

PART T  
ECHINODERMATA 2  
CRINOIDEA

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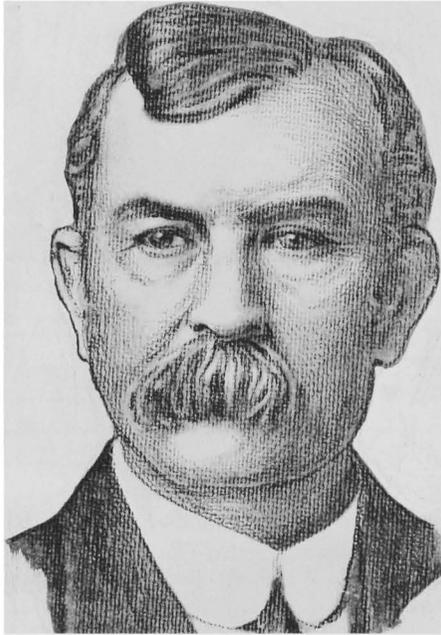
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**DEDICATION**By **RAYMOND C. MOORE**

The *Treatise* volumes on Crinoidea here published are dedicated appropriately to four paleontologists who have advanced knowledge of fossil representatives of these echinoderms most greatly. These outstanding contributors include one American, **FRANK SPRINGER** (1848-1927); one Britisher, **F. A. BATHER** (1863-1934); and two Germans, **OTTO JAEKEL** (1863-1929), and **JOHANNES WANNER** (1878-1956). (Portraits by **RAYMOND C. MOORE**.)

**FRANK SPRINGER**

**FRANK SPRINGER** was born at Wapello, Iowa, on June 17, 1848. He was graduated from the University of Iowa in 1867 and then, following his father, who was a distinguished judge prominent in gaining statehood for Iowa and in writing its constitution, studied law, followed by admission to the bar in 1869. At Burlington, some 30 miles south of his birthplace, young **SPRINGER** was chosen as county prosecuting attorney and served until 1873, when interest in opportunities offered by the rapidly expanding Southwest led him to move to Cimarron, New Mexico; he transferred residence to Las Vegas, New Mexico, and considered this city as home throughout the remainder of his life. Soon after his arrival in Cimarron he was chosen as attorney for a company that had acquired title to a Mexican land grant of more than 1,700,000 acres. Validation of the title required extensive litigation, however, leading ultimately to the U.S. Supreme Court where **SPRINGER** won a favorable decision. Also, he had to appear before committees of the U.S. House and Senate in order to obtain passage of needed legislation. In 1891, **SPRINGER** was elected president of the company, which by then had been proved to control huge reserves of valuable coking coal. Meanwhile, in 1878, he became counsel

for the Santa Fe railway when westward construction of the line reached New Mexico; his chief duty was the arranging of needed rights-of-way.

As a member of the New Mexico Legislative Council (1880, 1901) and Constitutional Convention (1889), SPRINGER promoted excellence in both lower and higher education within the State.

The scientific side of FRANK SPRINGER's career covers a span of approximately 63 years, running concurrently with his interest in the law and business activities, for it began early in his university student days and constantly was augmented up to the time of his death at age 79. During successive summers before his graduation from the University, the Iowa State Geologist, Dr. C. A. WHITE, and his assistant, ORESTES ST. JOHN, both paleontologists, left him in charge of the Survey's fossil collections and library while they were engaged in field work. Young FRANK used this opportunity to study the collections ardently and to search fossiliferous Devonian and Mississippian outcrops near Iowa City for specimens discovered by himself. When he moved to Burlington for the beginning of law practice, he continued paleontological work by making firsthand acquaintance with the crinoid-rich Burlington Limestone. Also, he met CHARLES WACHSMUTH, who had already made large collections of crinoids from the area. Together they undertook to compile information concerning all described fossil crinoids, especially from Paleozoic deposits of North America and Europe. This led to their first major written contribution entitled *Revision of the Palaeocrinoidea*, published in Proceedings of the Philadelphia Academy of Natural History (1880-86), which contained a comprehensive new classification of then-known species, genera, and families of these fossils.

In vacation periods after SPRINGER took up residence in New Mexico, he returned to Iowa for the purpose of continuing crinoid studies with WACHSMUTH. A very major result of this collaboration was publication in 1897 of the outstanding three-volume royal quarto monograph on *North American Crinoidea Camerata* (Harvard University). This is a landmark addition to paleontology which WACHSMUTH did not live to see, for he died in 1896. Its very many handsome illustrations consist of drawings made by CHARLES R. KEYES, a fellow student of SPRINGER at Iowa, who became State Geologist of Missouri in 1894-96.

Besides several large and important articles by SPRINGER on fossil crinoids, such as *Uintacrinus, its Structure and Relations* (1901), *The Crinoid Fauna of the Knobstone Formation* [Lower Mississippian of Kentucky] (1911), *Some New American Fossil Crinoids* (1911), *On a Trenton* [Middle Ordovician] *Echinoderm Fauna at Kirkfield, Ontario* (1911), *The Fossil Crinoid Dolatocrinus and its Allies* (1921), and *Unusual Forms of Fossil Crinoids* (1926), as well as the section on Crinoidea in ZITTEL-EASTMAN's *Textbook of Paleontology* (1913), he produced two large monographs published by the Smithsonian Institution. These are *The Crinoidea Flexibilia* (2 volumes, 1920), and *American Silurian Crinoids* (1926), both of them comprehensive and authoritative contributions of great value.

The crinoids gathered by WACHSMUTH prior to 1874, when a program of joint studies with SPRINGER was arranged, were sold in that year to Professor LOUIS AGASSIZ for the Museum of Comparative Zoology at Harvard University. Collections made by SPRINGER then were transferred to the fireproof brick-built laboratory located in the back yard of WACHSMUTH's home in Burlington and libraries of the two men were consolidated there. In 1911, SPRINGER gave both the collection and library to the Smithsonian Institution in Washington for display and further research in the United States National Museum. The collection of approximately 100,000 specimens, which included very many types and other illustrated, specially studied specimens, weighed more than 12 tons and may be valued conservatively at \$250,000. SPRINGER continued to augment the collections by purchases of fossil crinoids, especially from European localities, and by intensive collecting carried on by assistants working in many North American regions. The latter effort included the opening of quarries for the sole purpose of finding well-preserved crinoids, many consisting of complete crowns with attached stems, some with their distal holdfasts.

SPRINGER was named as Associate in Paleontology at Harvard University in 1901 and given the same title at the U.S. National Museum in 1914. He was chosen Foreign Correspondent of the Geological Society of London in 1906. Also, he was given an honorary Sc.D. degree by George Washington University in 1921 and a Ph.D. degree by the Universität Bonn, Germany, in 1924.

It is reasonable to judge that no one in the world excels FRANK SPRINGER in adding to knowledge of fossil crinoids. He died in 1927 at the home of one of his daughters in Overbrook, Pennsylvania, a suburb of Philadelphia.



### FRANCIS ARTHUR BATHER

A world leader in the study of fossil echinoderms, especially crinoids, was FRANCIS ARTHUR BATHER, whose entire career was based on his association with the British Museum (Natural History) in London. Born at Winchester, England, in 1863, he was educated in the Public School there and at New College, Oxford University, where he earned a bachelor's degree with first class honors in natural history (1886) and an A.M. degree (1890). His first scientific paper (on Jurassic rocks of Oxfordshire) was published (1886) in the *Journal of the Geological Society of London* and in 1887 he was chosen for curatorial work in geology and paleontology at the British Museum. The prolific nature of BATHER's pen was evidenced by the appearance of 16 publications by him in the four-year period 1887-90. Indeed, this pace was increased since the 48 years (1886-1934) of his entire career are represented by a total of 213 large and small contributions. Most important of these are his monographs on *The Crinoidea of Gotland* (Kongl. Svenska Vetenskapsakad., Handl., v. 25, 180 p., 10 pl., 1893), *Triassic Echinoderms of Băkonny* [Hungary] (Resultate d. Wissenschaftl. Erforsch. d. Balatonsees, v. 1, pt. 1, Paläont. Anhang, 280 p., 18 pl., 1909), and *Caradocian Cystidea from Girvan* [Scotland] (Roy. Soc. Edinburgh, Trans., v. 49, pt. 2, p. 359-529, pl. 1-6, 1913). Also of special

interest are BATHER's *Phylogenetic Classification of the Pelmatozoa* (Rept. British Assoc. 1898, p. 916-923, 1899) and *The Echinoderma* (E. R. Lankaster's Treatise on Zoology, viii + 344 p., 309 fig., Black, London, 1900).

