of rts. 25E and 131, near Thorn Hill, Grainger Co., Tenn. (Avondale 7½′ Quad.) *Nolichuckia casteri* plates.

WP-1A. (Westgard Pass, E. Calif.) Upper Poleta Fm. (*Nevadella-Holmia* zone), Lower Cambrian, gulley and SW side of 7821-ft. hill below helicoplacoid locality WP-1. which caps hill, SW¼, SW¼, sect. 5, T. 8 S, R. 35 E, W side of Cedar Flat in Westgard Pass area, Inyo Co., E. Calif. (Blanco Mountain 15′ Quad.) Eocrinoid(?) plates.

Plate 1. LEPIDOCYSTIS WANNERI

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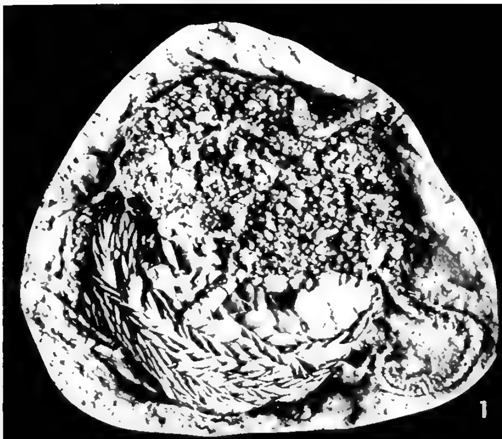
Figures 1–8. *Lepidocystis wanneri* Foerste. Original type suite. Fig. 1, adoral view of holotype showing circular oral surface with small, epispire-bearing plates, large imbricate calyx plates, five large brachioles at ends of ambulacra, and traces of larger plates underlying ambulacra and surrounding mouth. Fig. 2, counterpart of specimen in Fig. 1, aboral view; note large curved brachiole at lower left. Fig. 3, paratype showing part of calyx, 1–2 brachioles (right), and incomplete cylindrical holdfast (left) with small imbricate plates. Fig. 4, excellent paratype (side view) showing anal pyramid at edge of oral surface (right), two ambulacra (center and left) bearing numerous brachioles with cover plates, large imbricate calyx plates, and small epispire-bearing oral surface plates; note that center ambulacrum has brachioles attached on both sides of central food groove. Fig. 5, poorly preserved paratype. Fig. 6, counterpart to specimen in Fig. 5 (side view) showing conical calyx shape, portion of oral surface, and large curved brachiole. Fig. 7, small paratype with one brachiole visible and possible mouth in center of oral surface. Fig. 8, incomplete paratype with "stubs" for two large brachioles (top) at edge of imbricately plated calyx.

All figures latex casts. Specimen in Figs. 1–2 is holotype USNM 90773 (× 1.6) (Note: these two figures were inadvertently printed from reversed negatives and thus show mirror images of the correct views); Fig. 3, paratype USNM 90773-C1 (× 1.8); Fig. 4, paratype USNM 90773-B (× 1.4); Figs. 5–6, paratype USNM 90773-A (× 1.3); Fig. 7, paratype USNM 09773-C2 (× 1.6); Fig. 8, paratype USNM 90773-C3 (× 1.6). All specimens from the Kinzers Formation, Walcott locality 8q, near York, SE Pennsylvania.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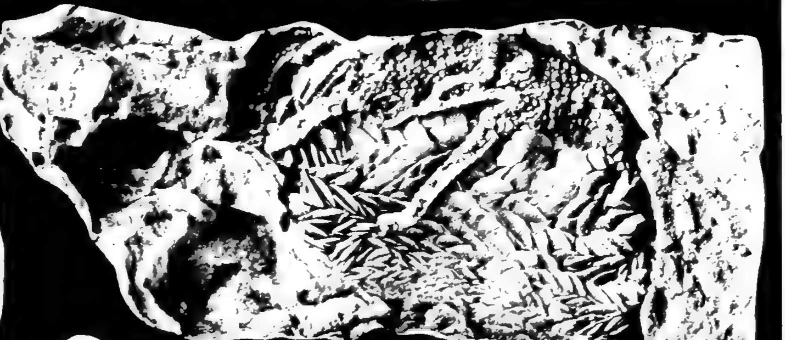
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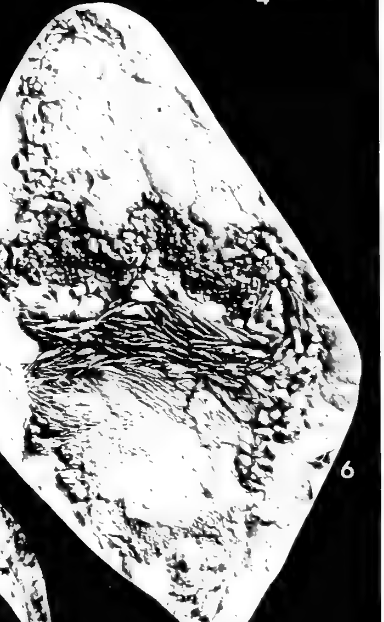
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Plate 2. LEPIDOCYSTIS WANNERI

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Figures 1–7. *Lepidocystis wanneri* Foerste. Additional specimens. Figs. 1–2, two counterparts of an excellently preserved specimen found on the same bedding plane as the holotype of *Kinzercystis durhami* n. gen., n. sp.; note (Fig. 1) well-preserved "CD" interradius showing small oral surface plates, elongate oral pyramid at top, slightly damaged anal pyramid at bottom, nearly complete "D" ambulacrum at left with brachioles attached, and poorly preserved possible hydropore-gonopore area just below mouth (top right), and (Fig. 2) disaggregated calyx plates and large terminal brachiole at left. Fig. 3, enlargement of "D" ambulacrum from Fig. 1 showing central food groove with brachioles attached to both sides, and marked increase in brachiole length and size between small first brachiole at top and large recurved terminal brachiole at bottom. Fig. 4, enlargement of holdfast from specimen in Fig. 5; note difference in plating size and shape between holdfast and calyx and possible distal termination on holdfast with tiny imbricate(?) plates. Fig. 5, side view of small calyx with cylindrical holdfast draped over it; note difference in plating and holdfast size and length. Fig. 6, top view of two specimens showing almost complete oral surfaces; note central mouth without oral pyramid, radiating ambulacral grooves and scattered brachioles. Fig. 7, matched counterpart of right specimen in Fig. 6 showing inside of oral surface with central mouth and radiating ambulacra underlain by large oral surface plates without epispires.

All figures latex casts. Specimen in Figs. 1–3 is plesiotype MCZ 588A and B from the Kinzers Formation, locality SH-1., SE Pennsylvania (× 2.0 and 3.4); Figs. 4–5, plesiotype MCZ 589, same locality as above (× 5.0 and 2.9); Figs. 6–7, plesiotypes MCZ 590A and B, Kinzers Formation, locality SH-2., SE Pennsylvania (× 1.6).

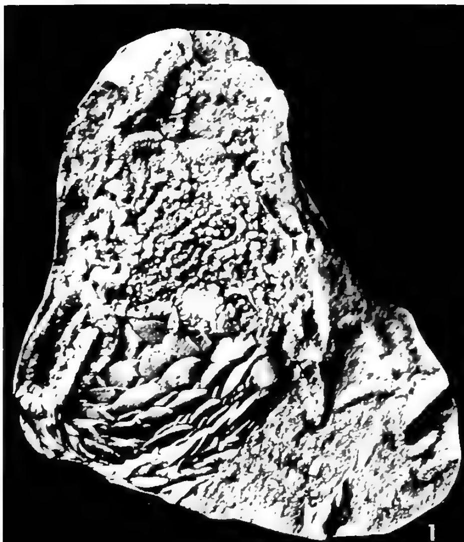
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Plate 3. LEPIDOCYSTIS, cf. L. WANNERI

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Figures 1–6. *Lepidocystis*, cf. *L. wanneri*. Long holdfast specimens. Figs. 1–2, aboral and adoral counterparts of Anné specimen showing long complete holdfast emerging from under calyx and attached at its distal end (bottom) to a small trilobite cephalon, "hole" through calyx wall (Fig. 1, top center) showing inside of opposite oral surface, and compressed oral surface (Fig. 2) with scattered brachioles. Fig. 3, enlarged view of "hole" through calyx wall in Fig. 1 showing inside of oral surface with tiny plates bearing epispires as well as large plates surrounding mouth and sending branches down each ambulacrum to floor food grooves; also note proximal end of holdfast at extreme left. Fig. 4, distal end of holdfast in Figs. 1 and 2; left counterpart shows holdfast attached to central raised glabella on convex dorsal side of small olenellid trilobite cephalon; right counterpart shows holdfast disappearing beneath ventral surface of cephalon. Figs. 5–6, aboral and adoral counterparts of Derstler specimen showing large calyx with well-preserved long holdfast alongside, constricted oral surface with "stubs" for largest brachioles at ends of all five ambulacra, and anal pyramid at bottom of oral surface.

Specimen in Figs. 1–4 is MCZ 628 (latex casts A1 and B1) collected by Martin Anné from Kinzers Formation, locality SH-2., SE Pennsylvania (Figs. 1–2, × 1.5; Fig. 3, × 3.2; Fig. 4, × 2.6); Figs. 5–6 is specimen PE 199 and 199A (latex casts MCZ 629-B1 and A0) collected by Kraig Derstler from Kinzers Formation, locality SH-1., SE Pennsylvania (× 1.6).

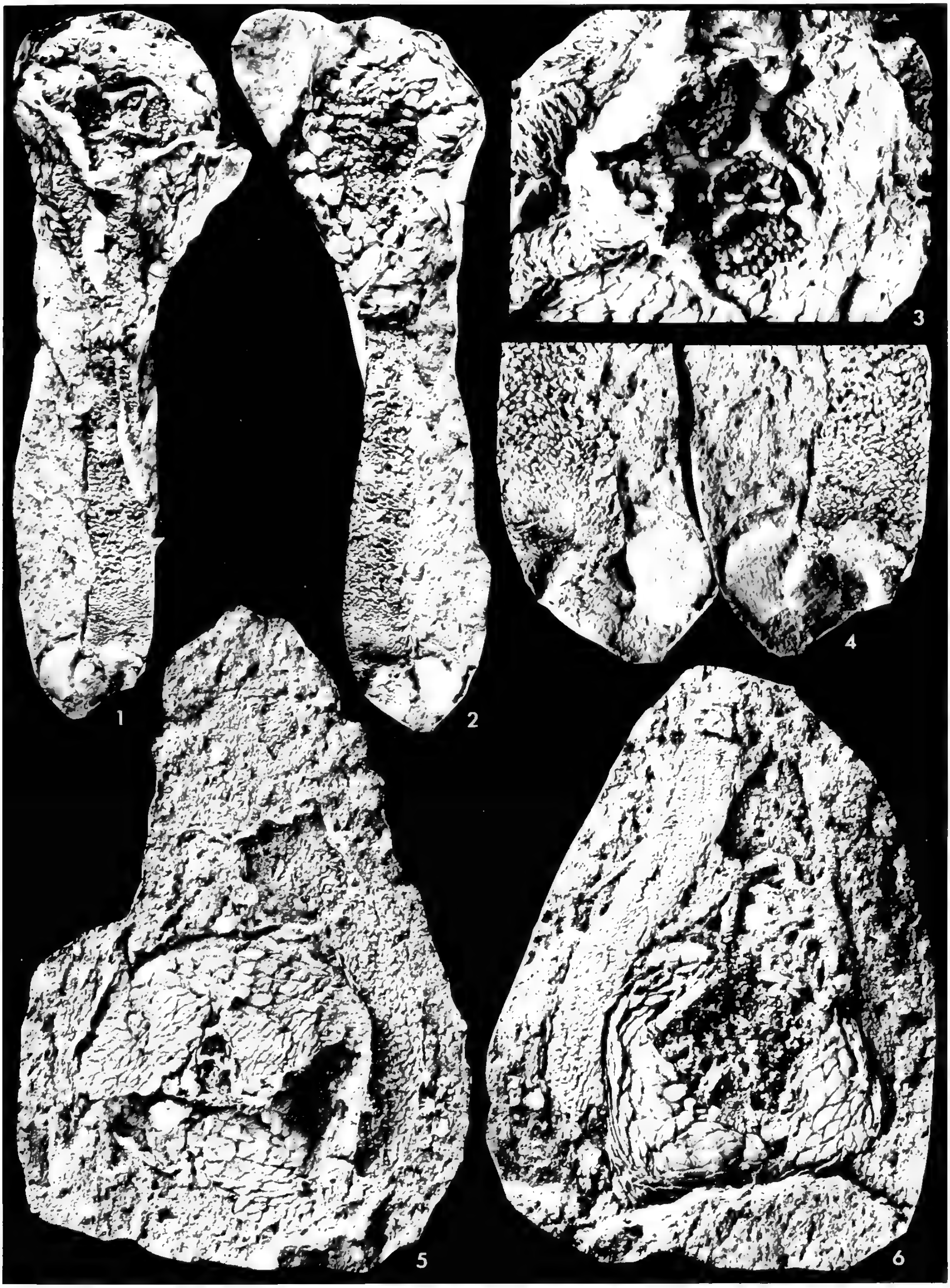
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Plate 4. KINZERCYSTIS

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Figures 1–4. *Kinzercystis durhami* n. gen., n. sp. Best preserved specimens. Fig. 1, oral and side view of excellent holotype specimen showing nearly complete, circular, oral surface with central oral pyramid, five radiating ambulacra with scattered brachioles, anal pyramid at lower edge of oral surface, and large oral surface plates bearing numerous epispires; also note conical calyx underlying oral surface, and short holdfast. Fig. 2, counterpart of Fig. 1 (aboral view) showing large conical calyx and short cylindrical holdfast with adjacent-plated attachment surface. Fig. 3, oral surface of best paratype showing oral pyramid at upper right, a nearly complete "D" ambulacrum (center) extending to the edge of the oral surface and having 11 brachiole "stubs" alternately attached beside it, and long brachioles attached to other ambulacra. Fig. 4, counterpart of Fig. 3 showing long brachioles with overlapping cover plates and a large "hole" (center) through this side of calyx showing interior of opposite oral surface including area lacking epispires and other openings under "D" ambulacrum.

Specimen in Figs. 1–2 is holotype MCZ 581 (latex casts A3 and B3) from the Kinzers Formation, locality SH-1., SE Pennsylvania (× 2.0); Figs. 3–4, paratype MCZ 582 (latex casts A2 and B7), same locality (× 2.4).


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Plate 5. KINZERCYSTIS

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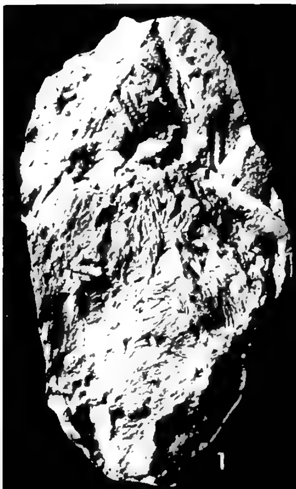
Figures 1–8. *Kinzercystis durhami* n. gen., n. sp. Additional specimens and isolated holdfasts. Figs. 1–2, two counterparts of a partially disarticulated specimen; note small imbricate calyx plates in Fig. 1 and oral surface plates with epispires in Fig. 2. Fig. 3, enlargement of Fig. 2 showing large, thick, disaggregated, oral surface plates with epispires penetrating all the way to interior. Figs. 4–5, another specimen showing badly crushed calyx (Fig. 4) and portion of oral surface (Fig. 5) with epispire-bearing plates and well-preserved brachioles. Fig. 6, lower portion of a calyx and holdfast showing small imbricate plates in both, and adjacent plates on bottom surface of holdfast (bottom). Figs. 7–8, slab bearing at least three incomplete *Kinzercystis*(?) holdfasts (Fig. 7), two of which (top and center) are attached to what appear to be arthropod(?) fragments, and the third (left and Fig. 8) showing the apparent bottom surface(?) with a trace of the plating.

All figures latex casts. Specimen in Figs. 1–3 is paratype MCZ 584 (× 1.4 and 2.9); Figs. 4–5, paratype MCZ 583 (× 1.8); Fig. 6, paratype MCZ 585 (× 2.6); Figs. 7–8, paratype MCZ 586 (× 1.6 and 3.7). All specimens from the Kinzers Formation, locality SH-1., SE Pennsylvania.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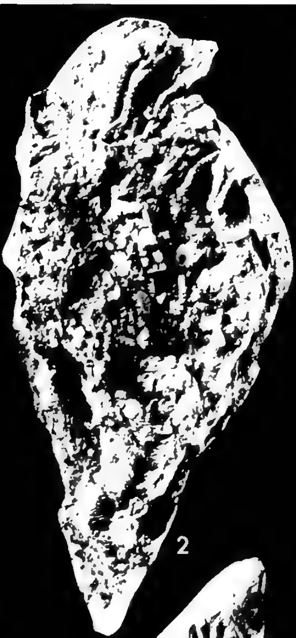
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Plate 6. KINZERCYSTIS

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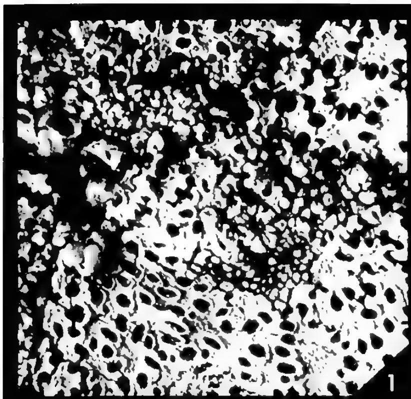
Figures 1–8. *Kinzercystis durhami* n. gen., n. sp. Detailed morphology of best specimens. Figs. 1–2, comparison of summit areas on first and ninth latex casts of holotype showing how latex rubber gradually excavates through to brachioles overlying the surface (Fig. 2) while showing critical summit features (hydropore-gonopore area) beneath these appendages on earlier casts (Fig. 1). Fig. 3, enlargement of hydropore-gonopore area from Fig. 1; note large oral surface plates with epispires surrounding tiny plated area bearing spoutlike structure (left, gonopore?) and pyramid- or sievelike structure (right center, hydropore?). Figs. 4–5, distal end of holdfast in holotype counterparts showing change from wide imbricate plating to wedge-shaped adjacent plating. Fig. 6, interior of oral surface in paratype showing that ridged oral surface plates beneath exterior ambulacrum lack epispires and other openings from calyx interior. Fig. 7, brachioles with distally imbricate, toothed, cover plates (right). Fig. 8, exterior of "D" ambulacrum shown in Fig. 6; note brachiole "stubs" mounted alternately alongside depressed food groove, oral pyramid (top), and well-preserved brachioles with cover plates at top.

All figures latex casts. Specimen in Figs. 1–2, 3, and 4–5 is holotype MCZ 581A and B (Fig. 4) (× 4.8, 14.7, and 7.4 respectively); Figs. 6 and 8, paratype MCZ 582B and A, respectively (×3.0 and 4.3); Fig. 7, paratype MCZ 583 (× 7.2). All specimens from the Kinzers Formation, locality SH-1., SE Pennsylvania.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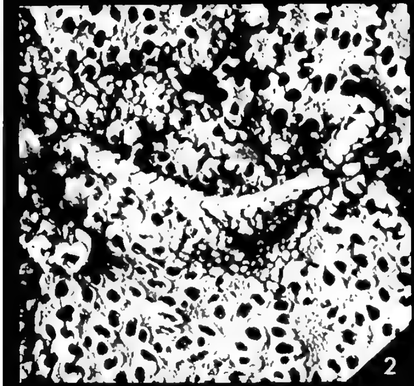
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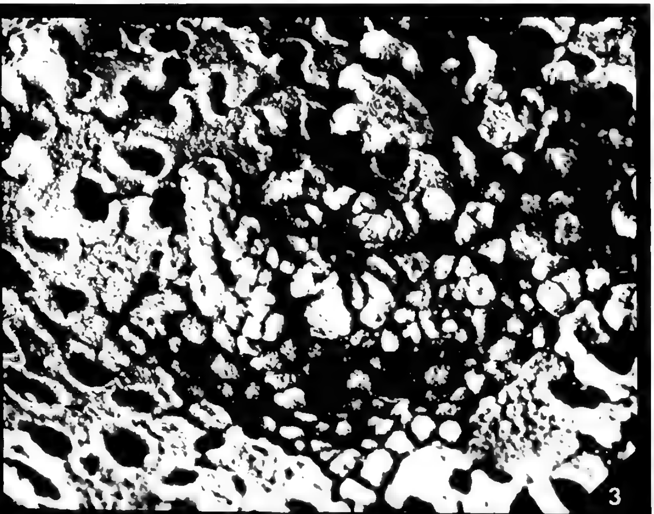
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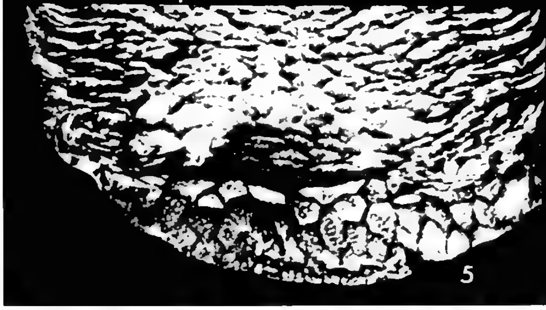
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Plate 7. GOGIA PROLIFICA

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Figures 1–6. *Gogia prolifica* Walcott. Lectotype and plesiotypes. Figs. 1–2, lectotype specimen before (Fig. 1) and after preparation (Fig. 2), showing how partially weathered calyx and buried brachioles and holdfast were greatly improved by acid etching and casting; note severe air bubbles in holdfast of Fig. 2 caused by not soaking specimen after acid etching. Fig. 3, small specimen having a conical calyx with few plates. Fig. 4, two specimens attached together to a thin fossil fragment (arthropod carapace?) lying vertically between them; note that both specimens have fallen over in the same direction. Fig. 5, large and well-preserved specimen showing calyx plates, epispires extending down to top of holdfast, and brachioles with small cover plates. Fig. 6, specimen showing common type of preservation with large calyx completely eroded away while holdfast and brachioles were still buried in matrix; note tapering holdfast with few plates per side.

All figures latex casts. Specimen in Figs. 1–2 is lectotype USNM 64350, latex casts from UC collection (Fig. 1) and USNM collection (Fig. 2) (× 1.2); Fig. 3, plesiotype MCZ 656 (× 1.9); Fig. 4, plesiotypes MCZ 657 (left) and 658 (× 2.0); Fig. 5, plesiotype MCZ 659 (× 1.7); Fig. 6, plesiotype MCZ 660 (× 1.7). All specimens from Mt. Whyte Formation, Walcott locality 62x (Figs. 1–2) and my locality GG-1., Assiniboine Prov. Park, British Columbia.

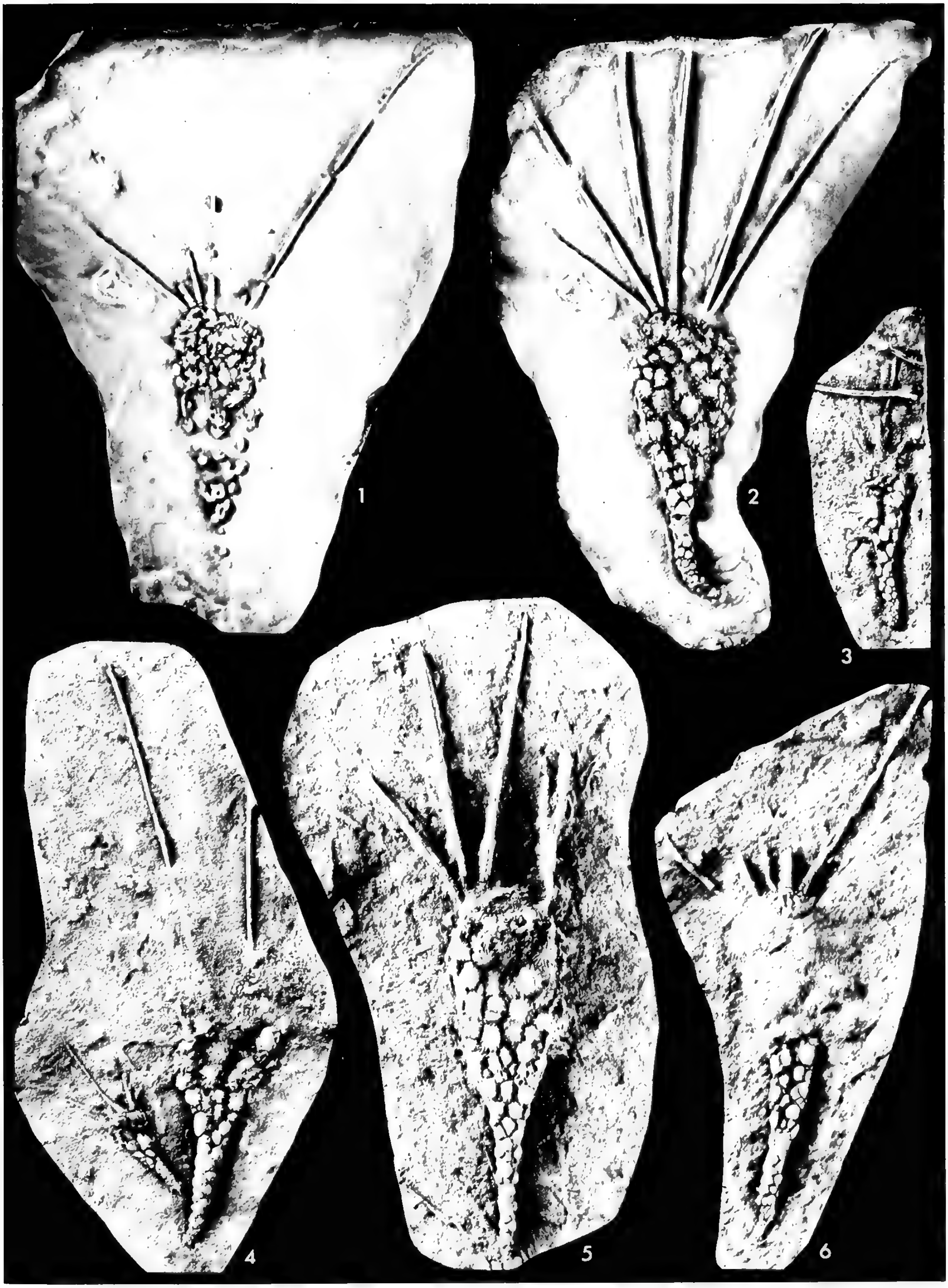
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Plate 8. GOGIA PROLIFICA

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Figures 1–8. *Gogia prolifica* Walcott. Plesiotype specimens showing morphology. Fig. 1, large, well-preserved specimen showing calyx plating and shape, tapering holdfast, and relatively few long straight brachioles. Fig. 2, two small specimens attached to a fossil fragment. Fig. 3, specimen showing curved and expanded holdfast tip as if specimen had been attached to sea bottom in this position. Fig. 4, distal holdfast tips of specimens figured in Figs. 1 and 3; note tiny plates at tip with relatively large and bulged holdfast plates above them. Fig. 5, enlargement of calyx in Fig. 1 showing calyx plating, epispires, probable anal pyramid in circular depressed area at top center of calyx, and five complete brachioles with small cover plates (in rear) plus three "stubs" (front), giving a "3-2-3" brachiole pattern. Fig. 6, small specimen with recurved brachiole. Fig. 7, enlarged specimen with brachioles showing biserial plating and small cover plates. Fig. 8, small specimen with eroded holdfast.

All figures (except Figs. 6 and 8) latex casts. Specimen in Figs. 1, 4 (pt.), and 5, is plesiotype MCZ 661 (× 1.7, 5.0, and 5.6, respectively); Fig. 2, plesiotypes MCZ 662 (left) and 663 (× 1.9); Figs. 3 and 4 (pt.), plesiotype MCZ 664 (× 1.9 and 5.0); Fig. 6, plesiotype NYSM 12758 (× 1.8); Fig. 7, plesiotype MCZ 665 (× 5.5); Fig. 8, plesiotype NYSM 12759 (× 1.8). Specimens in Figs. 1–5 and 7 from Mt. Whyte Formation, locality GG-1., Assiniboine Prov. Park, British Columbia; specimens in Figs. 6 and 8, from Titkana Formation, Mt. Mumm, British Columbia.


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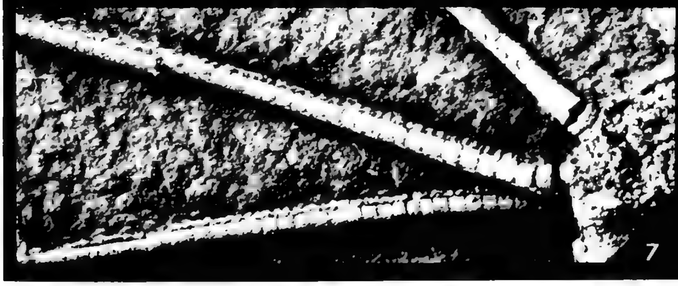
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Plate 9. *GOGIA LONGIDACTYLUS*

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Figures 1–14. *Gogia longidactylus* (Walcott). Brachiole, holdfast and calyx morphology. Figs. 1–2, two counterparts of a well-preserved specimen showing calyx, short holdfast segment, and at least 11 excellent brachioles. Fig. 3, enlargement of portion of summit area in Fig. 1 showing two small (probably immature) brachioles with curled tips; also note high cover plates on larger brachioles. Fig. 4, small specimen with relatively long holdfast. Fig. 5, specimen with complete holdfast and disarticulated calyx and brachioles; note that holdfast is nearly twice as long as the calyx. Fig. 6, enlargement of distal portion of holdfast in Fig. 5 showing tiny imbricate plates at the distal tip which is draped over (but not definitely attached to) a poorly preserved edrioasteriod. Fig. 7, large specimen with ornamented plates probably belonging to this species. Fig. 8, enlargement of brachioles in a large specimen; note arrangement of cover plates in brachiole at left (adoral view). Fig. 9, large specimen with a partially complete holdfast at lower right; note severe disarticulation of brachioles, lack of espispires from most of calyx, and trilobite fragments scattered around slab. Fig. 10, very large, well-preserved calyx and holdfast segment showing marked decrease in plate size near base and complete absence of epispires until at least half of distance to summit. Fig. 11, tiny specimen with rounded conical calyx bearing few plates, two very long brachioles, and an incomplete holdfast. Fig. 12, another specimen showing calyx plates without epispires. Fig. 13, relatively long but incomplete holdfast in a large specimen; note small plates in holdfast. Fig. 14, incomplete holdfast attached to a broken calyx.

All figures latex casts. Specimen in Figs. 1–3 is plesiotype MCZ 691A–B, locality Pl-2. (×1.3 and 4.0); Fig. 4, plesiotype MCZ 692, locality Pl-4. (× 1.8); Figs. 5–6, plesiotype MCZ 693, locality Pl-4. (× 1.5 and 3.3); Fig. 7, plesiotype MCZ 694, locality Pl-6. (× 1.2); Fig. 8, specimen in coll. of B. L. Stinchcomb (cast MCZ 695), (× 3.0); Fig. 9, plesiotype MCZ 696, locality Pl-7. (× 1.2); Fig. 10, plesiotype MCZ 697, locality Pl-2. (× 1.5); Fig. 11, plesiotype MCZ 698, locality Pl-1. (× 2.5); Fig. 12, plesiotype USNM 256500A (Fawcett Coll.) (× 1.5); Fig. 13, plesiotype MCZ 699, locality Pl-2. (× 1.2); Fig. 14, plesiotype MCZ 700, locality Pl-6. (× 1.8). All specimens from the Chisholm Shale, Pioche District, SE Nevada.


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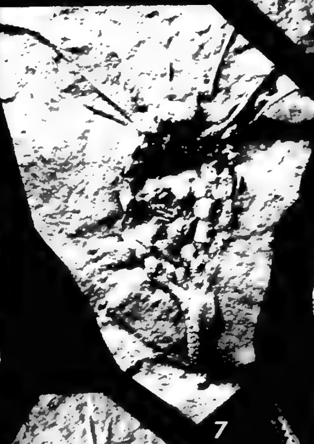
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Plate 10. GOGIA LONGIDACTYLUS

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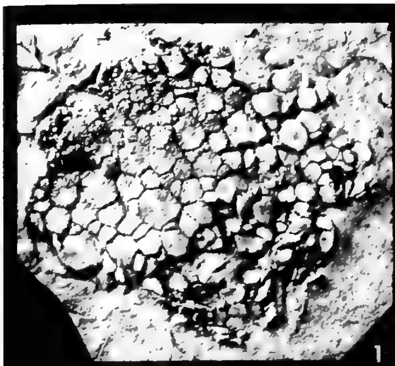
Figures 1–11. *Gogia longidactylus* (Walcott). Calyx morphology and isolated occurrence. Figs. 1–2, matched external and internal counterparts of lectotype selected by Robison; note incomplete calyx with epispires becoming more prominent (and elliptical) near summit, matching plates on external and internal casts, and thin bridges of calcite between epispires connecting plates together (Fig. 2, upper right). Fig. 3, small slab with two oriented specimens; note anal pyramid in specimen at left. Fig. 4, partial summit of an incomplete specimen showing many small plates with strongly developed epispires. Fig. 5, enlargement of summit of large specimen in Fig. 3, showing well-preserved, slightly domed anal pyramid just below edge of summit. Fig. 6, enlargement of smaller specimen in Fig. 3; note complete but relatively short holdfast, only 3–4 brachioles, and restriction of epispires to summit. Figs. 7–8, two fragments of a very large six-piece specimen showing large epispire-bearing plates near summit; this specimen shows the largest number of epispires per plate (between 10–33^{+}) ever observed in *Gogia*. Figs. 9–10, matched counterparts of another very large specimen with numerous brachioles ringing summit, trace of ambulacral food grooves leading to mouth (Fig. 10), and poorly exposed anal pyramid below summit at upper right (Fig. 10). Fig. 11, poorly preserved specimen from the Grand Canyon apparently belonging to this species; note long, thin proximal portion of holdfast, globular calyx shape, and apparent absence of epispires from most of calyx.

All figures latex casts. Specimen in Figs. 1–2 is lectotype USNM 15315 (× 1.1); Figs. 3, 5–6, plesiotypes MCZ 701–702, locality Pl-6. (× 1.2 and 3.2); Fig. 4, plesiotype MCZ 703, locality Pl-2. (× 1.8); Figs. 7–8, plesiotype MCZ 704A–B, locality Pl-1. (× 2.0); Figs. 9–10, plesiotype MCZ 705, locality Pl-2. (× 1.5); Fig. 11, plesiotype GCM 2641 (latex cast MCZ 706) (McKee Coll.) (× 1.2). Specimens in Figs. 1–10 all from the Chisholm Shale, Pioche District, SE Nevada; specimen in Fig. 11 from the Bright Angel Shale, locality on the Tonto Trail one half mi. NE of Indian Gardens, Grand Canyon Nat. Park, Arizona.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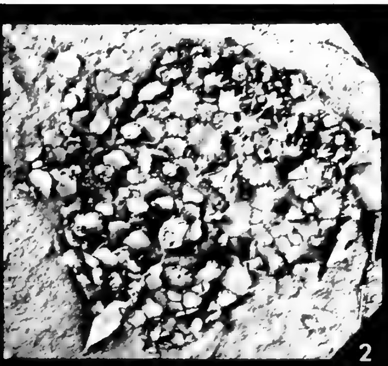
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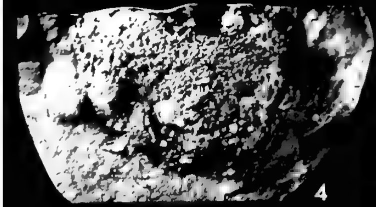
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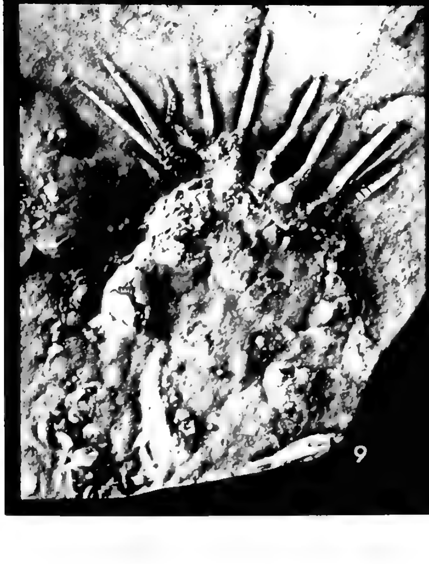
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Plate 11. GOGIA MULTIBRACHIATUS

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Figures 1–5. *Gogia multibrachiatus* (Kirk). Only known complete specimens. Figs. 1–2, negative and positive counterparts of holotype specimen showing cylindrical calyx with numerous plates bearing epispires, at least 24 long straight brachioles attached around rim of summit, and possible globular holdfast at base of calyx. Fig. 3, previously unfigured small specimen showing crushed and buried calyx, large biserial brachioles, and possible holdfast with small plates at bottom. Figs. 4–5, positive and negative counterparts of paratype showing calyx plates, six brachioles attached in a group at the edge of the summit, and possible globular holdfast at bottom of Fig. 4.

All figures latex casts. Specimen in Figs. 1–2 is holotype USNM 108556a (× 0.85); Fig. 3, plesiotype USNM 165425 (× 1.6); Figs. 4–5, paratype USNM 108556b (× 1.1). All specimens from the Bright Angel Shale, USNM locality 74e, Grand Canyon Nat. Park, Arizona.


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Plate 12. GOGIA SPIRALIS

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Figures 1–10. *Gogia spiralis* Robison. Attached and morphology specimens. Fig. 1, prepared slab of limestone bearing 5–6 specimens, one of which is definitely attached to a large flat trilobite pygidium. Fig. 2, enlargement of the two best specimens in Fig. 1 showing the doughnut-shaped inflated distal tips on the holdfasts; both specimens may still be attached in their original life positions. Fig. 3, a very large specimen again showing an inflated distal holdfast tip with tiny, apparently imbricate plates; also note rounded calyx and 11 spiralled brachioles. Fig. 4, shale slab with at least one eocrinoid attached to the fixed cheek of a large trilobite cephalon (upper right) and another specimen (lower left) apparently attached to an unidentified object (mud lump?, sponge?). Fig. 5, enlargement of the more complete specimen in Fig. 4 showing calyx plating with epispires, long spiralled brachioles, and attached holdfast. Fig. 6, very small specimen with few calyx plates, a short holdfast and five brachioles. Fig. 7, medium-sized specimen with a slightly inflated holdfast almost as long as the calyx. Fig. 8, another medium-sized specimen (compare with Fig. 7) having a short, strongly inflated holdfast, abrupt holdfast-calyx transition, and numerous epispires. Figs. 9–10, two brachioles from a single specimen showing left-handed spiral, normal biserial plating, large outside cover plates (note inside set not visible anywhere), and taper to distal tip in Fig. 10.

Specimen in Figs. 1–2 is plesiotype USNM 165421 from the Marjum Formation, Walcott locality 11q, House Range, W. Utah (× 1.0 and 2.0); Fig. 3, plesiotype USNM 165422 (C-802), indeterminate locality (× 1.9); Figs. 4–5, plesiotype MCZ 706–707, Wheeler Shale, locality AS-2., W. Utah (× 1.0 and 2.3); Fig. 6, plesiotype MCZ 708, locality AS-1., same formation and area as above (× 1.3); Fig. 7, plesiotype MCZ 709, locality AS-2. (× 1.3); Fig. 8, plesiotype MCZ 710, locality AS-1. (× 1.4); Figs. 9–10, plesiotype MCZ 711, same locality as above (× 3.5). Specimens in Figs. 8–10 prepared with hydrofluoric acid (HF).