BATHER received the Sc.D. degree (*honoris causa*) from Oxford University in 1909. He became a Fellow of the Geological Society of London and of the Royal Society. He had been president of the Geological Society of London, the Museum Associates, and the British Association for the Advancement of Science, and a correspondent of the Geological Society of America. In addition, he was awarded the Rolleston Prize of the Universities of Cambridge and Oxford, for researches in biology and the Lyell Medal of the Geological Society of London.

BATHER died at his home in London on March 20, 1934, aged 71.



### OTTO JAEKEL

A brilliant paleontologist who contributed innovatively to syntheses of knowledge concerning fossil crinoids was OTTO JAEKEL. Born on February 21, 1863, at Neusalz an der Oder, now known as Nowa Sól, in western Poland, he received training at an academy in nearby Liegnitz where he graduated in 1883 with intent to become a geologist. Studies then were undertaken at the Universität Berlin under FERDINAND ROEMER (1883-85) and Universität München under KARL VON ZITTEL, the most eminent paleontologist of Germany, who supervised completion of JAEKEL's work for the doctorate which he received in 1886. At once he was appointed as an assistant of E. W. BENECKE at the University of Strasburg where he continued to work (except for a lengthy visit to London) until in 1890 he was made a Professor of Geology at the Universität Berlin. He remained there until 1903 when he became Professor of Paleontology at the Universität Wien, but after only one year accepted a similar position at the Universität Greifswald in the northeastern part of present East Germany, not far from his birthplace. On his

retirement from the faculty at age 65, he was invited to continue teaching by transference of his work to Sun-Yat Sen University in Peking, China. This he did in 1928. He failed to complete a single academic year, however, for after a sudden illness he died on March 6, 1929.

Although JAEKEL's primary interest in paleontology was focused on fossil vertebrates, 27 of his publications dealt with echinoderms, chiefly crinoids. Among these, the most important are *Beiträge zur Kenntnis der paläozoischen Crinoiden Deutschlands* (Paläont. Abhandl., no. 7, p. 1-116, 29 fig., 10 pl., 1895) and *Phylogenie und System der Pelmatozoen* (Paläont. Zeitschr., v. 3, p. 1-128, fig. 1-114, 1918). The latter contains a new suprageneric classification of crinoids accompanied by diagnoses and illustrations of many new species and genera. A complete list of JAEKEL's long and short papers has a total of 211 titles (OTHENIO ABEL, *Veröffentlichungen von Otto Jaekel*, Palaeobiologica, v. 2, p. 156-186, 1929).



### JOHANNES WANNER

JOHANNES WANNER was born in the village of Scheidegg im Allgäu, southern Bavaria, on April 21, 1878, son of a high school teacher belonging to a well-known Allgäu family. His academic training included study as a pupil of the world-renowned paleontologist Professor KARL VON ZITTEL at the Universität München where he received his Ph.D. degree in 1901, based partly on a thesis describing Cretaceous fossils from Libya.

WANNER's work in subsequent years is divisible into two quite separate but partly complementary careers, one in petroleum geology and the other in paleontology. In 1902-05 he made his first visit to the East Indies for geological exploration wanted by the Dutch firm of Bataafsche Petroleum Maatschappij. He not only attained objectives for guiding search for oil deposits but made observations on several islands which advanced fundamentally knowledge of the geologic structure of the archipelago and its

development. On his return to Germany, he was appointed in 1906 as chief assistant of Professor GUSTAV STEINMANN at the Universität Bonn and published (1907) an important paper entitled *Hebungen und Senkungen der Erdkruste*. He then embarked on a second trip to the East Indies for reconnaissance of petroleum-development possibilities. On Timor he discovered exceptionally rich Permian and Triassic fossil localities. In 1911 a Bonn University expedition to Timor for the purpose of collecting fossils included WANNER with two other geologists and a zoologist. Their efforts were rewarded very richly.

During World War I, WANNER thought that because of his deafness he would not be called for military duty and thus he could devote himself to work on Timor crinoids. Instead, he was designated as a military geologist and assigned to mapping work in Alsace.

After the war, WANNER was elected in 1920 as Haniel Distinguished Professor of Applied Geology at Bonn Universität with permanent tenure, but in practice he supervised studies in paleontology and regional geology.

A monument signaling WANNER's scholarly work in the study of crinoids and other fossils is the series of monographs and long articles which he initiated in 1916 under the general title of *Paläontologie von Timor*. A host of new crinoid species, genera, and families is described and illustrated in this series (1916-29, 495 pages, 34 plates, 158 figures), in Netherlands publications (1920-40, 554 pages, 39 plates, 117 figures), and in *Palaeontographica* in the 1940's. In addition, several papers are devoted to Devonian crinoids of Germany. The entire list of WANNER's publications, chiefly on fossil crinoids, contains 83 titles.

In 1952 when I had the privilege of spending some days with him in Scheidegg, Professor Emeritus WANNER was in good health, but four years later on July 31, 1956, death overtook him.

## INTRODUCTION

By RAYMOND C. MOORE and CURT TEICHERT

[University of Kansas]

Echinoderms belonging to the class Crinoidea (from Gr. *κρινός*, lily) are among the most complexly organized, highly varied forms of all marine invertebrates. They are assigned to a subphylum variously named Crinozoa or Pelmatozoa. Both names are here regarded as synonyms, but preference of usage is given to the name Crinozoa to preserve continuity with previously established *Treatise* usage (see Part S).

Beyond an initial free-swimming larval stage, most fossil crinoids throughout life were attached by a stem to the sea bottom or, rarely, floating objects; however, most living species of crinoids are stemless. Only

the Antedonidae are active swimmers, whereas the comatulids are sluggish crawlers. These are the feather stars, whereas stem-bearing types, because of fancied resemblance to flowering plants, are known as sea lilies. Actually, the stemless forms are also fixed by a stem during part of their very early ontogeny, but by breaking away from this anchorage, they become able to crawl or swim about freely.

The crinoids are distinguished especially by their general form and by the structure of their skeleton. A relatively small disk-shaped or globular body enclosed by an armor of symmetrically arranged calcareous plates, forming the cup or calyx, bears ra-

dially outspread food-gathering appendages, which generally are branched. These appendages, called arms, and the stem are composed of many calcareous segments, joined together in a manner generally permitting differential movement and providing a degree of flexibility.

Adult crinoids range in size from a few millimeters, including length of stem and arms, to 18 m. or more; one Cretaceous species had arms at least 120 cm. long. Modern stemless crinoids have arms as much as 25 cm. in length.

Crinoids have worldwide distribution in present-day oceans, not only in tropical and temperate belts but in frigid waters of the Arctic and Antarctic. They are found at depths ranging from a few meters below sea level to a depth of about 9,000 m., though most stalked crinoids live between 180 and 5,000 meters. The occurrence of fossil crinoids generally suggests moderately shallow water as the habitat preferred by most species. None are found in freshwater deposits.

The number of living species of crinoids is approximately 650, only 80 of which are stalked. To date, about 5,500 fossil species of crinoids have been described, representing more than 1,000 genera (N. GARY LANE, pers. commun., 1976).

Remains of crinoids are widely distributed in many rock formations ranging in age from Middle Cambrian to Cenozoic, although commonly the hard parts are more or less dissociated. At many places, sedimentary deposits ranging in thickness to 30 m. or more are composed largely of crinoidal debris, with or without fossils consisting of articulated crinoid hard parts. Study of these remains has paleontological importance because the variety of fossils is extraordinarily great and the stratigraphic range of most individual species is very short.

Mass occurrences of crinoids are well known in present seas where CLARK (1915a) described the dredging of tens of thousands of individuals from single localities. Crinoid colonies, patches, and stands, sometimes also referred to as "gardens" or "meadows" have been described by LANE (1973) and earlier workers. Rocks that consist predominantly of crinoid remains

have been called "criquinite" (BISSELL & CHILINGAR, 1967).