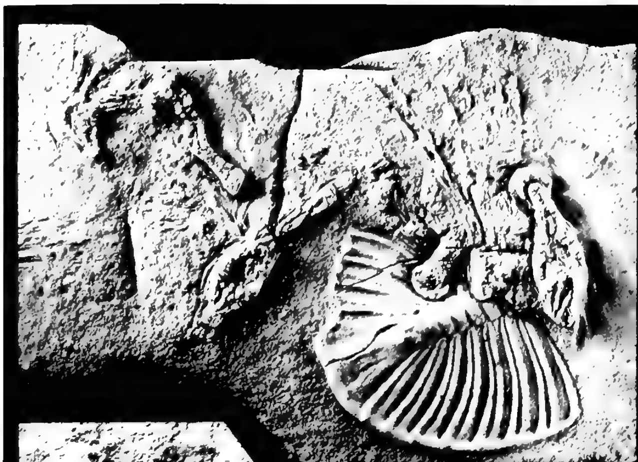
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Plate 13. GOGIA SPIRALIS

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Figures 1–9. *Gogia spiralis* Robison. Holdfast morphology and partial growth series. Fig. 1, large and well-preserved specimen showing long thin holdfast, rounded conical calyx with well-developed epispires and numerous long spiralled brachioles. Fig. 2, eroded distal tip of holdfast from Fig. 1; note tiny, apparently imbricate plates at tip. Figs. 3–4, isolated cylindrical holdfast showing plating and smaller plates around distal tip. Fig. 5, small specimen showing cylindrical holdfast and abrupt holdfast-calyx transition. Fig. 6, large, partially covered specimen immersed in water to show well-developed epispires (some 3-cornered) and long, slightly inflated holdfast. Fig. 7, small specimen showing cylindrical holdfast with flared distal tip. Fig. 8, medium-sized specimen with slightly inflated holdfast, disarticulated calyx, and numerous brachioles. Fig. 9, another medium-sized specimen with epispire-bearing calyx, poor anal pyramid in upper left-center, and many brachioles all spiralling in a left-handed direction.

Specimen in Figs. 1–2 is plesiotype MCZ 712 from the Wheeler Shale, locality AS-1., W. Utah (× 1.3 and 3.5); Figs. 3–4, plesiotype MCZ 713, locality AS-2., same formation and area as above (× 1.3 and 2.8); Fig. 5, plesiotype MCZ 714, locality AS-1. (× 3.0); Fig. 6, plesiotype MCZ 715, same locality as above (× 1.4); Fig. 7, plesiotype MCZ 716, same locality as above (× 1.3); Fig. 8, plesiotype USNM 111716, Wheeler Shale, Walcott locality 4, House Range, W. Utah (× 1.6); Fig. 9, plesiotype MCZ 717, locality AS-1. (× 1.6). Specimens in Figs. 3–5, 8–9 prepared with hydrofluoric acid (HF).


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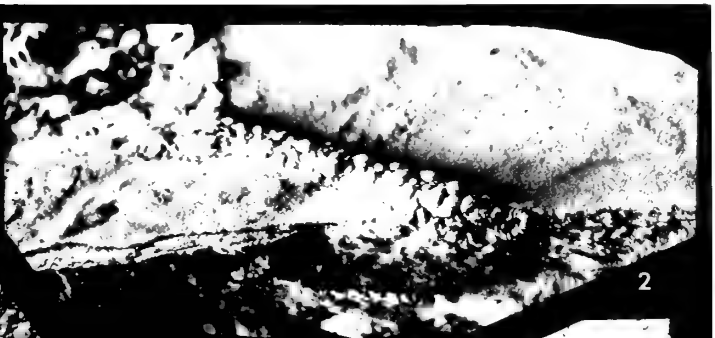
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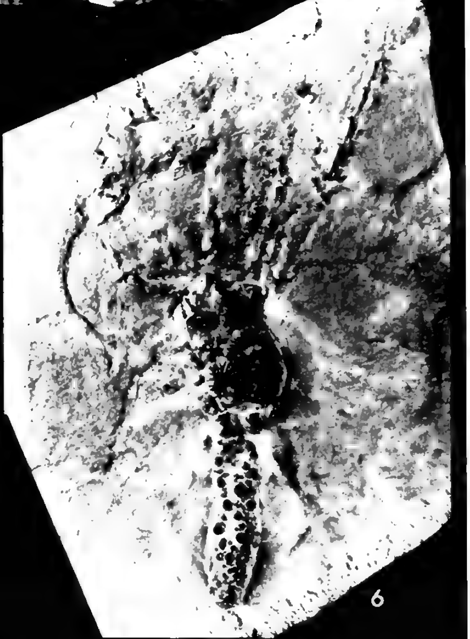
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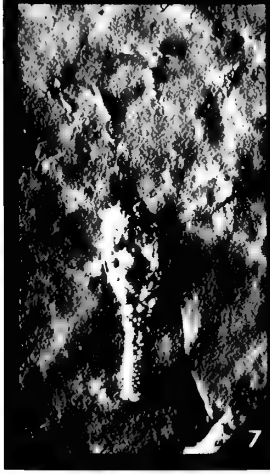
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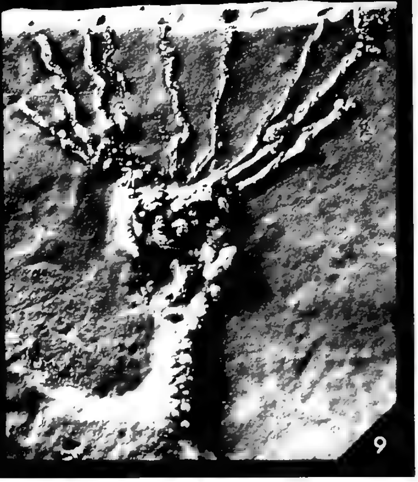
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Plate 14. GOGIA GRANULOSA

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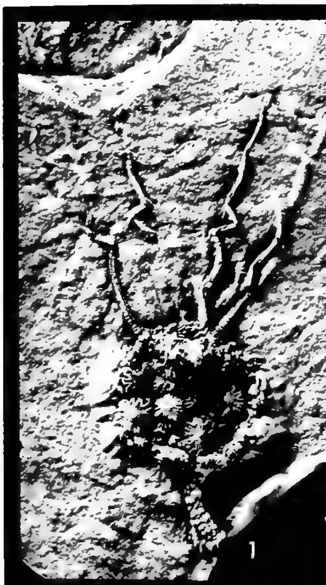
Figures 1–10. *Gogia granulosa* Robison. Type and other well-preserved specimens. Fig. 1, holotype specimen showing ornamented calyx plates with epispires, medium-length cylindrical holdfast, partially preserved spiralled brachioles, and shallow food grooves with cover plates on summit. Fig. 2, tiny specimen with short holdfast, few calyx plates, and only two brachioles. Fig. 3, large and well-preserved specimen showing the rounded conical calyx shape, summit plating, and numerous spiralled brachioles. Fig. 4, relatively small specimen with short spiral wavelength in brachioles. Fig. 5, medium-sized specimen with a short cylindrical holdfast. Fig. 6, specimen with very long complete brachioles and exposed base of holdfast; note that brachioles are nearly four times the calyx length and have 15 or more sprials. Fig. 7, weathered specimen with a relatively long thin holdfast. Fig. 8, medium-sized specimen with incomplete but well-preserved brachioles; note also that several calyx plates contain epispires inside their margins. Fig. 9, specimen with strong calyx plate ornament. Fig. 10, specimen with numerous brachioles mounted separately around edge of summit.

All figures latex casts. Specimen in Fig. 1 is holotype UU 1001 from the Spence Shale, near North Calls Fort, N. Utah (× 1.7); Fig. 2, plesiotype MCZ 733, Spence Shale, locality CF-1., N. Utah (× 1.4); Fig. 3, plesiotype UU 1010p, same locality as above (× 1.1); Fig. 4, plesiotype specimen PE-214 from Derstler Coll. (latex cast MCZ 732), near Brigham City, N. Utah (× 1.2); Fig. 5, plesiotype MCZ 734A, locality CF-1., N. Utah (× 1.3); Fig. 6, plesiotype USNM 165433, Spence Shale, USNM locality 55e, N. Utah (× 0.92); Fig. 7, plesiotype MCZ 735, locality CF-1., N. Utah (× 1.2); Fig. 8, plesiotype USNM 165434, Spence Shale, USNM locality 55e, N. Utah (× 1.2); Fig. 9, plesiotype MCZ 736, locality CF-1., N. Utah (× 1.7); Fig. 10, plesiotype MCZ 737, same locality as above (× 1.2).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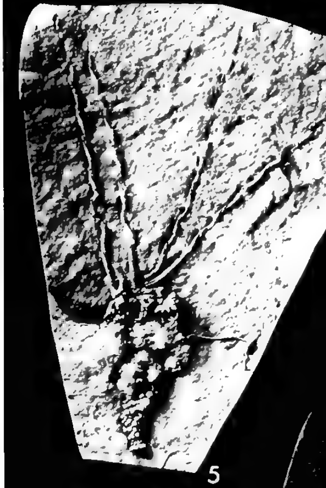
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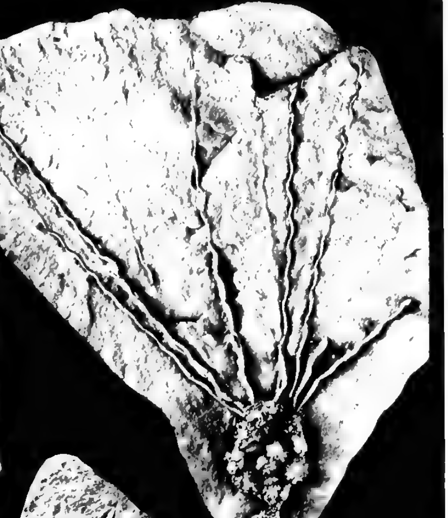
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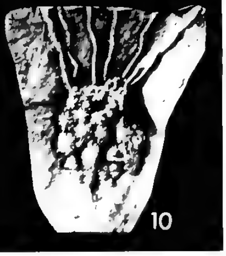
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Plate 15. GOGIA GRANULOSA

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Figures 1–8. *Gogia granulosa* Robison. Specimens showing holdfast and brachiole morphology. Fig. 1, enlargement of three specimens with expanded distal tips of holdfasts; note specimens at left and center have a curved margin of tiny plates surrounding a flattened pavement of somewhat larger plates at this distal tip. Fig. 2, specimen from Idaho apparently belonging to this species; note calyx plates with epispires and strong ornament, medium-length holdfast, and beginning of first spiral in brachiole with cover plates at left. Fig. 3, small specimen on slab with several ctenocystoid marginal plates (bottom and upper right). Fig. 4, weathered specimen having long brachioles with cover plates. Fig. 5, two specimens together; note variation in apparent holdfast length. Fig. 6, specimen with well-preserved articulated calyx and holdfast. Fig. 7, medium-sized globular specimen with an exposed summit and a relatively long holdfast. Fig. 8, counterpart of specimen on Pl. 14, fig. 5 showing a relatively short holdfast and missing brachioles.

All figures (except Fig. 2) are latex casts. Specimens in Fig. 1 are (left to right) plesiotypes USNM 165433, USNM 165435, and UU 1040p, Spence Shale, locality USNM 55e and exposures in Cataract Canyon, N. Utah (× 1.5); Fig. 2, ISU 1440 (Cutler Coll.), Spence Shale, Mill Creek, SE Idaho (× 2.0); Fig. 3, MCZ 738, Spence Shale, locality CF-1., N. Utah (× 1.2); Fig. 4, UU 1010w, same locality as above (× 1.4); Fig. 5, UU 1011d, same locality as above (× 1.2); Fig. 6, UU 1010x, same locality as above (× 1.3); Fig. 7, USNM 165436, Spence Shale, USNM locality 55e, N. Utah (× 1.3); Fig. 8, MCZ 734B, Spence Shale, locality CF-1., N. Utah (× 1.3).

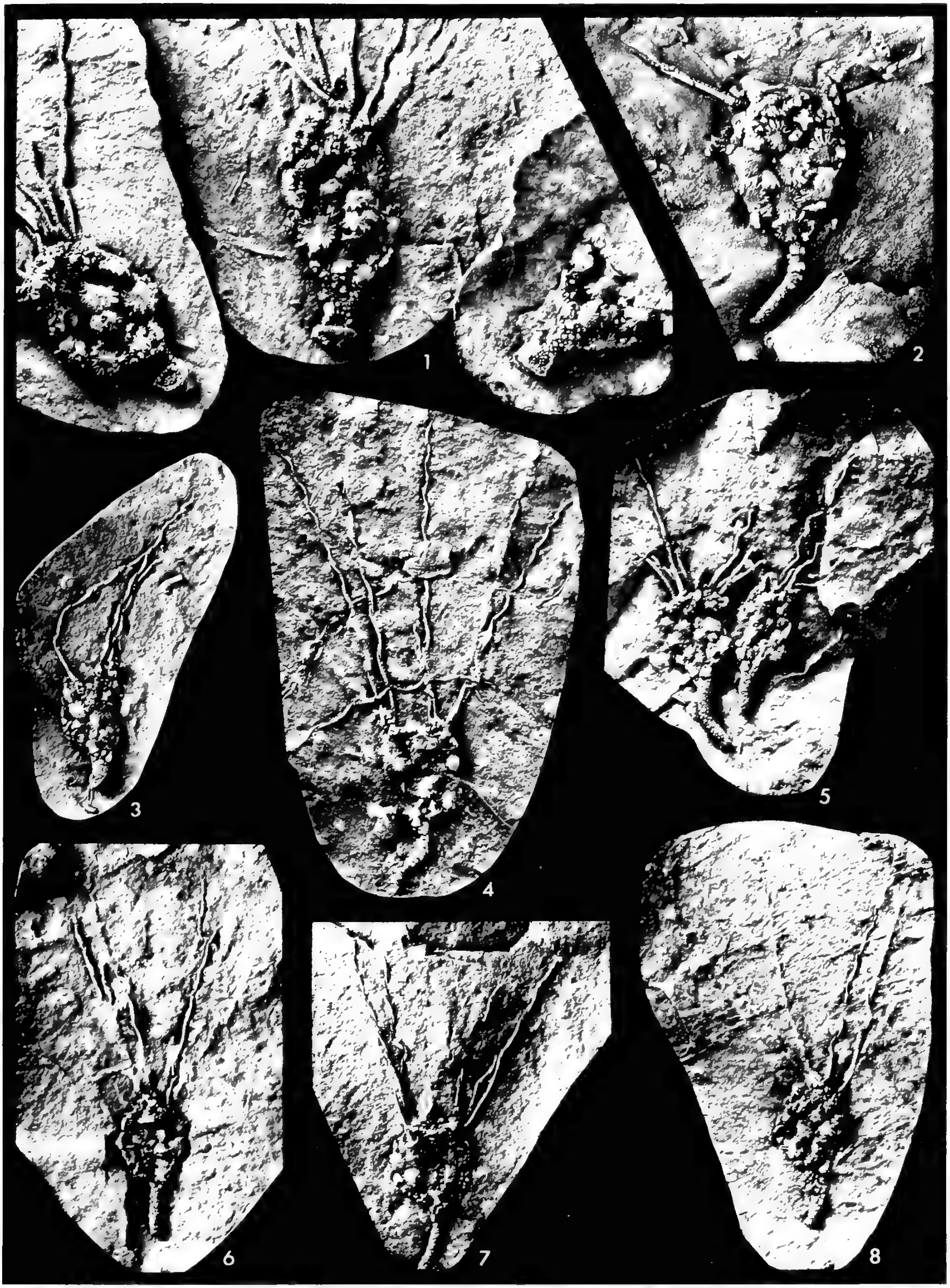
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Plate 16. GOGIA PALMERI

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Figures 1–6. *Gogia palmeri* n. sp. Holotype slab. Figs. 1–2, complete slab with large holotype and smaller paratype; note alignment of specimens, long medium-sized straight brachioles, curved holdfasts, and small "wedge" missing from counterpart in Fig. 2. Figs. 3–4, oblique side view of enlarged brachioles from Fig. 2 showing brachiolar plating and two sizes of cover plates. Fig. 5, enlargement of holotype showing barrel-shaped calyx with many plates, numerous very elliptical epispires, strong variation in calyx ornament, internal view of plates showing through from opposite calyx wall (small area near base), medium-length holdfast with "whorls" of larger and smaller plates, and distal attachment tip with tiny distally imbricate plates. Fig. 6, enlargement of small paratype in Fig. 2 showing single spiral in long straight brachiole; this is the only specimen in *G. palmeri* in which this has been observed.

All figures latex casts. Specimens in Figs. 1–6 are holotype USNM 165418 (large) and paratype USNM 165419 (small), from the "Spence Shale equivalent," USGS locality 6201 (my locality EC-1.), SE Idaho. (Figs. 1–2, × 1.05; Figs. 3–4, × 6.3; Fig. 5, × 2.3; Fig. 6, × 6.8).


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Plate 17. GOG*IA* PALMER*I*

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Figures 1–13. *Gogia palmeri* n. sp. Multiple and morphology specimens. Fig. 1, small specimen with three brachioles visible; Figs. 2–3, counterparts of a slab having four specimens of different sizes; note that all the eocrinoids have a similar orientation and undisturbed brachioles. Figs. 4–5, two counterparts of a specimen showing typical calyx plating and a portion of the ambulacral system with its attached brachioles. Fig. 6, enlargement of the summit area in Fig. 5. Note groups of two and three brachioles attached to the calyx summit on the right with a single covered food groove leading to the central mouth; more brachiole "stubs" are attached at the left and in front. Figs. 7–8, a very small complete specimen showing the rounded conical calyx shape and small holdfast characteristic of this size. Fig. 9, holdfast from a large but incomplete specimen showing the large "bulged" holdfast plates with rugose ornament sometimes found in this species. Figs. 10–11, two counterparts of a large, well-preserved specimen showing brachioles attached in groups of 3–4 to moderate "spouts" around the calyx summit with (Fig. 11) a single food groove leading from each spout to the mouth; note also that Fig. 11 shows the inside surface of some of the calyx plates in Fig. 10. Fig. 12, medium-sized specimen showing clusters of brachioles on the summit with the anal pyramid just below on the side of the calyx. Fig. 13, enlargement of summit region in Fig. 12 showing small and indistinct anal pyramid (center) between and below two groups of brachioles.

All figures latex casts. Specimen in Fig. 1 is paratype USNM 165414 (× 1.4); Figs. 2–3, paratypes MCZ 676a–d (× 1.2); Figs. 4–6, paratype USNM 165415 (× 1.5 and 3.0); Figs. 7–8, paratype MCZ 677 (× 1.4); Fig. 9, paratype USNM 165416 (× 2.1); Figs. 10–11, paratype MCZ 678 (× 2.3); Figs. 12–13, paratype MCZ 679 (× 1.2 and 3.3). All specimens from the "Spence Shale Equivalent," USGS locality 6201 (my locality EC-1.), SE Idaho.


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Plate 18. GOGIA PALMERI

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Figures 1–13. *Gogia palmeri* n. sp. Multiple specimens and growth series. Figs. 1–2, two counterparts of a slab with at least six aligned specimens packed together in close proximity; note bent holdfasts in several specimens and view of calyx interior in large central specimen in Fig. 2, showing epispires with thin "bridges" of plate material between them. Fig. 3, small specimen with globular calyx, five brachioles, and holdfast wtih inflated distal tip. Fig. 4, another small specimen; note that epispires are already present. Fig. 5, small specimen showing thin brachioles at least three times length of calyx. Fig. 6, larger specimen beginning to show trace of ornament. Fig. 7, medium-sized specimen with bent holdfast. Fig. 8, medium-sized specimen with long brachioles; note tiny specimen at upper right oriented in same direction. Fig. 9, larger specimen with long holdfast and rugose ornament over entire calyx. Fig. 10, large specimen showing brachiole "spouts" on summit and strongly developed epispires all over calyx. Fig. 11, large specimen with well-preserved holdfast; note tiny plates at distal tip. Fig. 12, very large specimen showing characteristic barrel-shaped calyx and part of summit. Fig. 13, another very large specimen with well-preserved calyx and holdfast.

All figures latex casts. Specimens in Figs. 1–2 are paratypes MCZ 680a–f; Fig. 3, paratype MCZ 681; Fig. 4, paratype USNM 165414; Fig. 5, paratype MCZ 682; Fig. 6, paratype MCZ 683; Fig. 7, paratype MCZ 684; Fig. 8, paratypes MCZ 685a–b; Fig. 9, paratype MCZ 686; Fig. 10, paratype MCZ 687; Fig. 11, paratype USNM 165417; Fig. 12, paratype MCZ 688; Fig. 13, paratype MCZ 689 (Figs. 1–2, 5–13, × 1.2; Figs. 3–4, × 1.4). All specimens from the "Spence Shale Equivalent," USGS locality 6201 and my locality EC-1., SE Idaho.

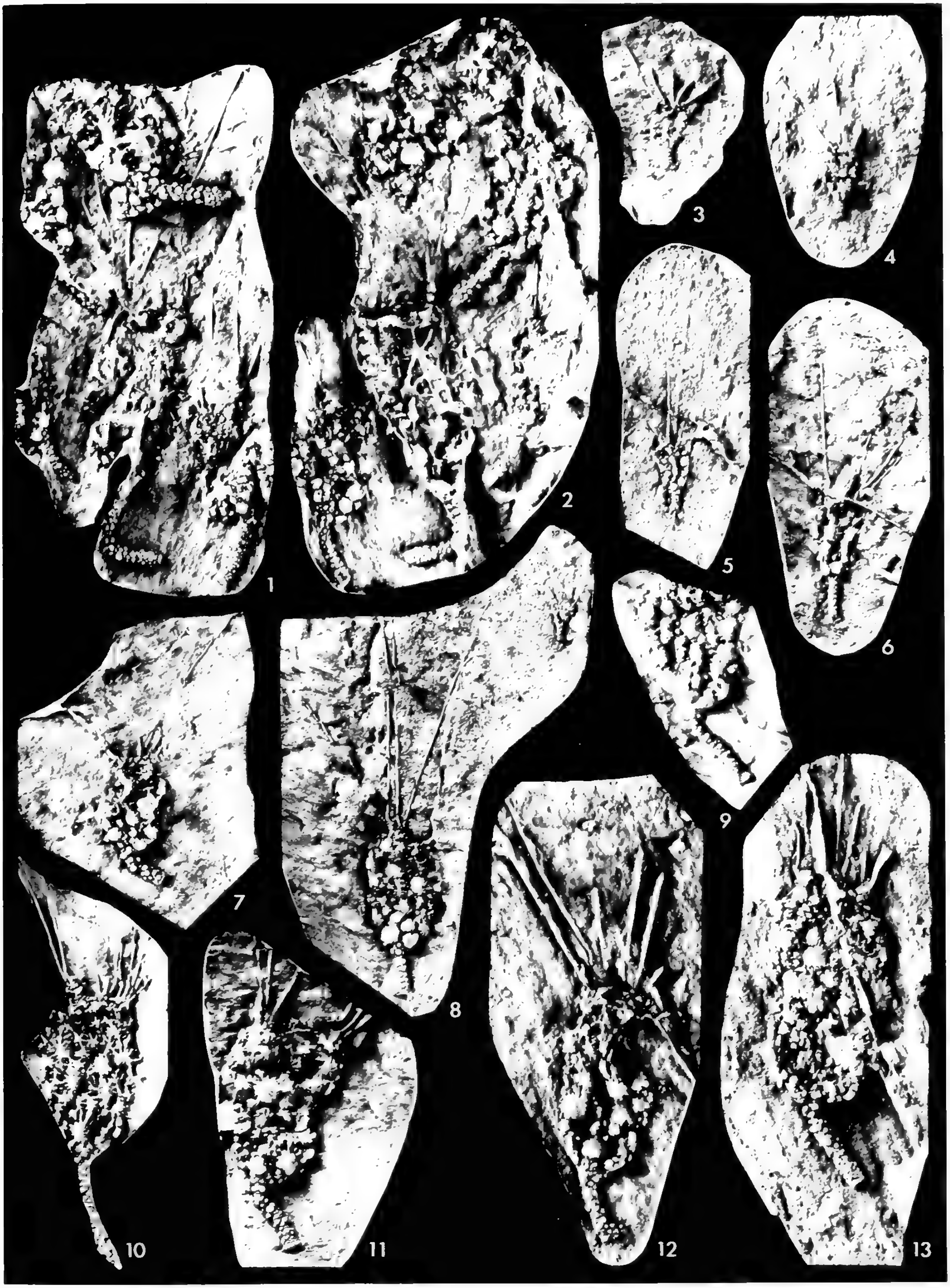
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Plate 19. GOGIA GUNTHERI

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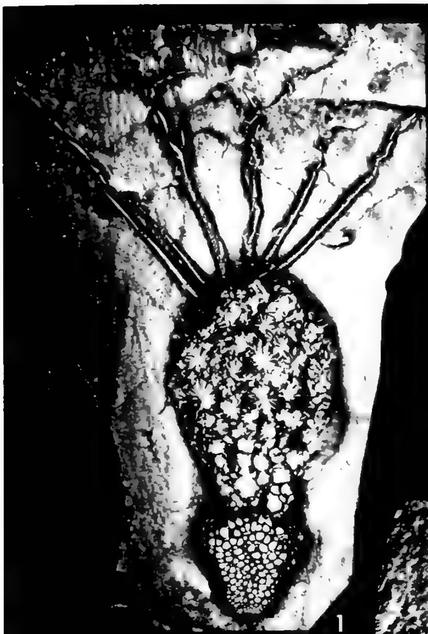
Figures 1–12. *Gogia guntheri* n. sp. Best type specimens. Fig. 1, large excellent holotype specimen showing ellipsoidal calyx with numerous epispire-bearing plates, large inflated holdfast with conical shape, and medium-sized brachioles which begin spiralling away from the calyx (top left). Figs. 2 and 4, specimen with poorly preserved calyx and globular inflated holdfast with a short cylindrical portion distally bearing whorls of tiny plates at the attachment tip. Fig. 3, small specimen having few calyx plates with nearly round epispires and a slightly inflated holdfast bearing epispires on its upper portion. Fig. 5, small separate holdfast with slight rugose ornament and inflated conical shape similar to Fig. 1. Fig. 6, specimen with calyx preserved as internal cast; note cover plates on straight portions of brachioles. Fig. 7, slightly inflated holdfast from a small specimen showing rotated and spread-out distal attachment tip. Fig. 8, relatively small specimen with a crushed calyx; scratches on matrix are from sliding of slabs on talus slope. Fig. 9, enlargement of spiralled brachioles from Fig. 11; note biserial brachiolar plates, tiny cover plates over food groove, constant spiral wavelength, long (but variable) straight region proximally, and attachment of four to five brachioles together to a spoutlike projection on the calyx summit. Figs. 10–11, medium-sized specimen with a well-preserved calyx bearing numerous elliptical and triangular epispires and an inflated holdfast with a well-exposed distal tip (Fig. 10). Fig. 12, another specimen showing the apparent anal opening (top center) covered by a few anal pyramid plates.

All figures latex casts. Specimen in Fig. 1 is holotype UU 1010a (× 1.3); Figs. 2 and 4, paratype UU 1010s (× 1.0 and 1.8); Fig. 3, paratype UU 1010h (× 1.1); Fig. 5, paratype UU 1040f (× 0.95); Fig. 6, paratype UU 1040b (× 0.90); Fig. 7, paratype MCZ 739 (× 5.4); Fig. 8, paratype UU 1010b (× 1.5); Figs. 9–11, paratype MCZ 740 (× 2.6, 1.8, and 1.1); Fig. 12, paratype MCZ 741 (× 2.7). All specimens from the Spence Shale, locality CF-1. (Figs. 1–4, 7–12) and exposures in Cataract Canyon (Figs. 5–6), N. Utah.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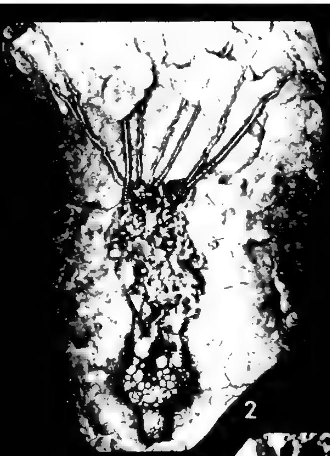
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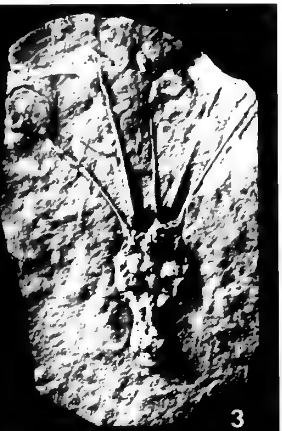
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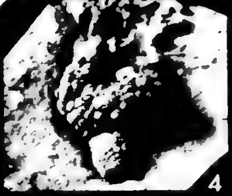
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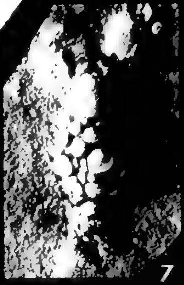
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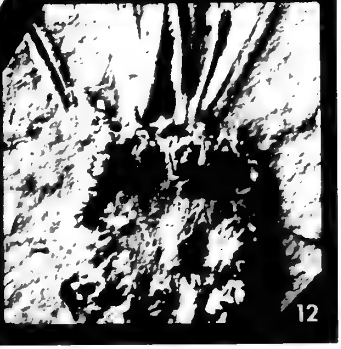
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Plate 20. GOGIA KITCHNERENSIS

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Figures 1–13. *Gogia kitchnerensis* n. sp. Latex casts and other specimens. Figs. 1, 5, and 7, holotype specimen showing disarticulated calyx with epispires most strongly developed near summit, very long cylindrical holdfast (Fig. 7) with slightly convex medium-sized plates and tiny plates at distal tip, long straight brachioles attached in groups, and large anal pyramid (Fig. 5) with tooth-shaped plates at edge of summit. Fig. 2, another anal pyramid (right) in a poorly preserved specimen. Fig. 3, medium-sized specimen with a rounded conical calyx and long holdfast. Fig. 4, group of three small specimens; note overlapping and strong alignment. Fig. 6, two specimens with well-preserved brachioles bearing cover plates. Fig. 8, poorly preserved specimen with a medium length holdfast. Figs. 9 and 11 well-preserved large specimen with a relatively short holdfast (compare with Fig. 1), a rounded conical calyx with epispires strongly restricted to the top one-third and best developed in the top one-sixth, and numerous brachioles branching off the summit in groups (Note "stubs" for three brachioles at top front of Fig. 11). Fig. 10, incomplete specimen showing what appear to be ambulacral grooves protected by cover plates on the summit. Fig. 12, another specimen with epispires restricted to the top portion of the calyx. Fig. 13, top view of weathered specimen with brachioles attached around edge of summit.

Figures 1, 3–5, 7, 9, and 11–12 are latex casts. Specimen in Figs. 1, 5, and 7 is holotype GSC 25934 (× 0.84, 2.7, and 2.7); Fig. 2, paratype GSC 25936 (× 3.1); Fig. 3, paratype GSC 25937 (× 0.78); Fig. 4, paratypes GSC 25938–40 (× 1.0); Fig. 6, paratypes GSC 25941–2 (× 1.3); Fig. 8, paratype GSC 25943 (× 1.6); Figs. 9 and 11, paratype GSC 25944 (× 1.0 and 2.4); Fig. 10, paratype GSC 25945 (× 3.4); Fig. 12, paratype GSC 25946 (× 1.1); Fig. 13, paratype GSC 25947 (× 2.7). All specimens from the "Stephen Formation," locality KT-1., Jasper Park, Alberta, Canada.

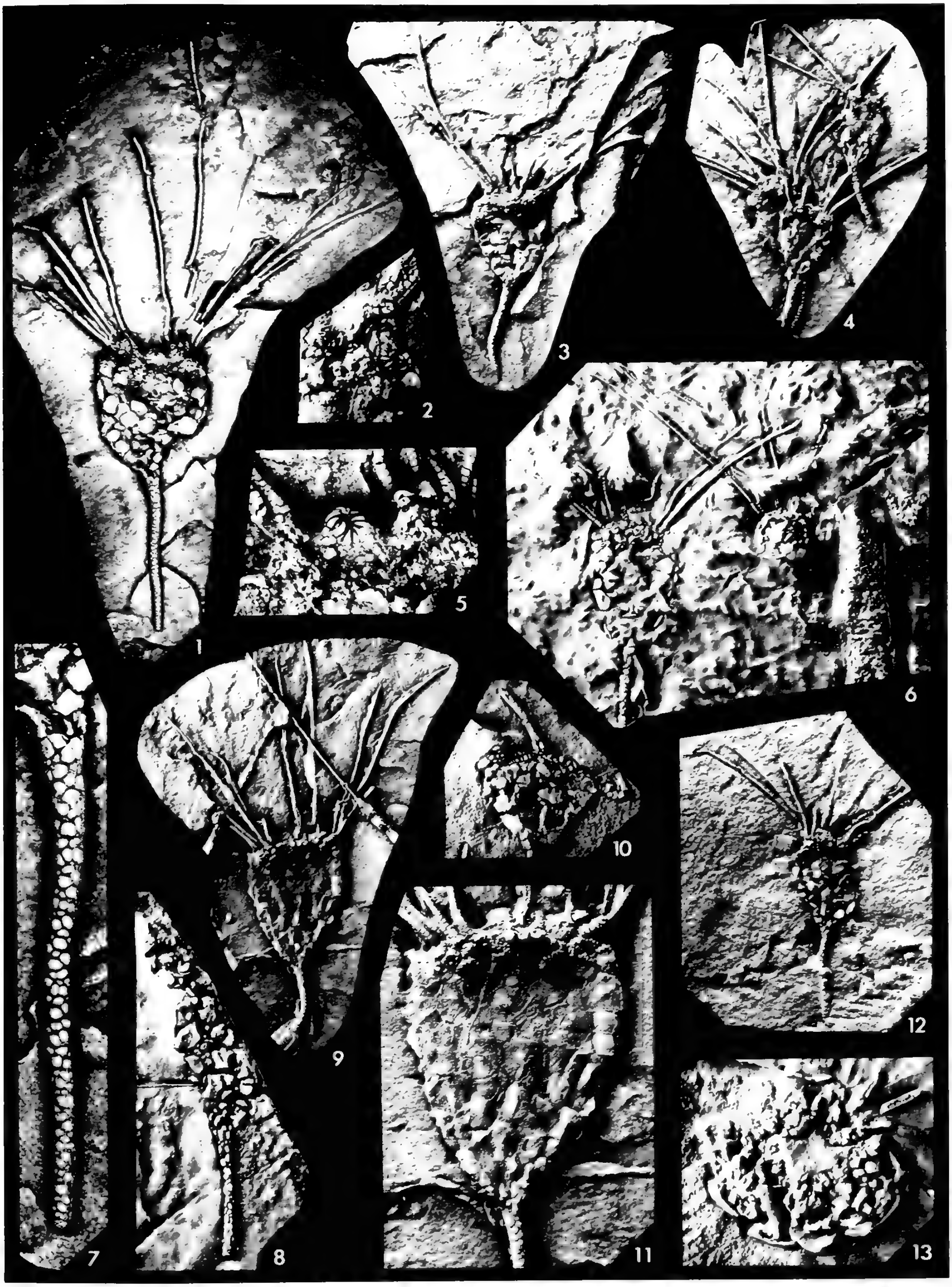
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Plate 21. GOGIA KITCHNERENSIS

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Figures 1–8. *Gogia kitchnerensis* n. sp. Additional slab specimens. Fig. 1, slab with six small, poorly preserved, but strongly oriented specimens. Fig. 2, nearly complete large specimen showing calyx plating and numerous long brachioles with cover plates; note worm burrow at lower left. Fig. 3, large but crushed specimen showing a portion of the summit with its brachioles. Fig. 4, enlargement of brachioles from another specimen; note tiny domed cover plates. Fig. 5, specimen showing badly weathered summit with brachioles branching off in groups. Fig. 6, small specimen (left) and tiny one (right) showing calyx shape and holdfast length; note other eocrinoid fragments. Fig. 7, large compressed fecal or regurgitation wad of unknown origin containing trilobite fragments and meraspid stages as well as separate *Gogia kitchnerensis* plates. Fig. 8, weathered specimen with long thin cylindrical holdfast.

Specimens in Fig. 1 are paratypes GSC 25948–53 (× 1.3); Fig. 2, paratype UC 24691 (× 1.0); Fig. 3, paratype GSC 25955 (× 2.4); Fig. 4, paratype GSC 25956 (× 2.4); Fig. 5, paratype GSC 25957 (× 3.2); Fig. 6, paratypes GSC 25958–9 (× 1.6); Fig. 7, figured specimen GSC 25960 (× 1.6); Fig. 8, paratype GSC 25961 (×1.5). All specimens (except Fig. 2) from the "Stephen Formation," locality KT-1., Jasper Park, Alberta, Canada. Specimen in Fig. 2 from moraine below Athabaska Glacier, Jasper Park, Alberta, Canada.


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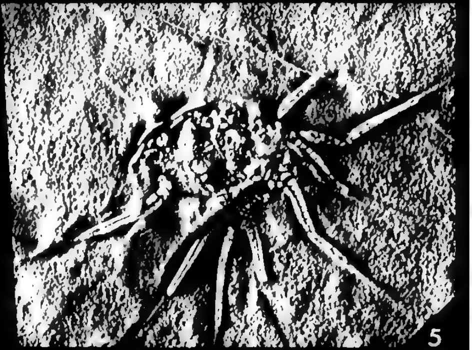
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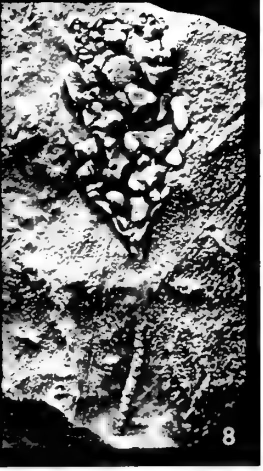
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Plate 22. GOGIA HOBBSI

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Figures 1–5. *Gogia hobbsi* n. sp. Holotype and other specimens. Figs. 1–2, well-preserved holotype specimen showing small calyx with few plates, epispires scattered all over calyx, short cylindrical holdfast, few small brachioles, and possible anal pyramid on right side of calyx near summit. Fig. 3, larger specimen showing gradation of calyx plates down into holdfast with loss of epispires. Fig. 4, poorly preserved specimen showing expanded distal tip of cylindrical holdfast. Fig. 5, another badly weathered specimen having 6–7 brachioles with cover plates (note possible spiralling(?) near distal end of upper brachiole), and holdfast with slightly expanded distal tip.

All figures latex casts. Specimen in Figs. 1–2 is holotype MCZ 631 (× 3.3 and 5.4); Fig. 3, paratype MCZ 632 (× 3.4); Fig. 4, paratype MCZ 633 (× 3.3); Fig. 5, paratype MCZ 634 (× 3.2). All specimens from the Cash Creek Quartzite, locality CL-1., central Idaho.


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Plate 23. GOGIA HOBBSI

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Figures 1–8. *Gogia hobbsi* n. sp. Attached specimens and other paratypes. Fig. 1, small weathered paratype attached to the fixed cheek of a trilobite cephalon just in front of the glabella. Fig. 2, enlargement of the attachment in this specimen. Fig. 3, another specimen attached in a similar position to a trilobite cephalon; note that holdfast seems to disappear beneath concave ventral surface of cephalon. Fig. 4, another well-preserved specimen attached in the same way showing broken brachioles and epispires in calyx. Fig. 5, enlargement of the attachment in this specimen; note trilobite cephalon is lying on bottom in most stable position (convex side up) and that the eocrinoid is attached to this upward-facing side. Fig. 6, another specimen apparently attached to a small inarticulate brachiopod. Fig. 7, a large and a small specimen apparently attached together (attachment lost); note well-developed epispires. Fig. 8, smallest specimen in collection, note only 14–16 plates on this side of calyx.

All figures latex casts. Specimen in Figs. 1–2 is paratype MCZ 635 (× 3.1 and 5.4); Fig. 3, paratype MCZ 636 (× 3.4); Figs. 4–5, paratype MCZ 637 (× 3.4 and 5.3); Fig. 6, paratype MCZ 638 (× 3.1); Fig. 7, paratypes MCZ 639 and 640 (large and small) (× 3.2); Fig. 8, paratype MCZ 641 (× 3.3). All specimens from the Cash Creek Quartzite, locality CL-1., central Idaho.


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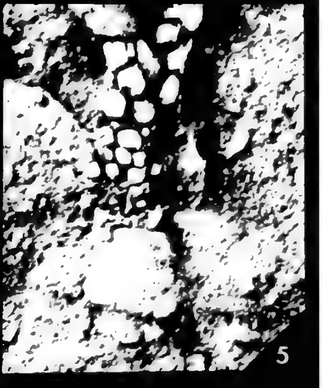
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Plate 24. GOG*IA*(?) *RADIATA* and BURGESS SHALE "ARMS"

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Figures 1–7. *Gogia*(?) *radiata* n. sp. Type collection. Fig. 1, holotype specimen showing base of large globular calyx bearing ridged plates with epispires, very large long holdfast with strongly bulged plates, slight "whorling," and rectangular calyx plate at proximal attachment; note two possible brachiolar(?) plates at top left of slab. Figs. 2–3, positive and negative counterparts of a small specimen having at least three brachioles with cover plates; note that calyx plating is very indistinct. Fig. 4, negative impression of very small and poorly preserved but perhaps complete specimen of this taxon; note cylindrical holdfast, globular calyx, and possible traces of brachioles(?). Figs. 5–6, positive and negative counterparts of another small specimen showing domed calyx plates with epispires, two brachioles, and a possible holdfast fragment at the bottom. Fig. 7, extremely long unattached holdfast showing original plating (center) and possible distal tip at bottom.