The distribution of crinoid limestones through time has been described for central and western Europe by DEECKE (1915). Crinoids occur as rock builders in many places from Ordovician to Jurassic time. Best known perhaps is the *Trochitenkalk* of the German Muschelkalk (MARTIN SCHMIDT, 1928). An excellent and detailed summary and annotated bibliography of crinoidal limestones, mainly from the Mississippian of the Midcontinent, was given by LAUDON (1957). Useful general discussions of formation and distribution of crinoidal limestones have been published by CAYEUX (1931) and JOHNSON (1951). In places, crinoidal fragments have accumulated in biohermal masses, especially in Mississippian time (HARBAUGH, 1957; CAROZZI & SODERMAN, 1962).

Crinoids have been persistent reef dwellers since at least Late Ordovician time, the most notable associations of this kind being known from the Silurian of central North America and the Baltic region of northern Europe (Gotland, Saaremaa), and the Devonian of central Europe (HADDING, 1933, 1941; LOWENSTAM, 1948; INGLES, 1963; LANE, 1971; RUHRMANN, 1971). Crinoids lived in vast numbers not only on these reefs but also in the offreef and interreef environments (MANTEN, 1970).

Crinoids are important indicators of depositional environments (CAIN, 1968) and their generally long, slender stems are excellently suited to serve as paleocurrent indicators (KLÄHN, 1929; WIMAN, 1933; SCHWARZACHER, 1963; ANDERSON, 1968).

The biostratonomy of recent and fossil crinoid associations has been studied by TEICHERT (1949), CAROZZI & SODERMAN (1962), RUHRMANN (1971), LANE (1973), LIDDELL (1975), and others. Preservation of entire cups of crinoids, other than camerates, indicates either very rapid burial or sedimentation in very quiet water.

Progressive modifications of crinoid structures during geologic time provide rich material for research on the nature of evolutionary trends. A point deserving stress is that completeness of fossil crinoid specimens is not a measure of their worth to paleon-

tology, because a surprisingly large volume of precise and useful knowledge can be gained from the study of crinoid fragments (MOORE, JEFFORDS, & MILLER, 1968; MOORE & JEFFORDS, 1968).

Because of their characteristic microstructure and optical properties, crinoid frag-

ments are generally easy to recognize in thin sections under the microscope (CAYEUX, 1931; HOROWITZ & POTTER, 1971).

Finally, crinoidal limestones have been found to be of commercial interest as reservoir rocks for oil and gas (IMBT & McCOLLUM, 1950).

## GENERAL FEATURES OF CRINOIDEA

By GEORGES U BAGHS, ALBERT BREIMER, N. GARY LANE, H. WIENBERG RASMUSSEN, R. C. MOORE, J. C. BROWER, HERTHA SIEVERTS-DORECK, H. L. STRIMPLE, D. B. MACURDA, JR., D. L. MEYER, and MICHEL ROUX

### GENERAL MORPHOLOGY

#### RECENT CRINOIDS<sup>1</sup>

By ALBERT BREIMER

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#### INTRODUCTION

Much of our knowledge of recent Crinoidea is based upon specialized forms generally known as the feather stars and systematically grouped as the Comatulida.

This group of crinoids, which is still flourishing, is regarded by paleontologists as not very typical, because they are vagile, stalkless crinoids, lacking a complete armoring

<sup>1</sup> The genus *Neocrinus* as used in this chapter is elsewhere placed in synonymy of *Chladocrinus*, except for the species *N. blakei* which is placed in *Isocrinus* (see p. T851, T857).—Eds.

of tegmen and ambulacra and in some (e.g., Comasteridae) having an excentric mouth and only partly developed ambulacra.

As a matter of fact, in zoological literature the comatulids are considered to be typical crinoids. This is not surprising, taking account of their occurrence in areas in which scientific zoology for almost 150 years could deal with them. They form the bulk of the extant crinoids, which partly live at moderate depths and are regularly caught at marine biological stations, biological expeditions, and even on fishermen's lines. Consequently they are readily available in zoological collections. As a result, the species *Antedon bifida* has developed in literature (CUÉNOT, 1948) as a model crinoid for zoologists.

In contrast, paleontological literature is almost exclusively devoted to sessile, stalked crinoids, generally known as sea lilies, which to the mind of paleontologists are better regarded as typical crinoids. They almost invariably have a complete armoring of the tegmen and ambulacra, a centrally located mouth, and fully developed ambulacra. However, extant stalked crinoids have the handicap of being rare organisms living mostly at appreciable depth, probably in a state of approaching extinction, and, almost exclusively, available specimens have been collected by zoological expeditions. Only a very few species inhabit shallow water. One of these is *Neocrinus decorus* in Caribbean waters. This species is fairly well represented in zoological collections and may occasionally be caught at marine biological stations. It has long been recorded in zoological literature and even has been

the subject of detailed anatomical and systematic studies. For use of paleontologists, *N. decorus* could very well serve as a model crinoid.

The aim of this chapter is to present information on the anatomy and morphology of recent crinoids with special emphasis on stalked forms belonging to the Isocrinida, Millericrinida, Bourgueticrinida, and Cyrtocrinida, which best may serve for comparison with similar fossil forms.

The section on anatomy is largely based on literature data, taken from older works on the subject. More recent and full accounts on anatomy have been published by CUÉNOT (1948) and HYMAN (1955). Morphological descriptions are largely based on my own observations. In preparing the text I have been able to study important collections of recent crinoids (Clark collection, U.S. National Museum, Washington; Agassiz collection, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; and the Challenger collection, British Museum of Natural History, London). Financial support for this study was received from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) in The Hague, The Netherlands.

Acknowledgments are due to N. GARY LANE (University of Indiana) and H. WIENBERG RASMUSSEN (Universitet København, Denmark), who critically read the manuscript and made many valuable comments.

New drawings in this chapter are *camera lucida* drawings made by the author *ad natura delicta*. A. HEINE (Amsterdam) prepared the drawings for final publication.

## ANATOMY

### BODY WALL

The body cavity in crinoids is enclosed within a firm, more or less leathery body wall (Fig. 1), which is usually heavily calcified in many parts. Only few openings perforate this wall: mouth and anus as openings for the digestive tract and hydro-pores or ciliated funnels in the interambulacral parts of the tegmen, as openings to serve the water-vascular system.

In parts of the body wall that are not

heavily calcified, this wall consists only of a thin outer **epithelium** of one cell layer in thickness, a layer of **connective tissue**, which gives the wall most of its substance and support, and a thin, inner **coelomic endothelium**, which lines the body cavity. This condition is found in naked tegmens, in lateral parts of the theca between the arms, and at the oral surfaces of arms and pinules outside the ambulacra.

Most parts of the body wall are heavily calcified, however. When skeletal elements