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Figures 8–16. Burgess Shale "Arms" from an otherwise unknown echinoderm. Figs. 8–9, positive and negative counterparts of best preserved and largest arm segment; note trace of brachiolar(?) plating (Fig. 9) and possible cover plates. Figs. 10–11, another specimen preserving only the brachioles(?). Figs. 12–13, negative and positive counterparts of a small arm with broken brachioles(?). Figs. 14–15, another small pyritized specimen with no plating preserved. Fig. 16, buried arm with tips of few brachioles(?) uncovered near top of slab.

Specimen in Fig. 1 (latex cast) is holotype USNM 165399 (× 1.7); Figs. 2–3, paratype USNM 165400 (× 1.3); Fig. 4, paratype USNM 165401 (× 1.1); Figs. 5–6, paratype GSC 25954 (× 1.4); Fig. 7, paratype USNM 165402 (× 1.2); Figs. 8–9, figured specimen USNM 165428 (× 1.1); Figs. 10–11, USNM 165429 (× 1.1); Figs. 12–13, GSC 25963 (× 0.86); Figs. 14–15, USNM 165430 (× 1.1); Fig. 16, USNM 165431 (× 1.2). All specimens from the Burgess Shale Member, Stephen Formation, Burgess Shale Quarry (Walcott locality 35k) and accessory quarry (Walcott locality 35k/10) (Fig. 1), SE British Columbia.


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Plate 25. GOG*IA Sp.* 1 and 2 and POLETA EOCRINOID(?) PLATES

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Figures 1–7. *Gogia* sp. 1. Fig. 1, only known complete specimen from the Carrara Formation showing long thin holdfast, conical calyx with epispires present only near summit, and brachiole segment with cover plates at upper left. Figs. 2–3, external and internal views of an isolated silicified plate from the Carrara Formation; note epispires and coarse surface ornament (caused by silicification?). Figs. 4–5, external and internal views of another plate showing well-delevoped epispires and nearly smooth exterior. Figs. 6–7, external and internal views of a small plate with deep epispire-like grooves on one margin similar to those in Figs. 12, 13, and 16.

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Figure 8. *Gogia* sp. 2. Only known specimen from the Ptarmigan Formation showing partially complete calyx and 7–8 brachioles heavily recrystallized with pyrite; note that little evidence of original plating now remains.

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Figures 9–22. Poleta eocrinoid(?) plates. Figs. 9–11 and 19, eocrinoid-like plates from the Lower Cambrian Poleta Formation showing well-developed epispires on plate margins, ridged or rugose exterior ornament (Figs. 9, 19), and smooth interior (Figs. 10–11). Figs. 12–13 and 16, plates with deep epispire-like grooves on one margin; note that plate in Fig. 12 has normal epispires on bottom margin. Figs. 14–15, 17–18, and 20–21, plates with half or complete ambulacra on their margins or surfaces; note single or alternating double row of pores not penetrating to interior, smooth ambulacral surface in contrast to rugose ornament elsewhere, and epispires on nonambulacral margins. Fig. 20, typical slab surface bearing one ambulacral plate and many others with and without epispires. Fig. 22, composite plate with a complete ambulacrum on the left margin and deep epispire-like grooves on the top margin.

All figures (except Figs. 2–7) latex casts. Specimen in Fig. 1 is USNM 165411 from the Carrara Formation, USGS locality 4148 CO, E. California (× 1.8); Figs. 2–7, MCZ 666a–c, Carrara Formation, locality FC-1., E. California (all × 5.3); Fig. 8, USNM 63712, Ptarmigan Formation, near Ross Lake, British Columbia (× 1.6); Figs. 9–22, MCZ 667a–n, Poleta Formation, locality WP-1A., E. California (all × 4.5).

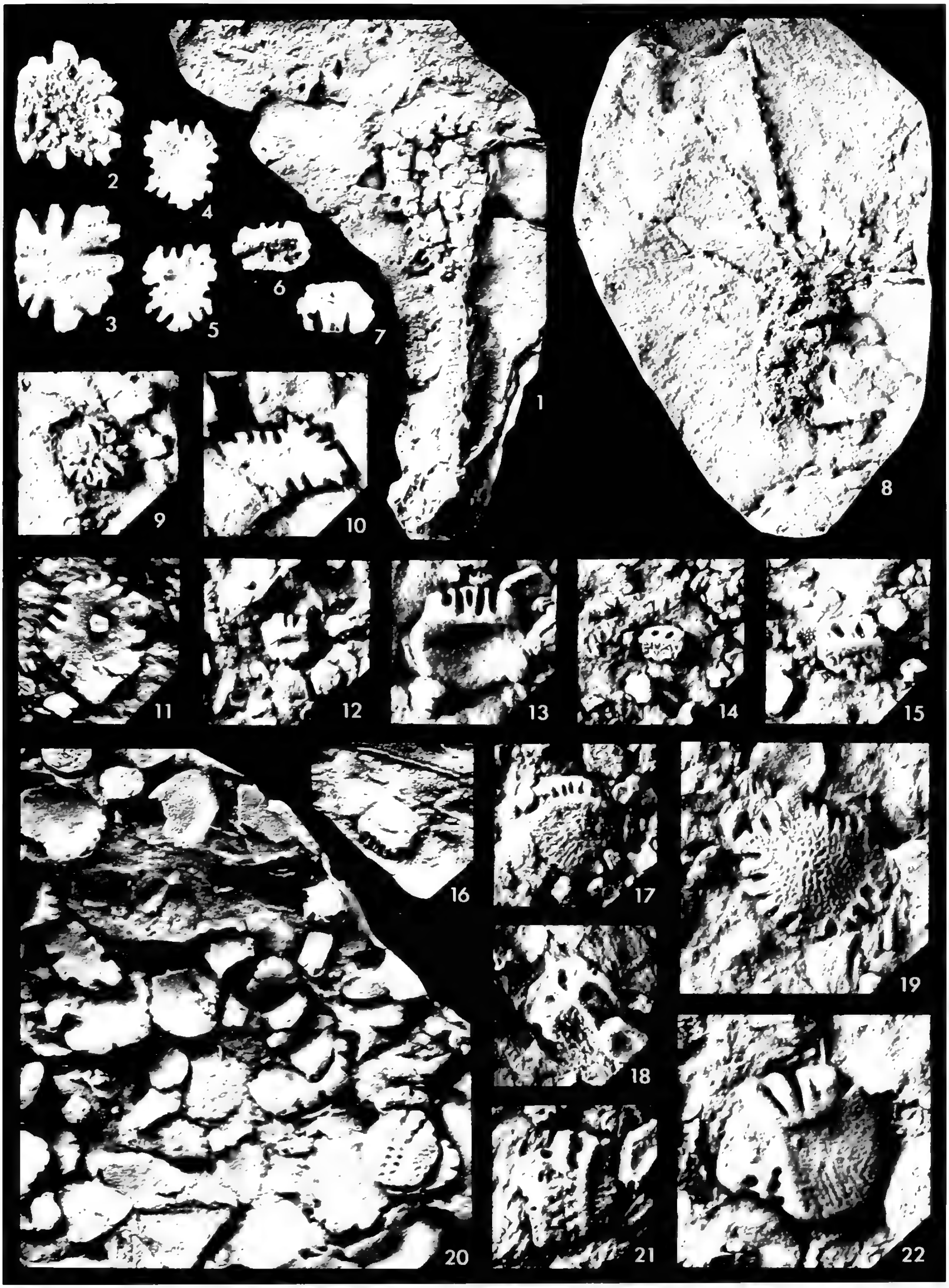
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Plate 26. AKADOCRINUS

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Figures 1–6. *Akadocrinus jani* Prokop. Morphology specimens. Figs. 1–3, two specimens together on a slab; inferred specimen of *A. jani* (left and Fig. 2) and holotype of *A. nuntius* (right and Fig. 3); note relatively poor preservation (the mold is somewhat weathered), slight irregularities in stem (Fig. 3), similar plating in both specimens, similar flattened summit with brachioles, and difference in shape apparently caused by slightly different modes of crushing. Fig. 4, lower part of calyx and crushed proximal stem showing gradual appearance of epispires above basals, slight fusular nature of columnals, and very large lumen. Figs. 5–6, another specimen in positive and negative (internal cast) counterparts; note prominent epispires well developed in middle of calyx but dying out towards summit and base, long biserial brachioles attached around summit and apparently having imbricate cover plates, and proximal end of stem attached to base in Fig. 6.

All figures latex casts from the Caster Coll., Univ. of Cincinnati. Specimen in Figs. 1–3 is cast E 62 (× 1.1 and 2.8); Fig. 4, cast E 41, (× 3.2); Figs. 5–6, casts E 40A and B (× 3.4). All specimens from the Middle Cambrian Jince Beds of Czechoslovakia and deposited in the National Museum, Prague.


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Plate 27. LICHENOIDES and CARDIOCYSTITES

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Figures 1–6. *Lichenoides priscus* Barrande. Calyx and brachiole morphology. Fig. 1, internal view of calyx plates; note massive nature of basals, epispires along all sutures, and that longest (oldest?) epispires are lateral on radials(?) at top of specimen. Fig. 2, complete but crushed specimen with at least eight brachioles, fine rugose plate ornament, and sutural epispires. Fig. 3, external and internal views of separate calyx plates; note two apparent overlayerings of secondary calcite on interior of lateral(?) at top center, and brachiole facet with food groove on its right on radial(?) at top right. Fig. 4, complete and well-preserved specimen; note brachioles with tiny imbricate(?) cover plates, possible change to biserial opposite or uniserial plating at base of second brachiole from right, epispires through calyx plates, and small basals near aboral pole. Fig. 5, oblique summit view of a weathered specimen showing central oral pyramid with covered food grooves leading to brachiole facets on radial(?) plates with a branch to the left (looking aborally) leading to the facets on the laterals(?). Fig. 6, large well-preserved specimen with well-developed epispires (note isolated epispire in left lateral(?) plate), bulbous basals, and broken brachioles.

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Figures 7–9. *Cardiocystites bohemicus* Barrande. Two known specimens. Fig. 7, better preserved specimen showing flattened shape, marginal and central plates with ridges, and normal stem. Fig. 8, enlargement of summit area from Fig. 7. Note "crests" at left and right, central flat area where appendages are attached and three stubby, heavily plated brachioles(?) (left, center [broken], and right) showing large food groove and muscle gaps; total number of brachioles was probably five. Fig. 9, other specimen showing same side of calyx, long stem, and missing summit.

All figures latex casts from the Caster Coll., Univ. of Cincinnati. Specimen in Fig. 1 is E 21 (× 2.1); Fig. 2, E 13 (× 2.1); Fig. 3, E 70A (× 2.2); Fig. 4, E 27 (× 2.2); Fig. 5, BC 141B (× 2.1); Fig. 6, E 25 (× 2.1); Figs. 7–8, E 51 (× 3.3 and 5.7); Fig. 9, E 39 (× 1.7). Specimens in Figs. 1–6 from the Middle Cambrian Jince Beds, Czechoslovakia; specimens in Figs. 7–9 from Middle Ordovician unit D_4, Czechoslovakia. All specimens in the National Museum, Prague.

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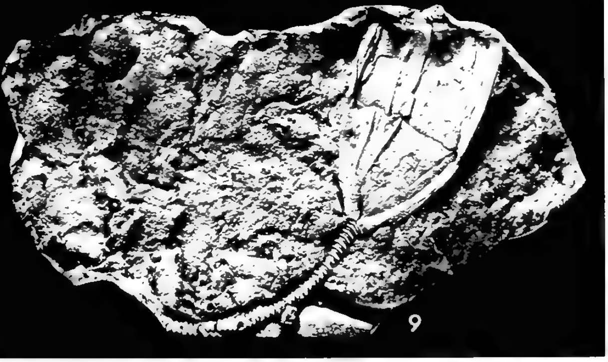

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Plate 28. EUSTYPOCYSTIS

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Figures 1–11. *Eustypocystis minor* n. gen., n. sp. Best preserved complete specimens. Figs. 1 and 3, three specimens extensively prepared by Edwin Kirk; note calyx shape, plating, lack of epispires, and badly damaged appendages. Fig. 2, holotype showing calyx plates, small stem with true columnals, and trace of brachioles. Fig. 4, very small specimen showing short stem segment, part of oral surface without brachioles, and apparent anal pyramid on right side of calyx; note unidentified echinoderm with biserial plating beneath eocrinoid. Fig. 5, partially complete specimen showing disarticulated calyx plates and short brachiole segments. Fig. 6, large but mostly buried specimen showing three brachioles with cover plates and short stem segment. Fig. 7, broken specimen showing short stem with columnals; note abundant worm burrows on rest of slab. Fig. 8, large broken specimen cut by quartz vein. Fig. 9, separate brachiole segment with cover plates. Figs. 10–11, two other complete but partially disarticulated specimens with short stem segments.

Specimens in Fig. 1 are paratypes USNM 165423a–b, locality USGS 835 (× 2.5); Fig. 2, holotype MCZ 719, locality SC-4A. (× 2.5); Fig. 3, paratype USNM 165424, locality USGS 834 (× 2.5); Fig. 4, paratype MCZ 720, locality SC-4A. (× 4.0); Fig. 5, paratype MCZ 721, locality SC-4A. (× 2.5); Fig. 6, paratype MCZ 722, locality SC-3. (× 2.0); Fig. 7, paratype MCZ 723, locality SC-4. (× 2.0); Fig. 8, paratype MCZ 724, locality SC-4. (× 2.0); Fig. 9, paratype MCZ 725, locality SC-1. (× 1.7); Fig. 10, paratype MCZ 726, locality SC-4A. (× 2.2); Fig. 11, paratype MCZ 727, locality SC-1. (× 1.9). All specimens from the Secret Canyon Formation, Eureka District, central Nevada.


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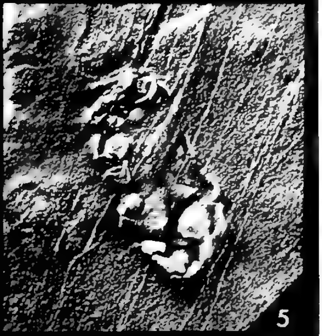
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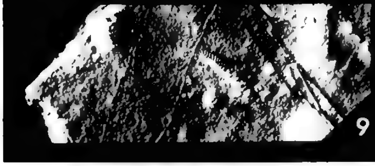
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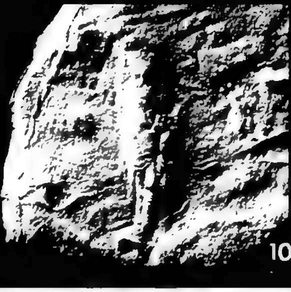
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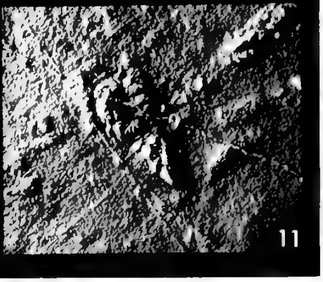
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Plate 29. NOLICHUCKIA

Plate 116

Figures 1–9. *Nolichuckia casteri* n. gen., n. sp. Complete specimens and fragmentary material. Fig. 1, holotype specimen showing incomplete calyx with holdfast (bottom) and large brachioles scattered around slab; note thinness of calyx plates and lack of epispires. Fig. 2, incomplete paratype showing articulated calyx plates and possible remains of holdfast (bottom). Fig. 3, enlargement of base of calyx and holdfast in Fig. 1; note tiny plates in proximal portion and badly damaged distal end. Fig. 4, short segment of another holdfast showing plating and small lumen; Figs. 5–6, separate "cystoid plates" from the Nolichucky Formation apparently belonging to this taxon; note polygonal shape, tiny growth lines, and "banding" into larger units. Figs. 7–9, enlargements of three brachioles from Fig. 1; note short brachiolar plates with slight gaps proximally (Fig. 7) and two types of cover plates (Fig. 8).

Specimen in Figs. 1, 3, and 7–9 is holotype MCZ 616 from the Nolichucky Formation, near Bristol, SW Virginia (× 1.8, 4.0, 4.0, 4.0, and 2.9 respectively); Fig. 2, latex cast of paratype USNM 165410, Nolichucky Formation, Walcott's locality 103a, NE Tennessee (× 1.9); Fig. 4, paratype MCZ 617, Nolichucky Formation, near Bristol, SW Virginia (× 3.0); Figs. 5–6, paratypes MCZ 618 and 619, Nolichucky Formation, locality HL-1., SW Virginia (both × 2.5).


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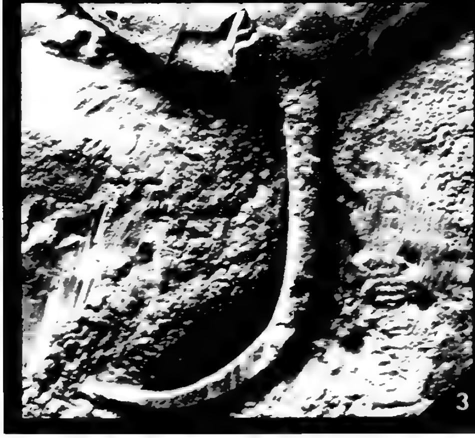
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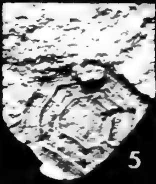
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Plate 30. TRACHELOCRINUS

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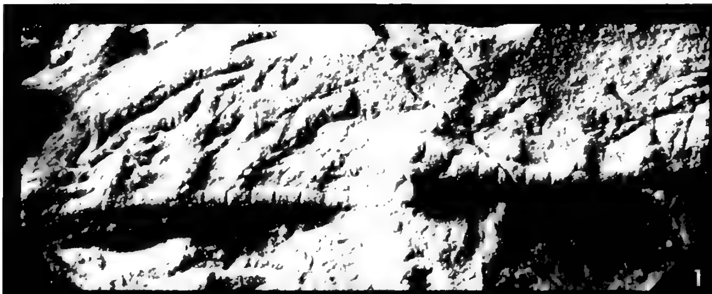
Figures 1–4. *Trachelocrinus resseri* Ulrich. Morphology of holotype and only known complete specimen. Fig. 1, enlargement of best preserved arm showing regular biserial arrangement of plates and smaller biserial brachioles(?) branching off every third (sometimes every second) arm plate. Fig. 2, spoutlike projection on summit of calyx bearing all of the arms; note small rectangular plates and tiny ornamental nodes. Fig. 3, complete specimen showing globular calyx, long arms branching off spoutlike projection on summit, and well-developed stem with flanged columnals. Fig. 4, enlargement of stem showing alternate arrangement of flanged and nonflanged columnals and short spines on flanges; note also that stem does not show any pronounced enlargement near calyx.

Specimen in Figs. 1–4 is holotype USNM 80490 from the Snowy Range Formation, Walcott's locality 37o, NW Wyoming. (Fig. 1, × 4.6; Figs. 2 and 4, × 4.0; Fig. 3, × 1.9).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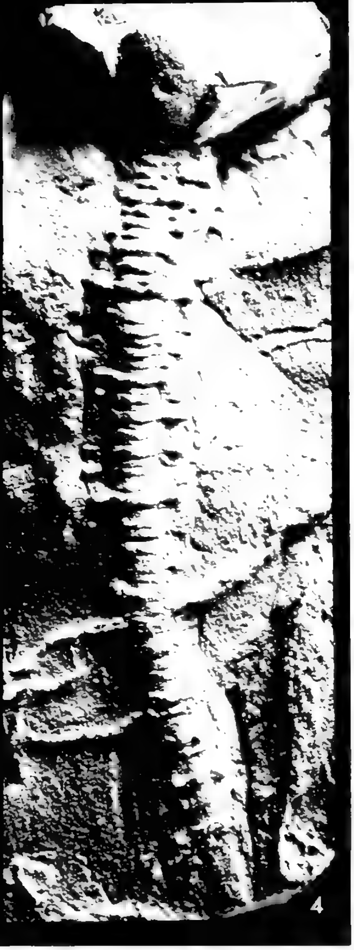
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Plate 31. PETALOCYSTITES

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Figures 1–3. *Petalocystites ikecanensis* n. gen., n. sp. Complete specimens. Fig. 1, holotype specimen showing calyx shape, plating, missing base, slanting summit area, round anal opening at upper left, and numerous long brachioles; Fig. 2, complete but partially buried paratype; note single columnal at base, similar plating to specimen in Fig. 1, and partially silicified brachioles. Fig. 3, broken base of another calyx showing single bullet-shaped columnal apparently attached to only two elongate basal plates.