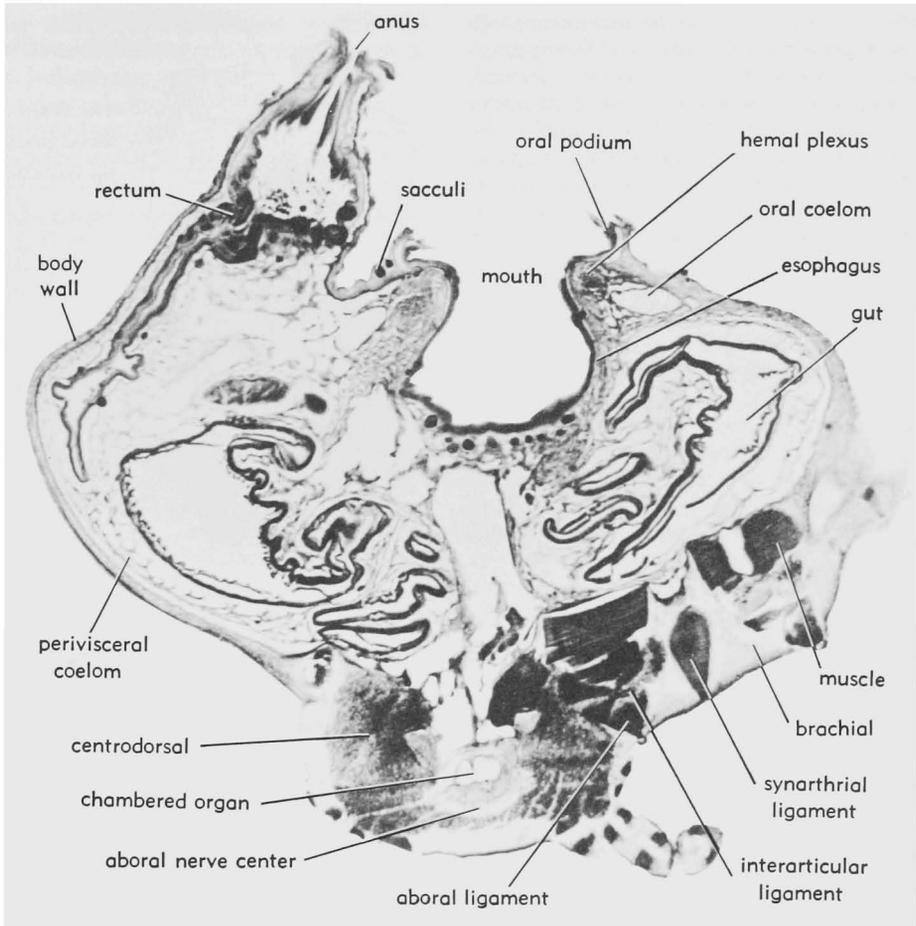


FIG. 1. Vertical sagittal section through theca of *Antedon bifida* [from preparations in the British Museum (Natural History), London] (Breimer, n).

are present, they have partially or entirely lost their epithelial covering over their aboral surfaces. If at all preserved, the epidermis is only a delicate cuticle covering these elements and difficultly separable from the underlying mesenchyme.

Highly differentiated and ciliated epithelia occur in the ambulacra and in the ciliated funnels or hydropores. In the ambulacra a firm and thick **ambulacral epidermis** is formed of very tall, slender cells which serve for support and highly attenuated sensory cells. The ambulacral epidermis has the nuclei of its component cells arranged at several different levels. The hydropores or ciliated funnels in the tegmen possess an epithelium composed of slender ciliated cells.

By far the most important part of the body wall is formed by mesenchyme cells, which may be differentiated into connective tissue, muscles, and elastic fibers (ligaments) or skeleton-secreting cells. Formation of the echinoderm skeleton has recently been studied by OKAZAKI (1960) from sea urchin larvae and by HEATFIELD (1971) from echinoid spines. It is thought that skeletal growth occurs in crinoids in a similar way.

First a rod or spicule of calcite is formed within a skeleton-secreting mesenchyme cell and later this calcitic particle comes to occupy nearly the whole cell. The cell then divides and starts to form a syncytial cell mass, which allows the contained skeletal element to grow. It does not grow as a

solid block, for growth increments are added preferentially in many different directions, so that a crystal meshwork is formed. The syncytial cell mass containing the nuclei occupies the spaces within and around the calcareous meshwork. This mode of growth allows the skeletal element ultimately to assume any shape needed. Each separate element forms a single crystal.

### BODY CAVITY

During individual development of the crinoid the body cavity arises from the larval left and right somatocoels, which—after rotation upon metamorphosis—take an adoral and aboral position, respectively. In the juvenile crinoid the adoral and aboral somatocoels meet along an equatorial plane and form a horizontal septum. Both somatocoels are crescentic in shape, with blind ends meeting at the posterior side, where they form the adoral and aboral vertical mesenteries, respectively. The aboral somatocoel is by far the largest of the two and surrounds the larval enteric sac. During postmetamorphic growth stages it retains this position and grows out as a perivisceral coelom. The smaller adoral somatocoel is situated around the adoral surface of the enteric sac and directly underlies the hydrocoel, to which it closely corresponds in form and position. During the postmetamorphic growth stages it follows growth patterns essentially similar to those of the hydrocoel and ambulacra. It grows out until it definitely takes a subambulacral position in the mature crinoid.

In the mature crinoid two major parts of the body cavity can be distinguished, namely an **adoral or subambulacral** coelomic compartment and an **aboral or perivisceral** coelomic compartment. The total body cavity in the theca is occupied for the most part by the extremely voluminous digestive tract. The aboral coelom is in contact with the aboral body wall and touches some interambulacral spaces of the oral or tegmental body wall. The hydropores or ciliated funnels in the interambulacral parts of the tegmen and lateral body wall open into the aboral coelom. In general, the aboral coelom surrounds the intestine (not the esophagus) and rectum. It is lined with coelomic endothelium and is filled in with numerous

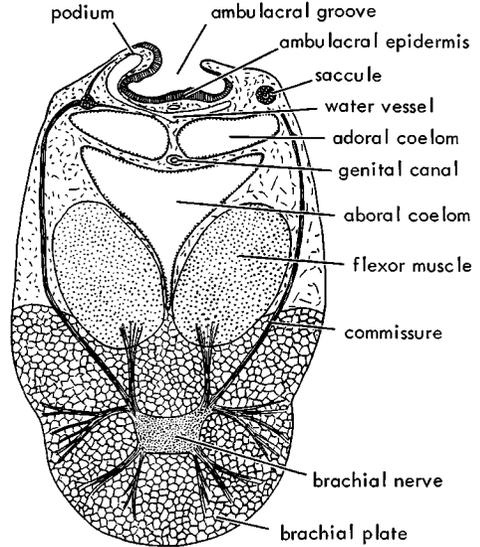


FIG. 2. Transverse section through arm of crinoid (after Hyman, 1955, and Hamann, 1889; from *The Invertebrates* by Libbie H. Hyman, copyright 1955, McGraw-Hill Book Company. Used with permission of McGraw-Hill Book Company).

strands and webs of connective tissue, thus giving it a spongy appearance. It is easily recognizable in anatomical sections. The aboral coelom continues into the arms (Fig. 2) and pinnules as **aboral coelomic canals**. In the pinnules the aboral walls of these canals are provided with typical **ciliated pits**, formed by differentiated endothelial cells, apparently for provisions of some movement in the coelomic fluid or for passage of coelomocytes.

The adoral coelom is distinguishable from the aboral one by its lack of spongy appearance. Some filaments of connective tissue do occur in it, but it is essentially an uninterrupted and unobstructed open space. It is separated from the aboral coelom by membranes of endothelium and connective tissue in which different organ systems (axial, genital, hemal) are developed. These membranes are apparently developed from the larval horizontal membrane between adoral and aboral somatocoels. They do not form a perfect separation of the two major coelomic compartments, for many pores and funnels interconnect the compartments. The adoral coelom has a large central or axial space at the left and an-

terior sides of the esophagus, with an extension to the central axis of the body cavity, just behind the axial organ. This aboral extension of the adoral coelom has erroneously been described by some authors as a separate coelomic compartment known as the axial sinus. From the main central space of the adoral coelom five large **adoral coelomic** canals are formed, everywhere underlying the water-vascular and ambulacral systems. The coelomic compartment is here called subambulacral (subtentacular in older literature) for this reason. The adoral coelomic canals continue in arms and pinnules. In the arm portions the canals are paired by a vertical septum. This septum is not present in the tegminal and pinnular parts of the adoral coelomic canals.

A minor coelomic canal is present between the radial water vessels and the ambulacra, directly beneath the epithelial nerve tract of the ambulacra. It is known as the **hyponeurial sinus**.

Another compartment, also of coelomic nature, known as the **chambered organ**, is found in the central axis of the calyx and in the stalk. It is lodged in a rosette-like structure formed by the basal or infrabasal circlets and is composed of five chambers, which are radially disposed in dicyclic crinoids, but interradially in monocyclic forms. The chambers are formed by mesenteries and adorally end blindly. There is a central strand from which the axial gland arises. Aborally the chambered organ continues into the axial canal of the stalk as a central tube with five compartments around the central cord. The compartments are continuous with the divisions of the chambered organ. At each nodal columnal cirrus canals branch off from the axial canal of the column and extend to tips of the cirri. The chambered organ ontogenetically develops as an evagination of the aboral coelom, from which it becomes entirely separated.