Specimen in Fig. 1 is holotype MCZ 646 (× 1.6); Fig. 2, paratype MCZ 647 (× 1.4); Fig. 3, paratype MCZ 648 (× 1.8). All specimens from the Antelope Valley Limestone, locality IK-2., central Nevada.

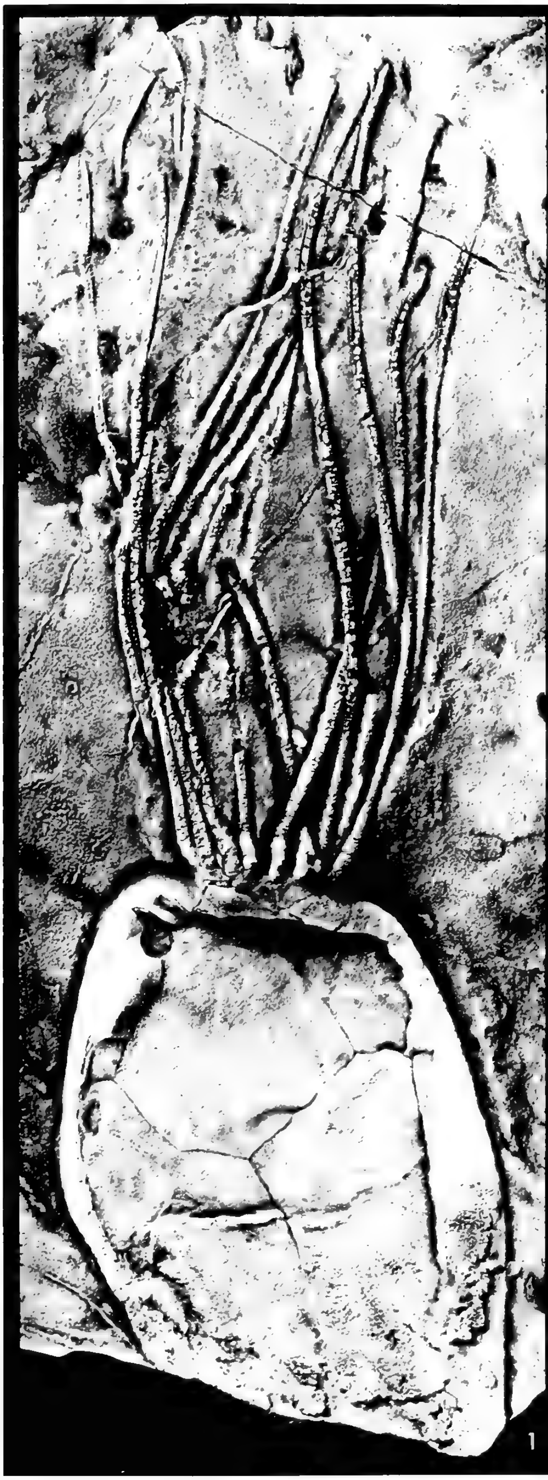
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Plate 32. PETALOCYSTITES and RHIPIDOCYSTID PLATES

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Figures 1–3. *Petalocystites ikecanensis* n. gen., n. sp. Details of summit and brachioles. Fig. 1, enlargement of summit area of holotype showing circular anal opening at left with several crushed anal pyramid plates, major horizontal crack below summit, and brachioles mounted on marginals and orals(?) in two ambulacral areas extending out from central mouth. Fig. 2, enlargement of distal portion of a brachiole in the holotype; note normal biserial plating. Fig. 3, oblique enlargement of holotype summit area showing change from biserial alternate to biserial opposite plating near base of two center brachioles, two sets of alternating cover plates (large and small) in brachiole at top left, and anal opening with its cover plates (left) surrounded by three marginals and one central.

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Figures 4–18. Silicified plates possibly belonging to *Petalocystites* or some other rhipidocystid genus. Fig. 4, adoral view of three-piece set of basal marginals; third plate is small wedge at bottom. Fig. 5, aboral view of same showing large columnal facet, central lumen, and sutures between three plates. Fig. 6, aboral view of basal columnal showing slightly elliptical shape and round facet for one or more additional columnals. Fig. 7, adoral view of same showing facet for basal marginals and widely elliptical lumen. Fig. 8, combined side view of specimens in Figs. 4–5 and 6–7 showing how basal marginals and columnal fit together. Figs. 9–10, side and oblique bottom views of another basal set (marginals & columnal) showing usual preservation. Figs. 11–13, internal, external, and upper end views of a separate marginal plate; note external ornament, shape in end view, and depressed facet for ligaments or muscles to hold marginals together. Figs. 14–16, internal, external, and upper end view of a separate (but broken) basal marginal showing (Fig. 14) short suture for other basal marginal and long suture where third wedge-shaped plate fits, as well as (Fig. 16) suture for part of basal columnal. Figs. 17–18, two other complete basal sets with broken marginal "limbs"; note differences in shape and plating between these and basals in *Petalocystites ikecanensis* (Pl. 31, figs. 2–3).

Specimen in Figs. 1–3 is holotype MCZ 646 (× 3.6, 6.1, and 5.8 respectively); Fig. 4–5 and 8 (part), MCZ 671 (× 2.2); Figs. 6–7 and 8 (part), MCZ 672 (× 2.2); Figs. 9–10, MCZ 673 (× 2.2); Figs. 11–13, USNM 165412 (× 2.7); Figs. 14–16, USNM 165413 (× 2.7); Figs. 17–18, MCZ 674–675 (× 1.7). All specimens from the Antelope Valley Limestone, localities IK-2., central Nevada and USGS D719i CO, SW Nevada (Figs. 11–16).

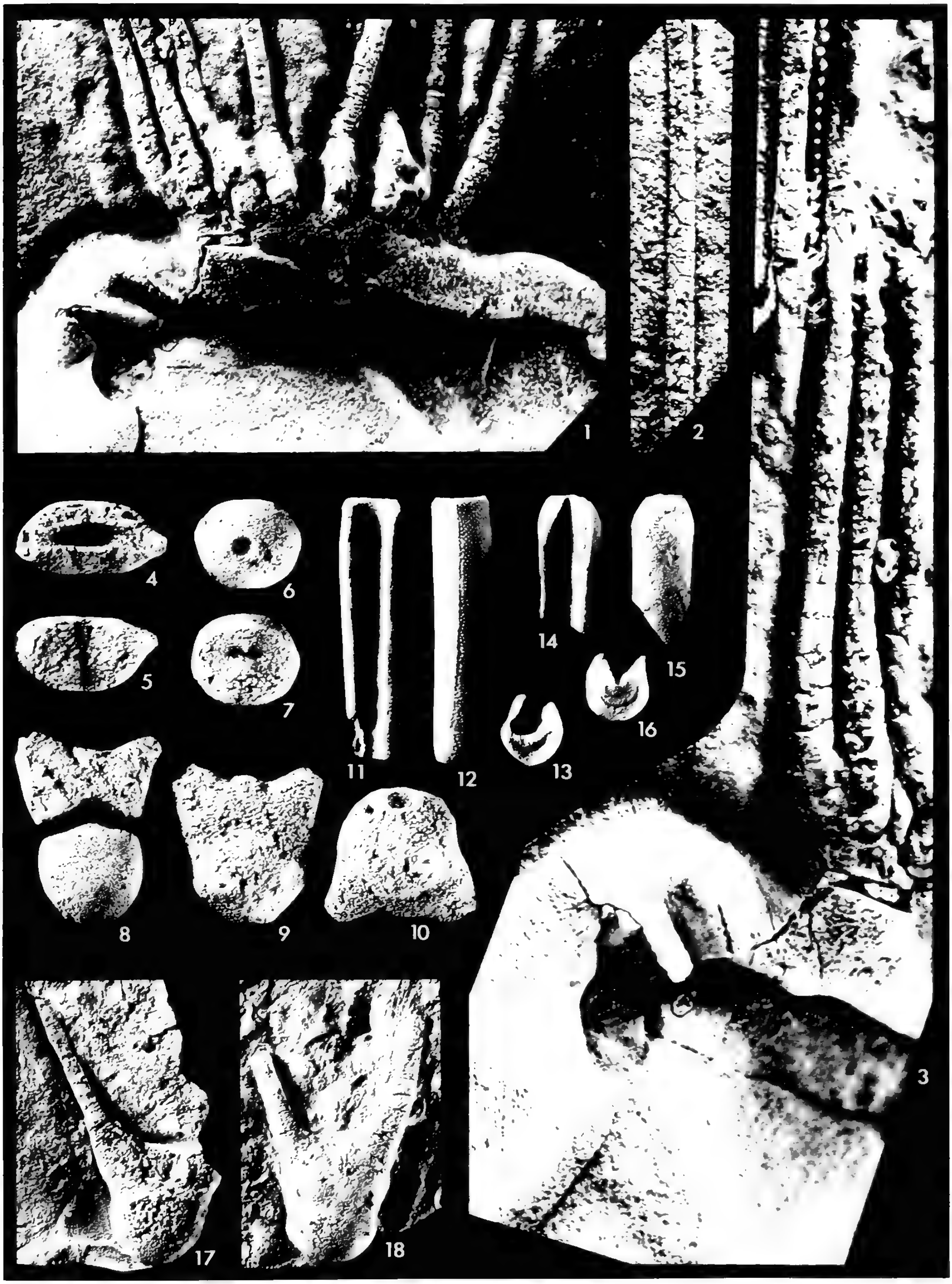
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Plate 33. LYSOCYSTITES, ARCHAEOCYSTITES, CYSTIDEA, and *CRYPTOCRINITES*

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Figures 1–8. *Lysocystites sculptus* (Miller). Springer plesiotype specimens. Figs. 1–3, summit, side, and basal views of best preserved plesiotype; note respiratory ridge system, calyx ornament, and small appendage facets around mouth. Figs. 4–5, another large plesiotype showing the exospire respiratory structures with the external covering nearly intact (Fig. 5, center, calyx inverted), and with the covering broken off (Fig. 4, center); note plate sutures, one large and two small lateral pores to interior, and high ridge between them which may have prevented mixing. Fig. 6, smallest specimen showing central mouth and lateral anus. Figs. 7–8, large weathered specimen shown smoked with ammonium chloride and wet; note thin ambulacral plates bearing appendage facets and extending down between orals, and two small pores between mouth and anus.

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Figures 9–10. *Archaeocystites medusa* Barrande. Only known specimens. Fig. 9, uniserial appendages with cover plates; note long appendage plates. Fig. 10, complete specimen showing poorly preserved calyx (mostly an internal cast), columnal-bearing spiny stem (bottom), and long uniserial appendages.

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Figure 11. *Cystidea nugatula* Barrande. Five- to six-part stem (top) attached to a basal attachment structure having irregular polygonal plating and a deep summit cavity (lower left) and attached to the glabella of a large trilobite.

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Figures 12–13. *Cryptocrinites laevis* Pander. Two complete specimens (summit views) showing the smooth calyx plating, mouth surrounded by appendage facets on small plates, and anal opening in "BC" interradius.

Figs. 9–11 latex casts. Specimen in Figs. 1–3 is plesiotype S3163b, Laurel Limestone, Indiana (× 2.7); Figs. 4–5, plesiotype S3163c, same locality as above (× 2.1); Fig. 6, plesiotype S3163a, same locality (× 2.7); Figs. 7–8, plesiotype S3163d, same locality (× 2.1); Fig. 9, E 33, Caster Coll., Univ. of Cincinnati (specimen in National Museum, Prague), middle Ordovician, Czechoslovakia (× 2.7); Fig. 10, holotype E 32, same collection as above (× 2.0); Fig. 11, S 31, same collection as above (× 1.3); Figs. 12–13, MCZ 743a–b, middle Ordovician, Estonia (U.S.S.R.) (× 2.4).


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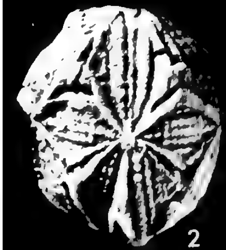
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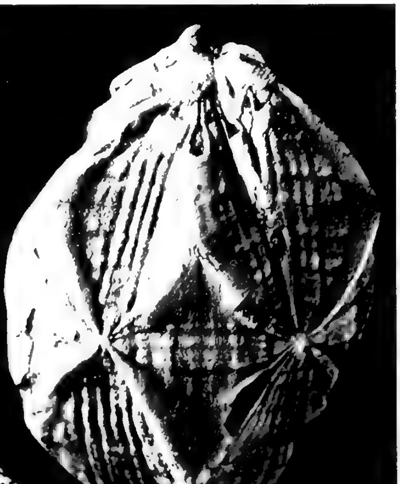
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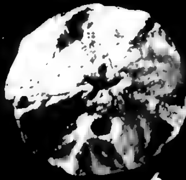
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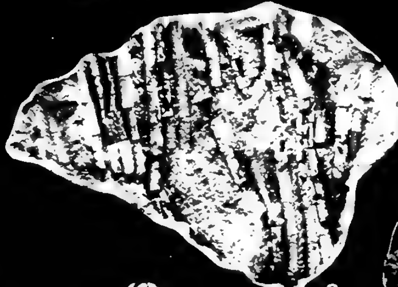
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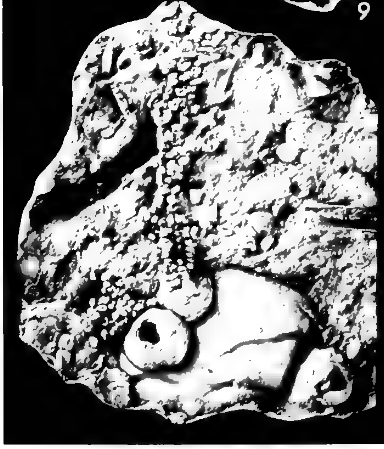
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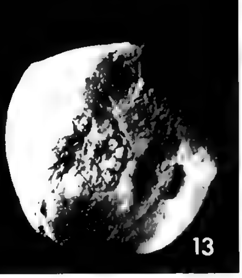
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Plate 34. BLASTOIDOCRINUS CARCHARIAEDENS

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Figures 1–38. *Blastoidocrinus carchariaedens* Billings. Hudson's complete specimen and separate plates. Figs. 1–5, basal, summit, oblique summit, ambulacral, and interambulacral views of Hudson's excellent complete specimen; note saw cuts for sections (now missing) used to study internal morphology, complex pelvis plating, large interradial deltoids with aboral cataspire slits, short brachioles folded in against flaring wing plates in protective ambulacral crest, ambulacral cover plates beneath wing plates (Fig. 3), oral crest plate covering mouth, and deep basal cavity with large stem. Figs. 6–10, partial deltoid growth series; note ornament, aboral cataspire slits, and change from bulged to flat or concave aboral margin. Figs. 11–14, interior, aboral, adoral, and side (ambulacral) views of specimens in Figs. 7–10 respectively; note thinness of deltoids, and strong convex shape in side view. Figs. 15–18, partial growth series of oral crest plates showing squat cylindrical shape, facets for abutting wing plates, and markings where brachioles fold into depressions. Figs. 19–21, oblique top, bottom, and top views of oral crest plates in Figs. 16–18 respectively; note shallow grooves on top and "2-1-2" pattern of sutures for oral(?) plates. Figs. 22–24, basal cavity, aboral interior, and side views of a large radial; note deepness of basal cavity and thickness of plate. Figs. 25–27, basal cavity, exterior, and lateral interior views of another radial; note exterior ornament and apparent sutures (Fig. 25) for interradial basals. Figs. 28–32, side, end, intersutural, top, and bottom views of a pair of bibrachials; note ornament, lack of opening in this plate for cataspires, and great thickness of inter-bibrachial suture. Figs. 33–38, side, top, and end views of an intermediate wing plate, and side, top, and bottom views of a terminal wing plate; note flaring shape in end view and apparent growth markings on the top surface indicating that during growth new wing plates were added aborally to the plate in Fig. 34, converting it from a terminal wing plate to an intermediate one.

Specimen in Figs. 1–5 is AMNH 25068 (× 2.7); Fig. 6, deltoid NYSM 7413; Figs. 7 and 11, NYSM 7407; Figs. 8 and 12, NYSM 7411; Figs. 9 and 13, NYSM 7412; Figs. 10 and 14, NYSM 7416; Fig. 15, NYSM 7431; Figs. 16 and 19, NYSM 7434; Figs. 17 and 20, NYSM 7437; Figs. 18 and 21, NYSM 7440; Figs. 22–24, NYSM 7396; Figs. 25–27, NYSM 7397; Figs. 28–32, NYSM 7401; Figs. 33–35, NYSM 7422; Figs. 36–38, NYSM 7427 (Figs. 6–38, all × 1.6). All specimens from the Chazy Group, Valcour Island, New York (Hudson Coll.).

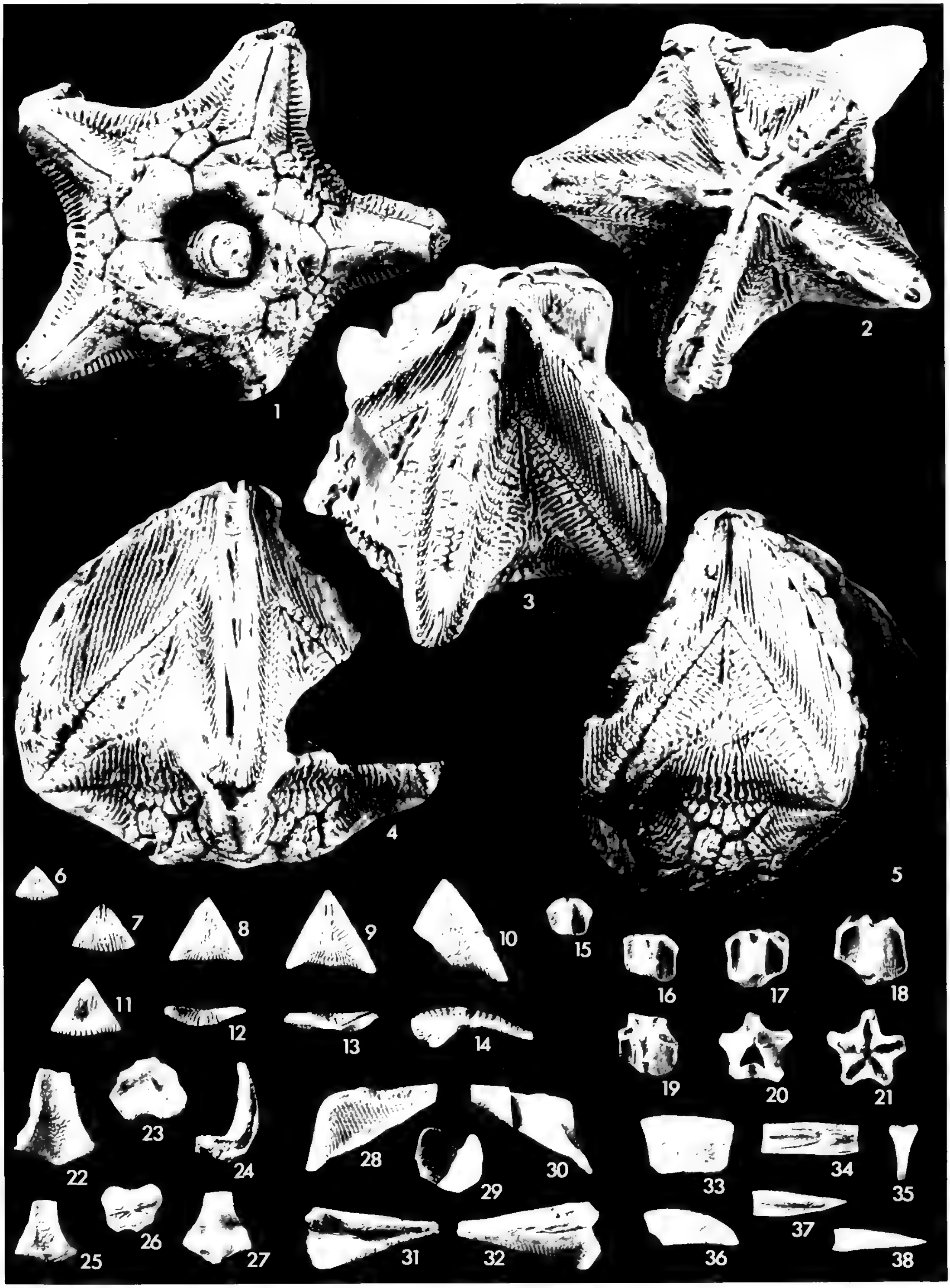
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Plate 35. BLASTOIDOCRINUS CARCHARIAEDENS

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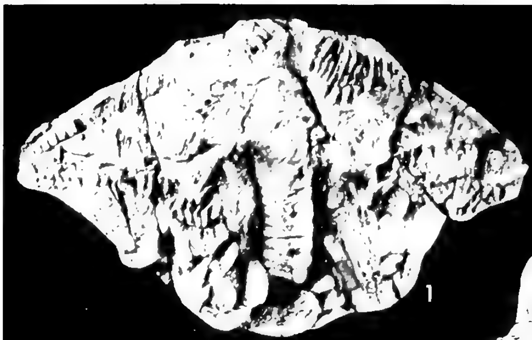
Figures 1–10. *Blastoidocrinus carchariaedens* Billings. Holotype and other complete Canadian specimens. Figs. 1–4, broken interior, exterior, summit, and basal views of the crushed and distorted holotype showing stem and basals pushed up into calyx, ambulacral areas with a few cover plates, and cataspire folds extending under deltoids. Fig. 5, summit view of a small specimen showing broken oral crest and brachioles and cover plates attached to top ambulacrum. Figs. 6–7, 9–10, basal, summit, and two side views of a large specimen that has been polished; note stem in basal cavity, large biserial cover plates (Fig. 10) over center of ambulacrum, and indistinct pelvis plating. Fig. 8, enlarged side view of large high cover plates which support the wing plates in the center of the ambulacrum.

Specimen in Figs. 1–4 is holotype GSC 1016, Chazy Group, Montreal, Canada (× 2.3); Fig. 5, UC 26022, Chazy Formation, Village Belanger, Que., Canada (× 2.3); Figs. 6–10, unnumbered GSC specimen at the Univ. of Kansas, Laval Formation (Chazy), Ile Jésus, Canada (× 2.0 and 3.0 (Fig. 8)).



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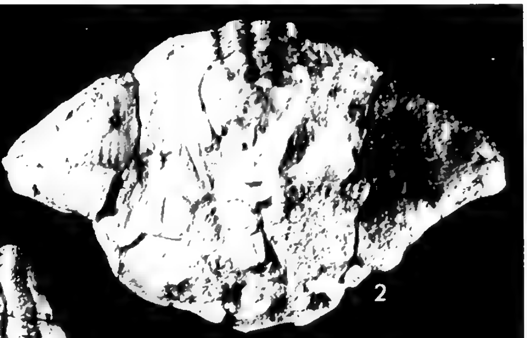

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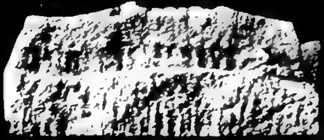

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Plate 36. BLASTOIDOCRINUS(?) ROSSI

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Figures 1–36. *Blastoidocrinus*(?) *rossi* n. sp. Plate morphology and deltoid growth series. Fig. 1, exterior of holotype deltoid showing shape of plate and overgrowths of silica. Fig. 2, aboral view of same showing cataspire slits; note that lateral slits on both sides are "slanted." Fig. 3, side view showing ambulacral facets and silica overgrowths on exterior. Fig. 4, adoral view of same; note thickness of plate. Fig. 5, interior view showing "bulged" aboral margin and greater spacing of central cataspire slits. Fig. 6, top view of oral crest. Fig. 7, same, bottom view, plate is broken near attachment area. Fig. 8, side view of same, note conical shape and lack of sutures for wing plates. Fig. 9, side view of another oral crest; note difference in shape. Fig. 10, side view of another very large, partially weathered, oral crest. Fig. 11, deltoid edge view of best preserved bibrachial; note strong curvature and thickness of plate. Fig. 12, exterior view of same showing radial ornament and asymmetrical shape of plate. Fig. 13, same, interior view. Fig. 14, deltoid edge view of another bibrachial; note trace of possible cataspire slit markings. Fig. 15, same, exterior view; compare shape with Fig. 12. Fig. 16, interior view of same showing cataspire slit markings. Fig. 17, aboral edge of possible oral (broken adorally); note large central projection and grooves. Fig. 18, aboral edge of another possible oral; note poorly preserved central projection (compare with Fig. 17). Fig. 19, exterior view of same showing shape of plate, lack of ornament, and depressed sutures around adoral and lateral margins. Fig. 20, adoral view of same showing possible food grooves on lateral edges. Fig. 21, side view of same. Fig. 22, interior view. Figs. 23–36, 14-plate deltoid growth series showing shape of plates, increase in number of cataspire slits and ambulacral facets, and retention of aboral "bulge" throughout size range.

Specimen in Figs. 1–5 is holotype USNM 165378 from the Garden City Formation, locality USGS D190d CO, N. Utah (all × 4.0); Figs. 6–8, paratype USNM 165392, same locality as above (× 4.1); Figs. 9–10, paratypes USNM 165393–4, same locality as above (× 4.1); Figs. 11–13, paratype USNM 165395, same locality as above (× 4.7); Figs. 14–16, paratype USNM 165396, Garden City Formation, locality USGS D190e CO, N. Utah (× 4.7); Fig. 17, paratype USNM 165397, Garden City Formation, locality LO-1., N. Utah (× 4.7); Figs. 18–22, paratype USNM 165398, locality USGS D190d CO (× 4.7); Figs. 23–36, paratypes USNM 165379–91 and holotype USNM 165378 (Fig. 35), localities LO-1. (Figs. 23–26, 28–29, 31–33), USGS D190d CO (Figs. 30, 34–36), and USGS D190e CO (Fig. 27) (all × 3.4).

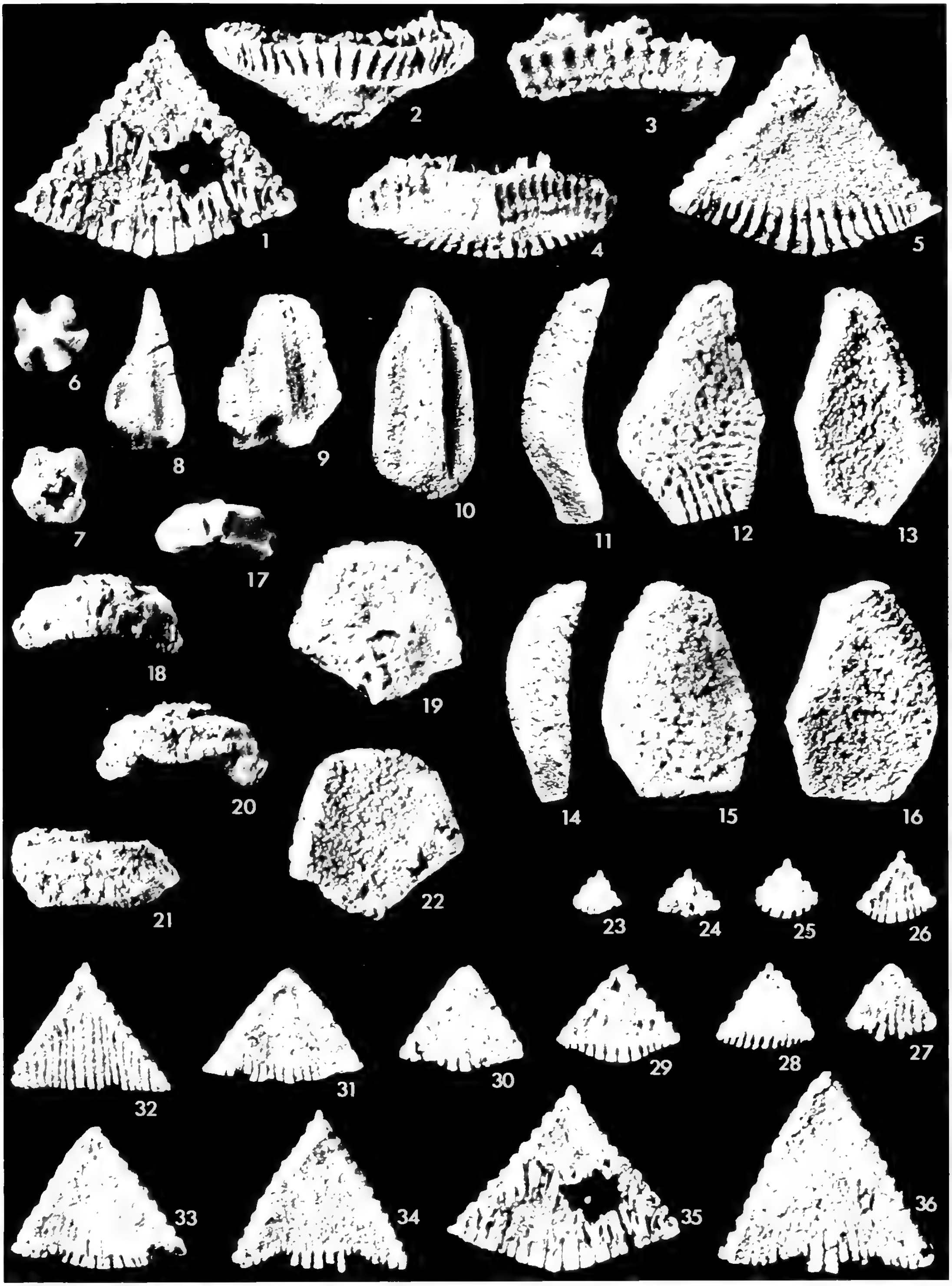
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Plate 37. BLASTOIDOCRINUS(?) NEVADENSIS and *B.(??) ELONGATUS*

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Figures 1–18. *Blastoidocrinus(?) nevadensis* n. sp. Plate morphology and deltoid growth series. Fig. 1, exterior of holotype deltoid showing shape and closely spaced, relatively long cataspire slits. Fig. 2, interior view of same; note trace of cataspire folds. Fig. 3, side view showing ambulacral facets. Fig. 4, aboral view of same; note that there is little "slanting" of the cataspire slits. Fig. 5, adoral view showing thickness of plate. Fig. 6, side view of small oral crest; note cylindrical shape and faceted edges where wing plates may have abutted. Fig. 7, oblique view of same showing hemispherical depression in top. Fig. 8, bottom view showing attachment area. Fig. 9, top view of same showing pentagonal shape and depressed top surface. Figs. 10–18, nine-plate deltoid growth series showing shape of deltoids, lack of a bulge on the aboral margin, and the closely spaced, relatively long cataspire slits.

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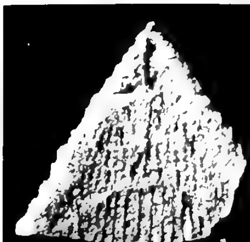
Figures 19–23. *Blastoidocrinus(??) elongatus* n. sp. Morphology of deltoids. Fig. 19, exterior view of silicified holotype deltoid showing shape of plate with long limbs and slight "twist" of these limbs aborally. Fig. 20, oblique bottom view of same showing numerous short cataspire slits. Fig. 21, exterior view of paratype deltoid (preserved in calcite); note strong pustular ornament. Fig. 22, side view of holotype showing shape of plate and numerous ambulacral facets. Fig. 23, side view of paratype deltoid showing both the ambulacral facets and the pores between them for the excurrent flow from the cataspires.

Specimen in Figs. 1–5 is holotype MCZ 613 from the Antelope Valley Limestone, locality MJ-1., SW Nevada (all × 3.9); Figs. 6–9, paratype MCZ 615, same locality as above (× 3.9); Figs. 10–19, paratypes MCZ 614-D1-6, 8–9 and holotype MCZ 613 (Fig. 16), same locality as above (× 3.2); Figs. 19–20, 22, holotype MCZ 610, same locality as above (all × 2.6); Figs. 21, 23, paratype MCZ 611, Antelope Valley Limestone, locality IK-3., central Nevada (× 2.3).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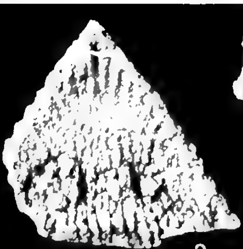
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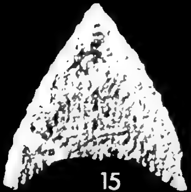
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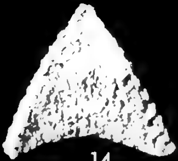
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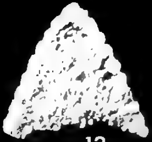
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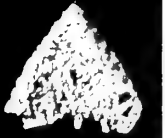
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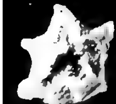
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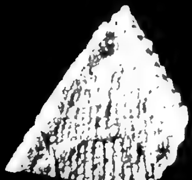
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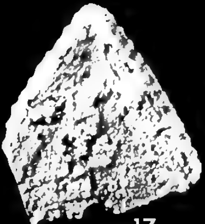
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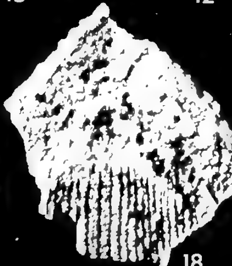
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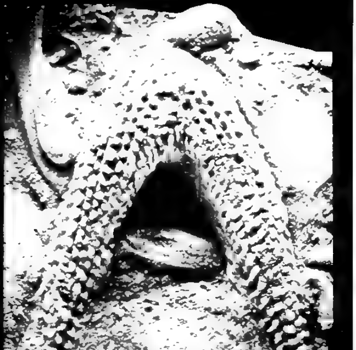
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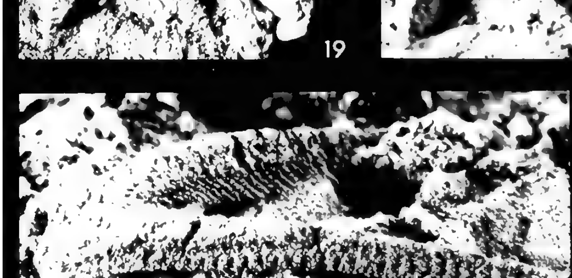
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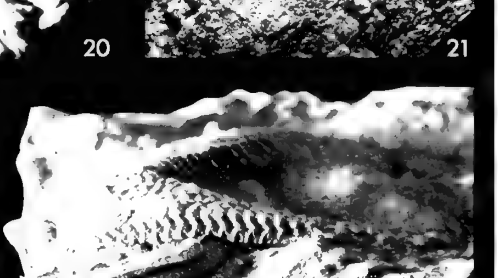
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Plate 38. MERISTOSCHISMA HUDSONI

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Figures 1–8. *Meristoschisma hudsoni* n. gen., n. sp. Two complete specimens. Fig. 1, aboral view of large complete holotype showing stem emerging from basal cavity. Fig. 2, oral view of same. Fig. 3, "A" ambulacral view; note calyx shape and brachioles attached to edges of wide ambulacra. Fig. 4, "CD" interradial view showing anal opening, cataspire slits in deltoid, and cataspire pores at edge of ambulacra. Fig. 5, oblique "D" ambulacral view showing oral plates, conical oral crest, and covered ambulacral food grooves leading to mouth. Fig. 6, interambulacral view of small paratype showing few cataspire slits in deltoid. Fig. 7, ambulacral view of same; note cataspire pores at edge of ambulacrum. Fig. 8, aboral view showing single columnal lodged in basal cavity.

Specimen in Figs. 1–5 is holotype MCZ 594 from the Benbolt Formation, locality LV-2., NE Tennessee (all × 2.2); Figs. 6–8, paratype MCZ 595, Benbolt Formation, locality RC-8., SW Virginia (all × 2.1).

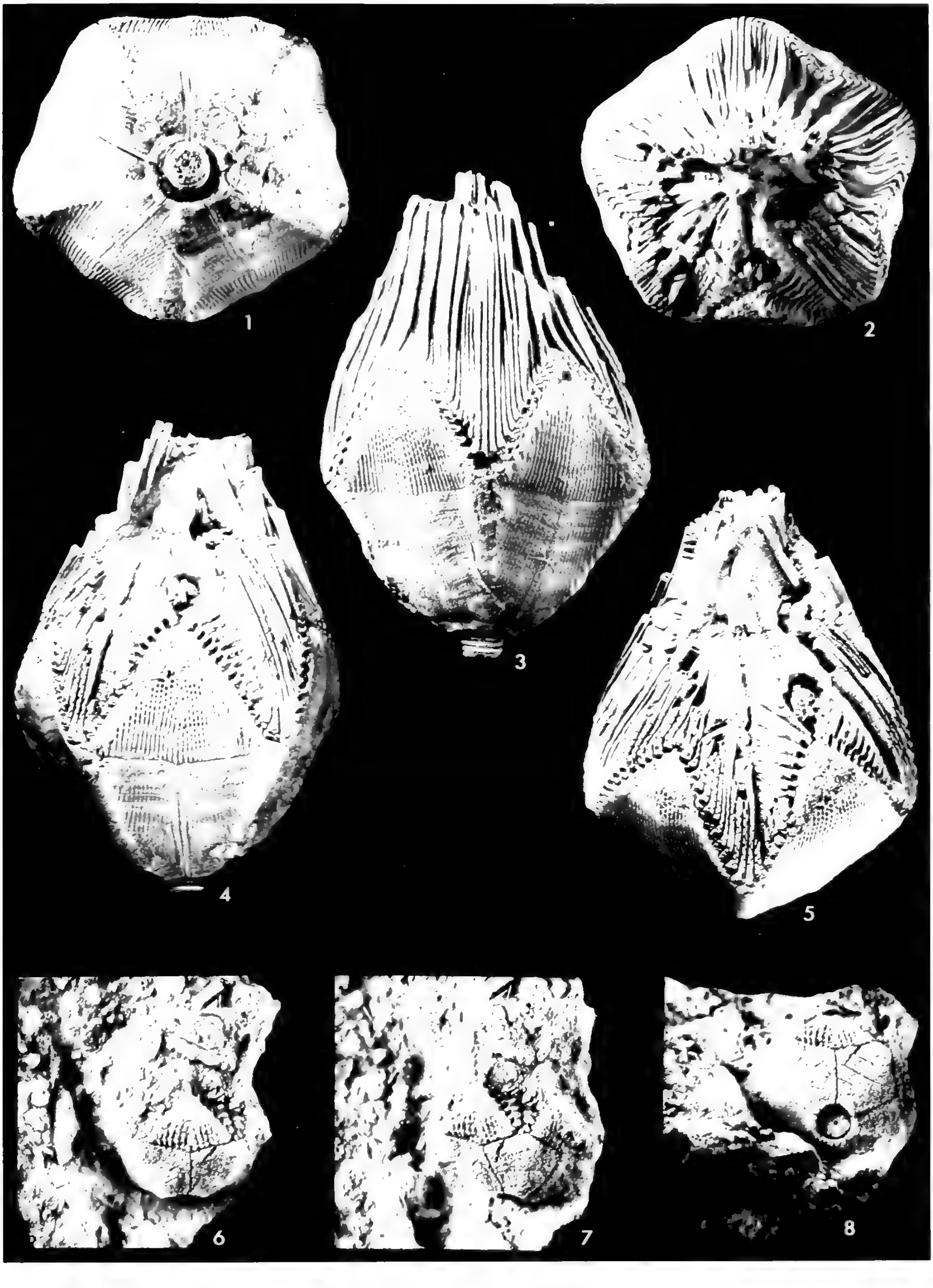
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Plate 39. MERISTOSCHISMA HUDSONI

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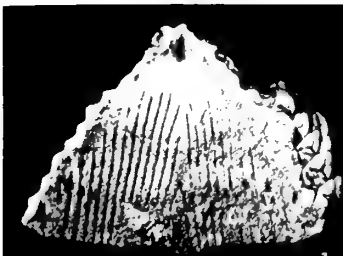
Figures 1–23. *Meristoschisma hudsoni* n. gen., n. sp. Morphology of calyx plates and brachioles. Fig. 1, exterior surface of a deltoid showing brachioles attached to edge. Fig. 2, interior of same deltoid showing ambulacral plates, traces of cataspire folds, and exit pores at edge of ambulacrum; note outward bend of cataspire folds near edge of deltoid. Figs. 3–4, oblique side views showing basal brachiolar plates attached to both ambulacral plates and deltoid margins, and pores between ambulacral plates. Fig. 5, external view of four ambulacral plates; note small brachiolar facets, pores for cataspire system between facets, and smooth side food grooves. Fig. 6, side view of same showing thickness of plates and pores. Figs. 7 and 11, external view of two oral plates; note large vertical ridges. Figs. 8 and 12, internal view of same; note small "nick" in center of aboral (lower) margin. Figs. 9 and 13, adoral view showing main food grooves to mouth on depressed edges of orals. Figs. 10 and 15, side view showing food grooves. Fig. 14, aboral view of larger oral showing prominent "nick" on interior aboral margin. Fig. 16, anal ("CD") side view of oral crest; note sutures. Fig. 17, same, "A" side view. Fig. 18, top view; note strong vertical ridges. Fig. 19, bottom view showing tiny lobes and sockets for cover plates over the main food grooves which are arranged in a standard "2-1-2" pattern around the mouth, and the facets for the adoral edges of the oral plates; Fig. 20, radiodeltoid suture on a radial with markings showing the aboralmost attachment of the internal cataspire folds and the location of the cataspire slits on the aboral edge of the deltoid; notice that not all of the folds and slits match up perfectly. Fig. 21, closeup of brachioles on the holotype showing tiny biserial cover plates protecting brachiolar food groove; oral crest in right foreground. Fig. 22, end view of same brachioles, note apparent lack of canals; four larger "abnormal" brachioles (top) protect many somewhat smaller ones. Fig. 23, side and aboral view of brachioles showing regular biserial plating and three short, apparently immature brachioles (center and left).