## AMBULACRAL AND DIGESTIVE SYSTEMS

The functions of food gathering and food conveying are carried out by the ambulacra and podia distributed along them. In extant stalked crinoids ambulacra are present on

all of the pinnules, on the arms, and on the tegmen. In certain comatulid species, however, the pinnules are specialized into groups distinguished as oral pinnules (with tactile function), genital pinnules, and distal pinnules. In such forms ambulacral grooves are absent on the oral pinnules and rudimentary on the genital pinnules; only the distal pinnules have well-developed ambulacra and podia. Several comasterid species entirely lack ambulacra in some of the arms, especially those belonging to the *C* and *D* rays.

The ambulacra are typically formed by a differentiated epithelium (Fig. 2), here spoken of as **ambulacral epidermis**, which is the only well-developed epithelium in the crinoid body wall. It consists of two sorts of cells: 1) very tall and slender ciliated cells, which serve for support, and 2) highly attenuated sensory cells, almost hairlike in form with a bulging nucleus. The ambulacral epidermis is fairly thick and has the nuclei of its component cells arranged at several different levels. The epidermis contains numerous mucus-gland cells, which secrete mucus as a conveying medium for the food particles. The ambulacral epidermis is everywhere underlain by a thick nervous layer to which the sensory cells of the epidermis connect.

The ambulacra are everywhere accompanied by the podia (Fig. 2), placed in triads along both sides of the ambulacral grooves. The typical ambulacral epidermis and underlying nerve tract pass laterally onto the adambulacral sides of the podia, which in this way have a thicker epithelium on the inner side than on the outer. Groups of four or five tall attenuated cells project beyond the podial wall to form papillae with presumably a combined glandular and sensory function. Some of its cells are gland cells, secreting mucus as an adhesive for food particles which happen to come to contact with the podia. Nerve and muscle fibrils are also present in the papillae.

The podia or tube feet are arranged in triads, each individual podium of a group differing in length from the others. The longest tube feet are the main food-gathering organs. They possess muscle cells on their adoral sides and are thus able to bend in toward the ambulacrum and pass food particles to the smaller tube feet. The tube

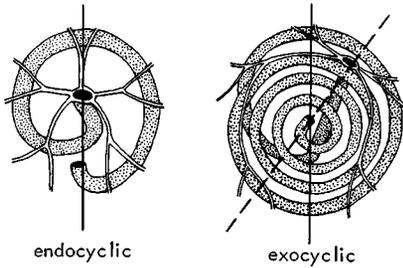


FIG. 3. Digestive systems in crinoids; examples of endocyclic and exocyclic conditions (after Ubaghs, 1953, and Carpenter, 1884a). [Vertical line indicates normal crinoid plane of symmetry; broken line indicates secondary axis.]

feet of intermediate length have muscle cells on their adoral and aboral sides and thus are able to move toward the ambulacra or away from it, receiving food particles from the longer podia and sticking them into the ambulacral groove. The smallest podia have muscles all around their walls and are capable of lateral movement in any direction. They probably serve for conveying food along the ambulacra. The muscle cells in the tube feet are innervated by branches from the hyponereal lateral nerves in the arms and pinnules. The podia embody the terminal branches of the water-vascular system. It is logical to suppose that erection of the podia (which occurs as feeding starts) is brought about by regulation of the water pressure in the water vessels. NICHOLS (1960, 1966) has described the possible mechanism that could be responsible for water-pressure regulation in the water-vascular system (see section on water-vascular system).

The mouth of crinoids usually is placed at the center of the tegmen, this position being defined as **endocyclic** (Fig. 3). In some comasterids, however, the mouth is displaced to a position in the *AB* interray and location of the mouth then is called **exocyclic**. In this condition the anus is placed at the center of the tegmen.

The mouth leads to a long or short **esophagus**, which runs obliquely in an aboral direction under the *C* ambulacrum. The ambulacral epithelium and the underlying nervous layer of the ectoneural system continue down the esophagus (Fig. 4). In this way the esophageal and intestinal epithelia consist of tall attenuated cells, which

are ciliated everywhere in the intestine, except in the rectum. The esophagus is sheathed by a nervous layer and by well-developed circular muscle fibers forming a sphincter around the esophagus. The same is true for the rectum.

In endocyclic forms the esophagus is followed by a voluminous **intestine** of larger diameter than the esophagus, which in part is lobed and plicated. It describes one complete spiral volution clockwise if viewed from the adoral side. The terminal part of the intestine is vertical and forms the **rectum**, which opens through the anus on the tegmen. The intestine has several branched **diverticula**.

In exocyclic forms the digestive tract describes up to four spiral windings or

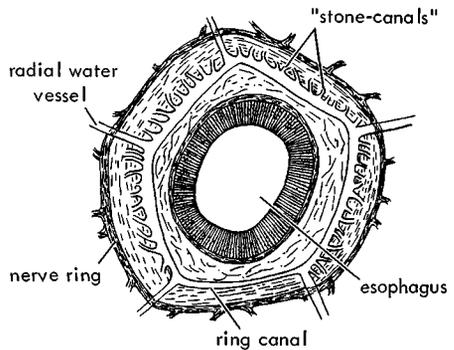


FIG. 4. Ring canal of water-vascular system with "stone-canals" along four sides (after Hamann, 1889).

volutions. Such a digestive tract has the same diameter as the esophagus, is not lobed or plicated and has no diverticula.

The anus may be situated on a special elevation of the tegmen, known as the **anal tube**. This is (frequently reported to be) engaged in rhythmic pulsations by which water is intermittently brought into the rectum and again ejected. The interpretation of this is probably twofold: by water movements the elimination of fecal pellets probably is aided and at the same time a kind of rectal respiration is carried out.

## WATER-VASCULAR SYSTEM

In adult extant crinoids the water-vascular system is internally discontinuous because of lack of a direct connection between its

two component parts: a system of hydropores, mainly located in the tegmen and a system of definite canals everywhere accompanying the ambulacral grooves and podia.

The distribution of **hydropores** in various genera may be different. In primitive forms such as *Rhizocrinus lofotensis* the juvenile condition of five hydropores persists during maturity, one in each interray, that located in the *CD* interray apparently being the original hydropore formed by the axocoel. In this genus the five hydropores are connected with the ring canal by five stone canals.

In stalked as well as nonstalked extant crinoids large numbers of hydropores occur in the four normal interrays and five interbrachial areas (see Fig. 33). Hydropores are positively absent in the *CD* interray in *Neocrinus*, *Endoxocrinus* and *Calamocrinus*. They may be present in narrow zones bordering the posterior side of the *C* and *D* ambulacra in stalked crinoids (e.g., *Saracrinus*), and are reported to occur in the anal tube and arm bases of comatulid genera. The hydropores penetrate the tegmental wall and are lined with a heavily ciliated and very vibratile epithelium (Fig. 5). The hydropores open into the aboral peri-intestinal coelomic compartment.

The central element of the water vascular system is the **ring canal** (Fig. 4). It is circumesophageal in position and directly underlies the tegmen. In perradial position five main **radial canals** originate from it. Also, many small canals or tubes are given off from the ring canal and on four of the interradial sides many (up to 30) so-called **stone canals** emerge. These open into the axial space of the adoral coelomic compartment. In the accompanying illustration (Fig. 4) attention may be called to the lack of stone canals along one interradial side, which presumably is the *CD* interray. Absence of stone canals in one interray coincides with absence of hydropores in the *CD* interray. No correlation exists between the number of stone canals and the number of hydropores in each interray, the latter being far more numerous. The number of hydropores is variable in adult crinoids, ranging from approximately 500 to 1,500. Apparently in many extant stalked crinoids, after reduction of the original posterior

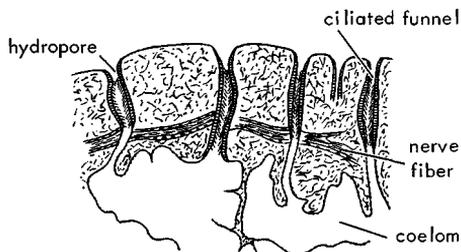


FIG. 5. Section through adoral body wall with ciliated water canals (after Hamann, 1889).

stone canal no additional stone canals and hydropores are evaginated from the posterior side of the ring canal, nor are additional hydropores formed in the posterior tegmental wall.

Adorally, the ring canal gives off many delicate tubes leading into the labial podia surrounding the ambulacral depression around the mouth. Five main **radial** or **brachial water canals** diverge from the ring canal. These canals penetrate into the arms and pinnules, closely accompanying the ambulacra which they immediately underlie, only separated from them by the epithelial ambulacral nerve tract. Where ambulacra are tegmental, the water canals occur immediately beneath the tegmen, following the ambulacral tract. In each arm the brachial water canal has a similar subambulacral position and is situated between the ambulacral groove and the two coelomic canals. The brachial water canal has branches to each of the podia bordering the ambulacral groove, and to each of the pinnules in alternating order. From the pinnular water canal terminal branches lead to the groups of three podia, which are placed in alternating order along the pinnular ambulacral groove. As the number of podial groups is generally the same as the number of side plates or lappets on each pinnular and as side plate numbers per pinnular may vary, individual pinnulars may bear different numbers of podia. Consequently, on each pinnular various terminal water canals are given off to the podial groups in alternating order. Each group of three podia receives one terminal water canal, which branches to become the lumen of each podium.

The wall of the water-vascular canals is made up of coelomic endothelium and

some connective tissue. Circular muscles do not occur in their walls but some longitudinal muscle cells are present. Muscle cells also are found to traverse the lumen of the water canal obliquely. The wall of the water canals may be described as weakly muscled. Apparently it is not capable of much contraction of the canals.

The function of the water-vascular system in crinoids is still subject to some uncertainty. Recently, NICHOLS (1960, 1966) has made new studies on this subject. As the podia or tube feet are capable of contraction by muscular activity, another mechanism is needed as an antagonist to protract them. In echinoderms this mechanism is generally present in the form of a regulation system that controls the water pressure in the tube feet. The radial water canals of crinoids are compartmented for this purpose, and each compartment may be contracted by the muscles traversing the lumen of the compartment. Contraction of the compartment sends water into the tube feet, and makes them protract.

### HEMAL SYSTEM

The hemal system in crinoids is not formed by definite canals, but by many intercommunicating spaces in the filaments and mesenteries of connective tissue which are present in the body cavity. The system is therefore best described as a **blood-lacunar system**. It is only known from anatomical studies. The blood substance is a colorless liquid rich in proteins, which in preparation coagulates and hence becomes visible. It is reported not to possess any typical cells other than coelomocytes.

Surrounding the esophagus, not far from the ring canal, is a **periesophageal plexus** in the form of an irregular network of anastomosing lacunae. From this plexus many branches pass aborally to connect with the intestinal wall. These are absorbing lacunae and are especially frequent along the inner wall of the first half of the digestive tract. The blood lacunae have an intimate relation to the intestinal wall. The strands and webs of connective tissue in which the blood substance circulates is continuous with the connective tissue of the intestinal wall. The same is true for the endothelial covering. The periesophageal plexus sends branches to another circu-

lar plexus of blood lacunae, which is situated immediately beneath the tegmen. This plexus is called the **subtegminal plexus**. Five radially disposed hemal canals are given off from the subtegminal plexus which continue into the arms. The hemal canal is situated in the center of the arm between the two adoral coelomic canals and the single aboral coelomic canal. This canal lodges the genital cord and is so called the genital tube. It is the only part of the hemal system in the arms.

In the posterior (*CD*) interray the periesophageal plexus is connected with the **spongy organ**, which consists of lacunae with much thickened walls, while the lacunar cavities are filled in with many rounded cells, leaving hardly any open space. This organ extends aborally and has an intimate relation with the axial organ, to which it is connected by a network of blood lacunae. In *Neocrinus decorus* it extends aborally all along the posterior side of the axial organ, but in comatulids it covers only the oral part of the gland. In older literature the spongy organ is interpreted as a labial plexus, but its status as an ordinary hemal plexus is doubtful. CUÉNOT interpreted it as a lymphoid organ. The periesophageal plexus also has a direct connection with the axial gland from which it receives a mesh of efferent blood lacunae.

HOLLAND (1970) described the fine structure of the axial organ and the extracellular hemal fluid from *Nemaster*. The gland cells of the glandular tubules of the axial organ have the characteristic fine structure of protein exporting cells and may produce granular and filamentous components of the hemal fluid.

In the literature (CUÉNOT, 1948; NICHOLS, 1962), part of the coelomic canal system is interpreted as a perihemal system. The first to draw attention to the presence of a perihemal system in crinoids was HAMANN (1889). In his view the small coelomic canal between the epithelial nerve band of the ambulacra and the radial water canal is a schizocoelous canal, which he compared to the perihemal canals of asteroids. This canal, termed hyponeurial sinus by HYMAN (1955), in rare cases has been observed to continue into a subtegminal ring canal. Later, CUÉNOT (1948) drew further at-

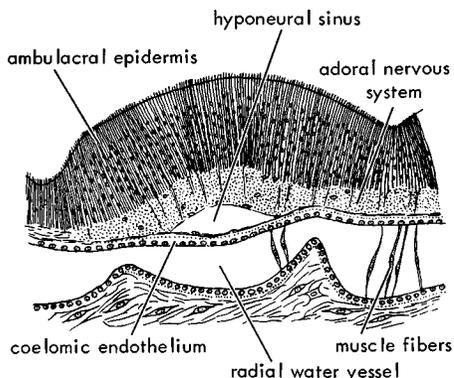


FIG. 6. Transverse section through ambulacrum (after Hamann, 1889).

tention to possible perihemal structures in crinoids. He interpreted the sheath surrounding the genital canal in the arms as a perihemal sheath. He also stated that all the organs traversing the body cavity as the digestive tract, the water-vascular system and the blood-lacunar system are ensheathed. NICHOLS (1962) interpreted these sheaths as perihemal lacunae.

## NERVOUS SYSTEM

The nervous system in crinoids is complex and divisible according to its ontogenetic development, to its position in the adult animal, and to its function.

According to ontogenetic development, two different nervous systems can be distinguished. The first is of ectodermal origin, developed in an early larval stage as a thickening of the ectoderm along the course of the hydrocoel and podia. In juvenile and adult crinoids this nervous system is adorally disposed. It is known as the **adoral** or **ectoneural system**. This superficial nervous system is present as a band of nerve cells and longitudinal fibers just beneath the strongly differentiated epidermis of the ambulacral grooves (Fig. 6). It continues to the internal sides of the podia. It is in contact with the sensory cells in the ambulacral epidermis and the sensory papillae on the podia. The five ectoneural bands coming from the primary arms proceed on the aboral side of the tegmen and meet around the mouth. They continue downward as

an epithelial nerve sheath around the esophagus. In contrast to other echinoderm groups, the ectoneural system is weakly developed in crinoids.

The second nervous system is of mesodermal origin and probably appears very late in ontogeny, as larval stages possess only an ectoneural nervous system. The ontogenetic development of the mesodermal nervous system is poorly known. According to its position in adult crinoids the mesodermal nervous system is divisible into two parts: 1) an **adoral** or **hyponeural system** and 2) an **aboral** or **entoneural system**, which are strongly intercommunicating.

The hyponeural system is located in the connective tissues of the tegmen and arms. Its center is a pentagonal circumesophageal nerve ring in connective tissues of the tegmen. The nerve ring is situated lateral to the circumesophageal rings of other organ systems. From the nerve ring some smaller nerves run to the labial podia on the tegmen. Larger nerves are given off directly from the ring to serve the internal organs, among which are two prominent nerves leading to the anal tube. Ten main nerve branches depart from the nerve ring to the arm bases. They continue in each arm as two longitudinal nerves, located laterally in the connective tissues of the adoral surface of arms and pinnules. These longitudinal nerves innervate the musculature of the wall of the radial water canal and the external sides of the podia.