Specimen in Figs. 1–4 is paratype MCZ 596 from the Benbolt Formation, locality RC-7., SW Virginia (all × 3.3); Figs. 5–6, paratype MCZ 597, Benbolt Formation, locality RC-9., SW Virginia (both × 5.6); Figs. 7–10 and 11–15, paratypes MCZ 601A and B, respectively, same locality as above (all × 3.6); Figs. 16–19, paratype MCZ 598, same locality as above (all × 3.7); Fig. 20, paratype MCZ 601C, same locality as above (× 3.7); Figs. 21–23, holotype MCZ 594, Benbolt Formation, locality LV-2., NE Tennessee (× 7.8, 6.9, and 6.8, respectively).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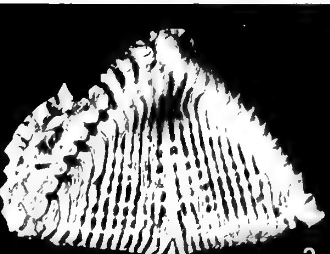
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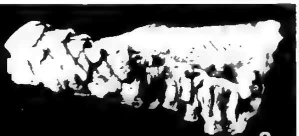
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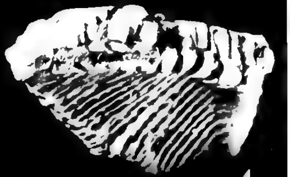
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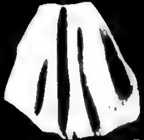
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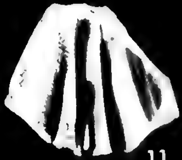
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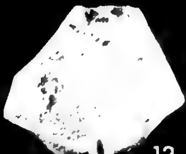
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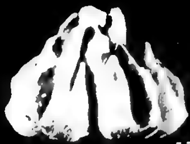
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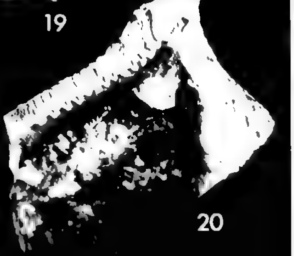
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Plate 40. MERISTOSCHISMA HUDSONI and M. FAYI

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Figures 1–10. *Meristoschisma hudsoni* n. gen., n. sp. Deltoid and radial morphology. Fig. 1, external view of deltoid showing cataspire slits. Fig. 2, aboral view of same; note slight irregularities in slits. Fig. 3, side view showing ambulacral facets. Fig. 4, adoral view; note possible secondary thickening of deltoid along ambulacral margins. Fig. 5, internal view showing cataspire slits divided into pores and minor branching medially for new short slits. Fig. 6, external view of radial; note subdued ornament, fine holoperipheral growth lines, and 4–5 larger "bands" or groupings (perhaps seasonal) of these growth lines. Fig. 7, side view of same; note thinness of plate. Fig. 8, aboral view showing basal cavity and suture for two basals. Fig. 9, adoral view showing very angular shape of plate transversely and markings for the aboral attachment of the cataspire folds (see also Pl. 39, fig. 20). Fig. 10, interior of radial; note absence of growth lines and traces of cataspire fold attachments along the deltoid margins.

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Figures 11–20. *Meristoschisma fayi* n. sp. Deltoid and radial morphology. Fig. 11, external view of deltoid showing coarse ornament between cataspire slits. Fig. 12, aboral view of same showing cataspire slits and somewhat greater plate thickness (compare with Fig. 2). Fig. 13, side view showing ambulacral facets and traces of excurrent cataspire pores in between. Fig. 14, adoral view of deltoid. Fig. 15, internal view showing elongate pores in cataspire slits. Fig. 16, external view of radial showing coarse ornament, much different ornament along RR sutures, and apparent absence of growth lines and bands. Fig. 17, side view of same; note very thick nature of plate (compare with Fig. 7) and somewhat different longitudinal shape. Fig. 18, aboral view showing larger basal cavity. Fig. 19, adoral view; note slightly convex transverse section of plate and faint traces of cataspire fold attachments. Fig. 20, interior of radial showing massive nature of plate and larger basal cavity.

Specimen in Figs. 1–5 is paratype MCZ 599-D7 from the Benbolt Formation, locality RC-9., SW Virginia; Figs. 6–10, paratype MCZ 600-R10, same locality as above; Figs. 11–15, holotype MCZ 602-D1, Benbolt Formation, locality DT-3., NE Tennessee; Figs. 16–20, paratype MCZ 602-R3, Benbolt Formation, locality MC-3., SW Virginia (Figs. 1–20 all × 3.5).

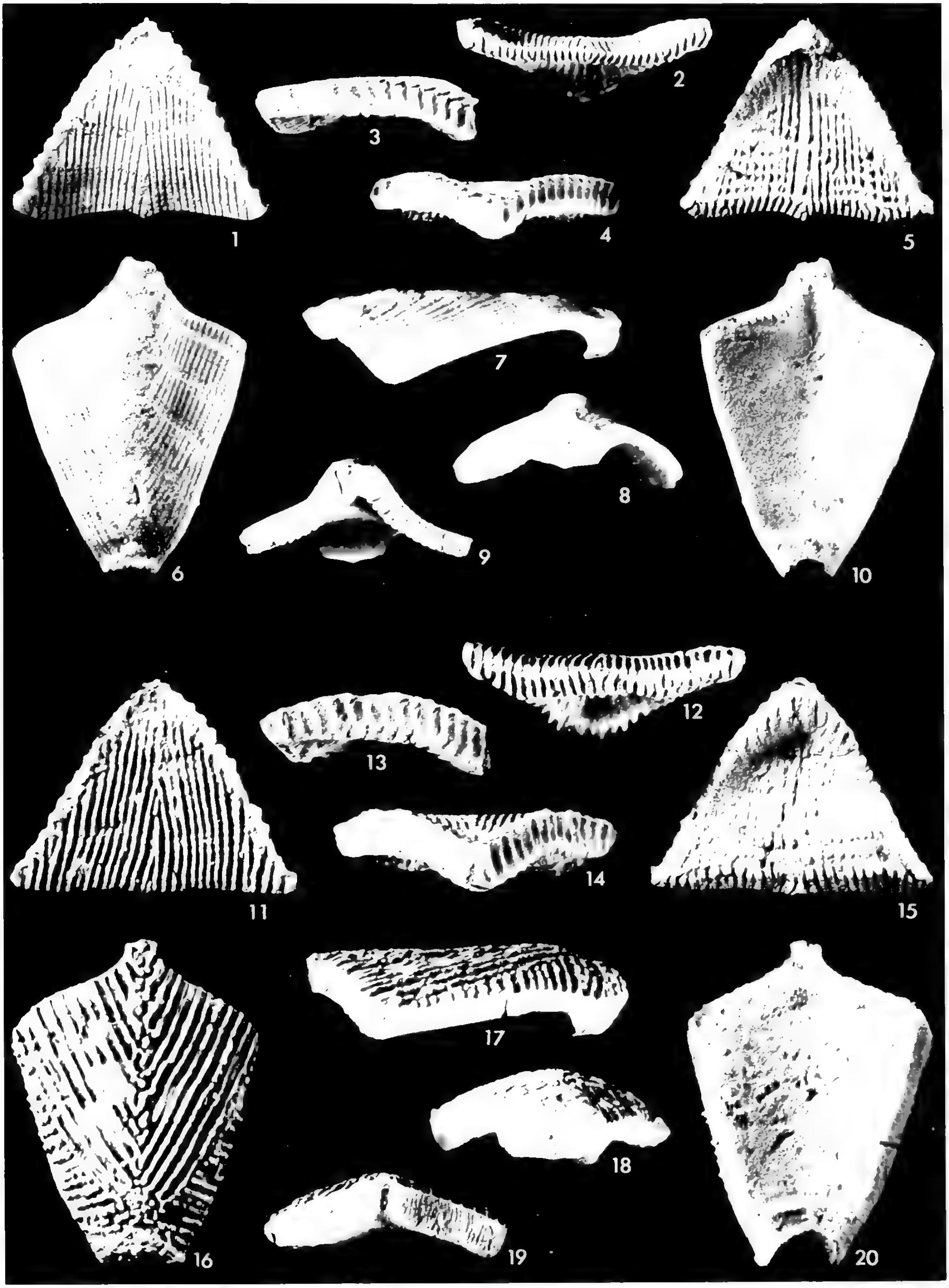
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Plate 41. MERISTOSCHISMA HUDSONI and *M. FAYI*

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Figures 1–20. *Meristoschisma hudsoni* n. gen., n. sp. Deltoid and radial growth series. Figs. 1–10, deltoids; note gradual increase in L/W ratio, and addition of new cataspire slits at edges and center of deltoid with increasing size. Figs. 11–20, radials; note gradual change in plate shape because of faster growth toward deltoids than toward adjacent radials.

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Figures 21–27. *Meristoschisma fayi* n. sp. Deltoid and radial growth series. Figs. 21–23, partial deltoid growth series showing similar shape to the deltoids of *M. hudsoni* (Figs. 1–10) but with stronger rugose ornament. Figs. 24–27, partial radial growth series showing strong rugose ornament and large basal cavity throughout all growth stages.

Specimens in Figs. 1–20 are paratypes MCZ 599-D1-10 (deltoids) and MCZ 600-R1-10 (radials), all from the Benbolt Formation, locality RC-9., SW Virginia (except MCZ 599-D10 which is from locality LV-2., NE Tennessee); Figs. 21–27, holotype MCZ 602-D1 (Fig. 21) and paratypes MCZ 602-D2-3 (deltoids), and paratypes MCZ 602-R1-4 (radials), Benbolt Formation, locality MC-3., SW Virginia (Figs. 22, 25–27), and localities DT-3. (Figs. 21, 23) and DT-3A. (Fig. 24), NE Tennessee. (Figs. 1–27 all × 2.3)

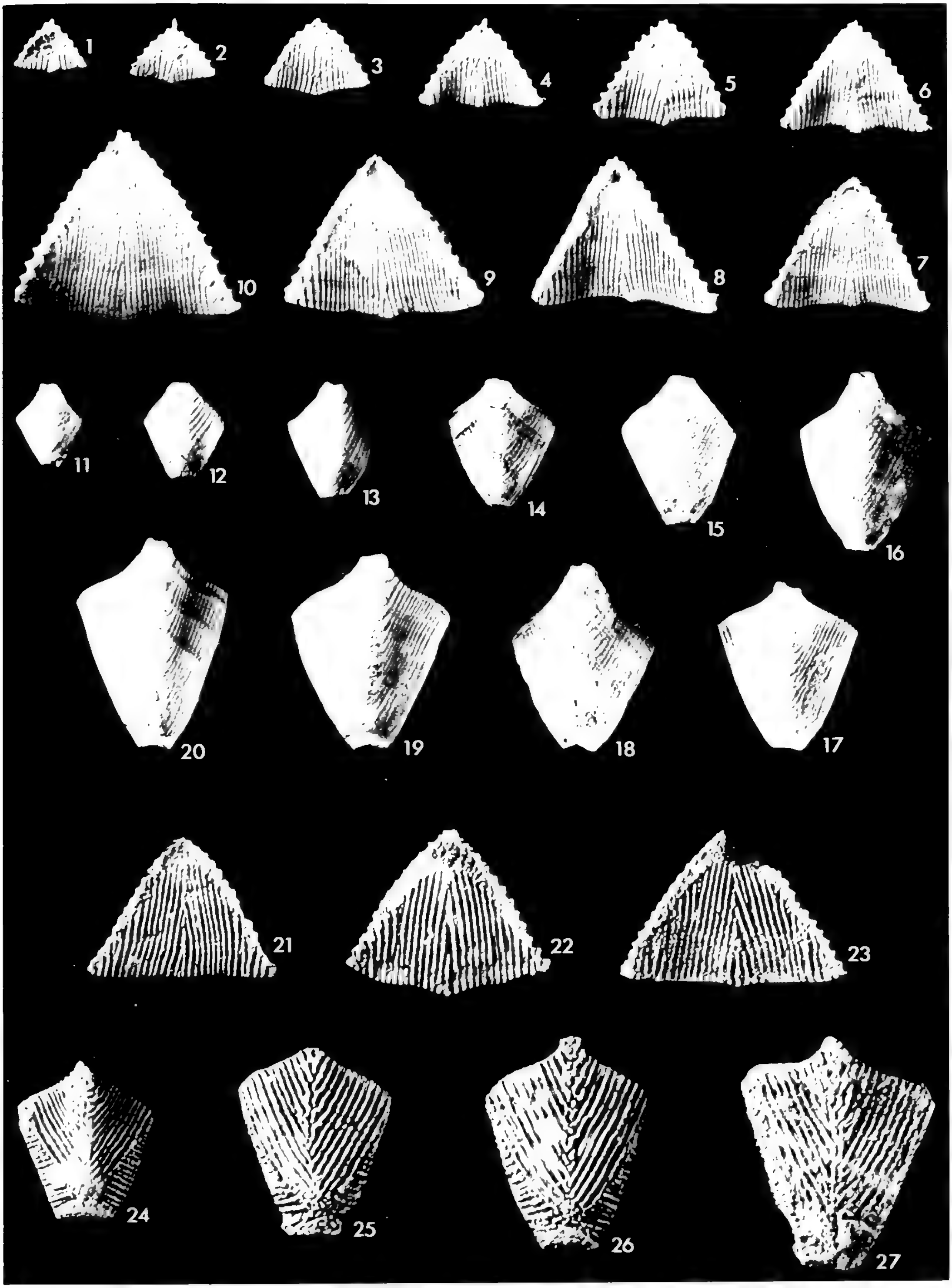
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Plate 42. ECHMATOCRINUS

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Figures 1–3. *Echmatocrinus brachiatus* n. gen., n. sp. Holotype and large holdfast. Figs. 1–2, two counterparts of large complete holotype immersed under water; note conical calyx with irregular plating, long tapering holdfast attached to a *Selkirkia* worm tube, and the large uniserial arms bearing apparently soft tube feet. Fig. 3, isolated crushed holdfast with missing calyx; specimen may be attached to a hyolithid(?) at the distal end and shows some of the thin irregular plating.

Specimen in Figs. 1–2 is holotype GSC 25962B and A (× 1.5); Fig. 3, paratype USNM 165408 (× 1.2). Both specimens from the Burgess Shale Member, Stephen Formation, Walcott's Quarry, USNM localities 35k and 35k/10, near Field, British Columbia.


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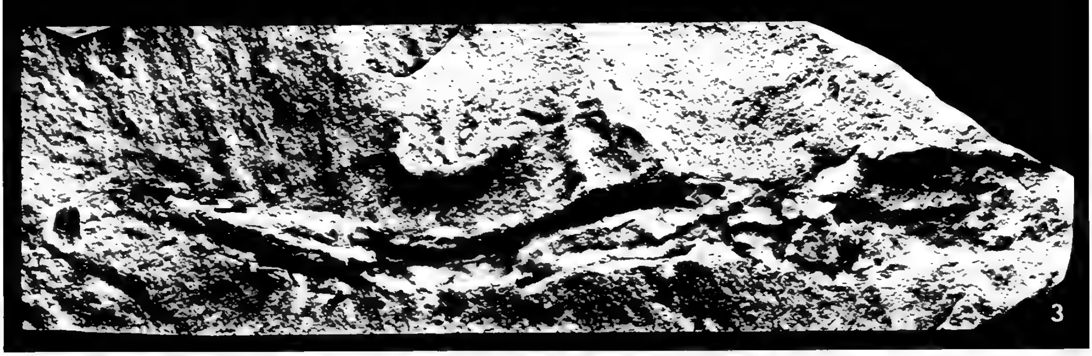
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Plate 43. ECHMATOCRINUS

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Figures 1–8. *Echmatocrinus brachiatus* n. gen., n. sp. Specimens showing relief and preservation. Figs. 1–2, positive and negative counterparts of a well-preserved specimen having a short holdfast attached to an unidentified pyritized object, irregular calyx plating with granular ornamentation, and at least seven arms. Fig. 3, very poorly preserved specimen showing part of calyx and holdfast. Figs. 4–5, specimen with conical calyx and short arms showing little relief or morphology. Fig. 6, holotype specimen (negative counterpart—smoked) showing calyx proportions and plating; compare with Figs. 1–2. Fig. 7, indistinct specimen lacking characteristic granular ornament; may possibly belong to the edrioasteroid *Walcottidiscus*. Fig. 8, single arm plate showing darker V-shaped area at top.

Specimen in Figs. 1–2 is paratype USNM 165405A and B (× 1.3); Fig. 3, USNM 165407 (× 1.1); Figs. 4–5, USNM 165406B and A (× 1.1); Fig. 6, holotype GSC 25962B (× 1.3); Fig. 7, paratype(?) USNM 165427 (× 1.0); Fig. 8, paratype USNM 165426 (× 1.0). All specimens from the Burgess Shale Member, Stephen Formation, Walcott's Quarry (USNM locality 35k), near Field, British Columbia.


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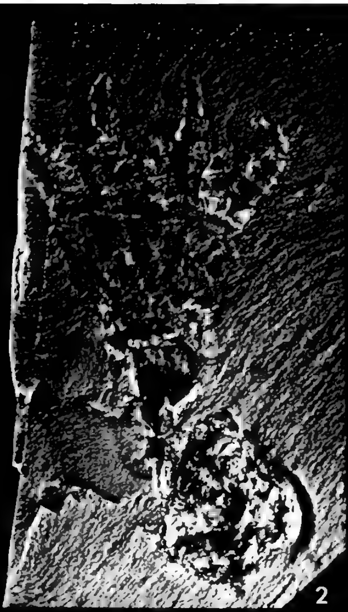
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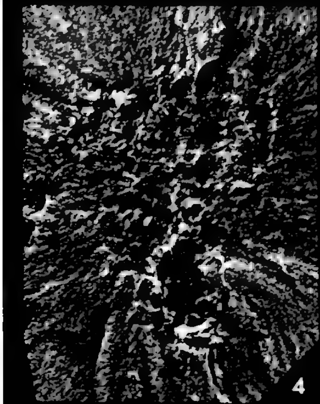
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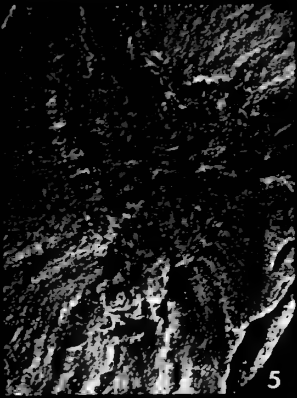
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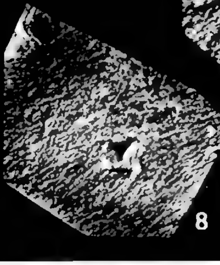
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