The entoneural system (Fig. 7) has its center in a compact, cup-shaped, ganglionated nerve mass in the central axis of the body cavity, embedding the base of the chambered organ. A sheath of nervous tissue descends from this mass into the stem surrounding each of the compartments of the axial canal and the coelomic cirral canals. From the aboral cuplike nerve mass ten small trunks are given off, which soon unite in five radial trunks. The five radial trunks are interconnected by a pentagonal commissure lodged in the calcareous bodies of the radials. Five main brachial nerve trunks depart from the edges of the pentagonal commissure, leading into the arms. In each axillary plate this aboral nerve trunk bifurcates. The two trunks produced by the bifurcation are interconnected by one

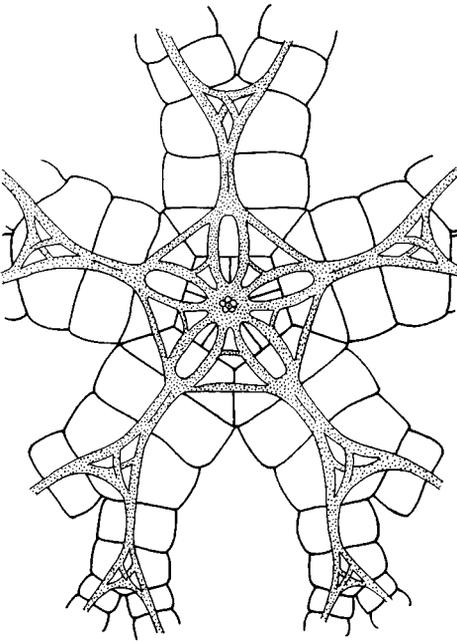


Fig. 7. Aboral nervous system in *Neocrinus decorus* (after Reichensperger, 1905).

transverse commissure and two crossing commissures. The aboral brachial nerve trunk traverses the skeletal elements (brachials) through a nerve canal. This canal has been formed during growth by lateral ingrowth of skeletal material of a deep groove which originally housed part of the coelomic canals of the arm. The aboral brachial nerve trunk has a thickening in the center of each brachial. From this node nerve branches are given off to innervate the articular muscles. Other branches connect the aboral brachial nerve trunk with the orally disposed longitudinal nerves of the hyponeural system. In this way a firm interconnection joins the hyponeural and ectoneural systems.

The entoneural system in crinoids is by far the most important of the three. Experiments have shown that this system is to be regarded as the motor nervous system. The cup-shaped nerve mass in the central axis apparently controls and coordinates the movements of arms and pinnules, stem and cirri, necessary for swimming and feeding. If the aboral nerve center is damaged, movement of arms and cirri stops. On the

contrary, if parts of the hyponeural or ectoneural systems are damaged, no such an effect is produced. A purely sensory function is attributed to the ectoneural system.

HOLLAND (1970) described the fine structure of all constituent cell types in the axial organ of *Nemaster*. The neurons (perikarya and axons) of the axial organ may possibly be neurosecretory, since they are filled with electron-dense granules.

## REPRODUCTIVE SYSTEM

The genital system in crinoids consists of a system of genital cords, located in genital tubes, which are sheathed by genital canals. This system is mainly located in the arms and pinnules. The **genital canal** is situated in the arms between the two adoral coelomic canals and the single aboral coelomic canal at the junction of the horizontal and vertical mesenteries. The genital canal is part of the perihemal system and has many interconnections with the coelomic canals. The genital canal contains a **genital tube** suspended in it by filaments of connective tissue. The genital tube is part of the hemal system and the only blood lacuna in the arms. In the axis of the genital tube is a **genital cord** composed of cells with large nuclei, identical with young genital cells. At the level of each pinnule the genital cord gives off a lateral branch, which has an enormous volume and constitutes a **gonad** or **genital cavity**, occupying almost all of the aboral coelomic space in the pinnule. It is probable that the cells of the genital cords multiply and displace themselves along the genital cords and only arrive at maturity in the gonads, which are rather storage compartments for mature sex cells. In a few crinoids the gonads are lodged in the arms (e.g., *Holopus*) and are exceptionally found in the tegmen, evidently along the tract of the genital cord. Toward the tegmen the course of the genital cords can be traced only with much difficulty. The genital canal meets the subtegmenal plexus but the genital cords are ultimately lost in the meshes of this plexus.

In some comatulid species the gonads are situated in special **genital pinnules**, much inflated structures in breeding time, which more or less completely lose their ambulacra and podia, but in connection with this the

sterile distal pinnules have strongly developed ambulacra and podia. The gonads usually lack an opening to the external medium; only in *Notocrinus* is such an opening present in the testes at the base of the pinnules. Usually the sex cells escape by rupture of the pinnular wall and the eggs are stuck to the pinnules by the secretion of cement glands present as a longitudinal band of mucus-secreting cells on the external side of the pinnular wall. In some species rupture occurs through preformed spots on elevated areas of the pinnules. It is recorded that rupture of the ovarian wall is stimulated by the spawning products of male individuals, thus providing for fertilization immediately after rupture of the ovarian wall. Several Antarctic species are known to brood their eggs. In these species a **brood pouch** or **marsupium** is present on the base of the pinnules, and in them fertilized eggs develop to the pentacrinoid larval stage.

The ontogenetic development of the gonads in crinoids is insufficiently known. Russo (1902) has discovered in the larva of a comatulid the primary gonad, a cellular

network situated in the *CD* interray in the horizontal mesentery close to the primary stone canal. DAWYDOFF (1948) has described a similar primary gonad in the aboral vertical mesentery. From these primary gonads sex cells migrate into the arms and later atrophy. Much speculation is found in the literature concerning the original primary gonad. As the axial gland also appears to arise in the aboral vertical mesentery, this gland is sometimes (PERRIER, 1886-90) interpreted as a sterile genital stolon. REICHENSPERGER (1905) has interpreted the spongy organ of *Neocrinus decorus* as a primary gonad. Speculation on the phylogenetic significance of a supposed single primary gonad in crinoids has spread among textbooks. This primary gonad is believed to be significant in interpretation of a single pore of the *CD* interray of some cystoids and primary crinoids (e.g., *Hybocystites*, *Hybocrinus*, *Porocrinus*). This pore is interpreted as a gonopore on the weak grounds of ontogenetic development of primary gonads in recent crinoids. However, a gonopore is not shown to exist in crinoid ontogeny.

## MORPHOLOGY

### GENERAL STATEMENT

Morphologically the crinoid organism is divisible into several major parts: the stalk or **column**, the **theca** which may be divided into an aboral cup or **calyx**, and an oral membrane or **tegmen**, and pinnule-bearing arms or **brachia**. The crinoid organism consists of a very voluminous body wall and only a relatively small body cavity. By far the largest part of the body cavity is lodged in the theca and only extensions of it consisting of small canals penetrate the stalk, arms, and pinnules. The bulk of the volume of the several internal organ systems is found in the central body cavity of the theca. The crinoid body wall is supported by a voluminous mesodermal endoskeleton, the form of which determines the total shape of the organism. Describing the crinoid form is practically the same as describing the form of its skeleton.

Traditionally the crinoid skeleton has been described as consisting of a primary

skeleton, a secondary or perisomic skeleton, and a visceral skeleton. In this chapter, however, the crinoid skeleton is divided into an **aboral skeleton**, an **adoral** or **perisomic skeleton**, and a **visceral skeleton**.

1) The aboral skeleton comprises elements distinguished as **columnals**, **centrodorsal**, **infrabasals**, **basals**, **radials**, **brachials**, and **pinnulars**. Definition given in this way differs from that of the primary skeleton in that the orals are not included. Also, because adult recent crinoids lack an anal plate or plates, such elements are unmentioned. The new distinction is purely topologic, and not ontogenetic, as the traditional one. Topologic criteria derived from adult crinoid specimens are thought to be best suited for describing crinoid morphology. The aboral skeleton is by far the largest part of the total skeletal mass; as a rule it is always well developed. It is the main supporting skeleton and determines the overall body form.

2) The adoral or perisomic skeleton com-

prises the orals, tegmen plates or scales, ambulacral and adambulacral plates, and interradial and interbrachial plates or scales. Thus defined, the perisome is the adoral body wall, penetrating between the arm bases to complete the central thecal cavity in conjunction with the aboral skeleton. The adoral skeleton is not always well developed. In the Isocrinida the perisome is generally highly calcified and almost completely occupied by skeletal plates or scales, but in the Comatulida the perisome is reinforced only with incoherent calcareous spicules and rods and appears as a leathery body wall.

3) The visceral skeleton is formed by spicules and rods of calcite together with smaller calcareous meshworks found in the connective tissues around the visceral mass. Complete calcification of internal membranes to form structures such as the so-called convoluted organ in some fossil crinoids (e.g., *Teleocrinus*, Miss., N. Am.) are unknown in extant crinoids.

For descriptive purposes we have distinguished between adoral and aboral sides of the crinoid organism. It is agreed with HYMAN (1955) that use of the terms dorsal and ventral for the description of crinoids is conjectural. The position of the mouth in crinoids is always very well observable. In a vast majority of the forms the mouth is located in the center of the tegmen. Hence the mouth is the starting point for considerations on orientation and symmetry.

In describing orientation and symmetry of the crinoid body, it is convenient to distinguish a **central axis**, which is the line connecting the centers of the adoral and aboral skeletons. Through this axis pass five reference planes, each of which is called a **radius**. A radius is expressed in the skeleton by the structures forming a **ray** (see Glossary for definition). Ideally the radius passes through the central axis and the median line of the ray-structures.

Orientation of modern crinoids is usually only possible from the adoral surface, on which mouth and anus are invariably located. The anus, which usually is placed interradially, generally is recognized to indicate the **posterior side**. The ray or radius opposite to it is termed **anterior**. **Left and right sides** of the crinoid then correspond to the left and right sides of the observer if

the tegmen is directed upward. In the system of designations introduced by CARPENTER (1884a), the five rays are termed *A* (anterior), *B*, *C*, *D*, and *E*, respectively, in a clockwise direction when the crinoid is viewed from the adoral side. The anus thus is in the *CD* interradius.

The obvious symmetry of the adult crinoid is **pentaradial**, as is evident from both the aboral and the adoral skeletons. In the aboral skeleton the five radii are expressed by the five prominent series of proximal arm segments, and in the adoral skeleton by the five ambulacra that radiate from the mouth. In aboral view nothing disturbs the pentaradial symmetry because the interradial areas normally are not differentiated.

The posterior interradius can be recognized in aboral view of the larval stages of some recent crinoids (e.g., *Promachocrinus*), where anal plates may exist for some time in postmetamorphic stages of development. It is also known to exist in postmetamorphic growth stages (e.g., *Thaumatocrinus*), where a sixth or posterior "arm" exists in the posterior interradius. In adoral view, too, it is noted that the crinoid symmetry is not perfectly pentaradial, for the anus is situated in one of the interradial areas of the tegmen. This disturbs the pentaradial symmetry and in fact gives the organism a **bilateral symmetry**. This is the original type of symmetry in crinoids, since embryonic growth stages lack any trace of pentaradial symmetry. During the larval growth stages a strong pentaradial symmetry is steadily imposed on the original bilateral symmetry. In the adult crinoid bilateral symmetry is expressed by a sagittal plane through the *A* radius, mouth, anus, and aboral pole of the calyx. This plane is known as the **crinoid plane of symmetry**. The symmetry pattern described is normally present in representatives of the orders of the stalked crinoids and also in many Comatulida.

Two marked deviations from the normal crinoid plane of symmetry are known. The first is represented by the comatulid family Comasteridae. The mouth is excentric in these crinoids and displaced some distance in the direction of the *AB* interradius. Consequently the radius opposite to it is modified. In this way a symmetry plane is created which is at 36 degrees to

the normal crinoid plane of symmetry. The second aberration in symmetry is exemplified by the genus *Holopus*. In this form the five arms are unequally developed. Two small arms form the so-called **bivium** and the three larger arms are clustered to make the **trivium**.

In paleontology, morphological descriptions of crinoids conventionally are organized in the order of the major morphological parts of the organism: stem, calyx, tegmen, arms, and pinnules. In zoology, it is hardly desirable to follow this arrangement, since major morphological parts—very well defined in fossil crinoids—may not be differentiated or may even be non-existent in recent crinoids. The stem is not present in most adults of the latter group, since all comatulids lack it. Also, the calyx is frequently very difficult to identify in recent crinoids, for such well-differentiated calices as characterize *Camerata* and *Flexibilia* are absent. The only recent crinoid having a well-marked calyx as well as a tegmen, together forming a complete skeletal case, is *Calamocrinus diomedae*. The radials in this form are specially differentiated to form the largest part of the calyx, and the orals are preserved to form the major part of the tegmen. The spacious theca thus formed has the same rigid nature as is found in *Camerata*. Commonly the radials—and in some crinoids the orals—are the essential components of a theca. Good development of the radials—and to a lesser degree the basals—does not exist in the *Isocrinida* and the *Comatulida*, but may be found in the *Millericrinida*, *Bourgueticrinida*, and the *Cyrtocrinida*. Hence calices are identifiable in the three last-mentioned groups, but a tegmen is hardly developed and a theca still poorly defined. In the comatulids a theca is found, composed of a more or less inflated adoral membrane or tegmen, which is usually not calcified, sitting on the central part of the aboral skeleton, thus providing the necessary space for the voluminous digestive tract. Comatulids are crinoids which almost exclusively are composed of their arms.

In this chapter morphological descriptions are arranged according to location of the elements in the aboral and adoral skeletons.

## ABORAL SKELETON

### COLUMN

In most crinoids other than extant forms, the stem or stalk, designated as the **column**, is a very characteristic part of the body. It serves the purpose of fixing the animal to the sea bottom or to any available or suitable object that might serve as a substrate. For example, telegraph cables are sometimes found to have crinoid specimens attached to them.

The column is composed of many different skeletal elements called **columnals**. Some of these may bear short and unbranched appendages named **cirri**. Such cirrus-bearing columnals are termed **nodals**, in contrast to the non-cirrus-bearing **internodals**. The cirri, like the stem, are supported by a row of skeletal pieces, called **cirrals**. Both the stem and the cirri are pierced by an axial canal, containing extensions of the coelom (**chambered organ**) and the aboral nervous system. Columnals and cirrals are bound together by bundles of elastic fibrils or **ligaments**, which provide the column and cirri with a degree of flexibility. Muscles are entirely absent in crinoid stems and cirri.

The distal extremity of the stalk has special modifications for fixation to the bottom or a substrate. Primarily—and even ontogenetically—attachment is obtained by a disclike columnal, which may be retained during further life as an **attachment disc** (e.g., *Phrynocrinus*). In some genera (e.g., *Democrinus*, *Rhizocrinus*) the distal columnals bear special rootlike, unbranched appendages for fixation (Fig. 8,1). These are named **radicular cirri**. In the *Isocrinida* (e.g., *Neocrinus decorus*) the normal cirri may also serve for attachment. The British Museum (Natural History) in London has a specimen attached to a telegraph cable with its cirri. CARPENTER (1884a) figured the terminal part of a stem of *Hypalocrinus naresianus* with something like an attachment disc (Fig. 8,2). A very special way of attachment occurs in *Holopus*, for it is cemented to rocky substrates by means of its highly modified basal and radial circllets, which form a sort of foot. Permanent attachment to the bottom is abandoned in the *Comatulida*. These crinoids may freely

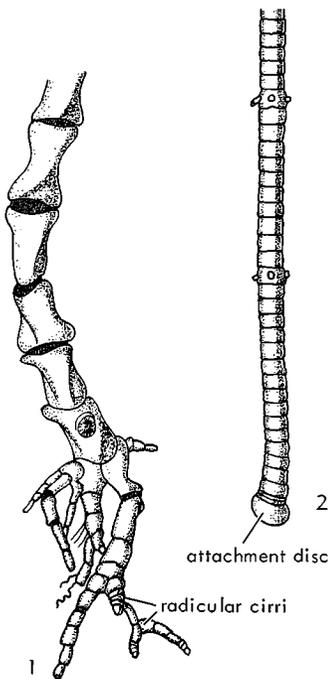


FIG. 8. Mode of attachment of crinoid columns. —1. Radicular cirri of *Rhizocrinus lofotensis* (Breimer, n).—2. Attachment disc of *Hypalocrinus naresianus* (Carpenter, 1884a).

swim, crawl, or creep with aid of the arms, but throughout most of their lives they are sedentary, fixing themselves to the bottom or a substrate by their cirri or even by some of their arms (e.g., in some comasterids).

One may confidently expect that, at least ontogenetically, a stalk occurs in all crinoids. Development of a stalk is known to occur in the ontogeny of the non-stalked feather stars (e.g., *Antedon*, *Pro-machocrinus*). In these crinoids the juvenile stem is cut off by autotomy (except in *Thiolliericrinus*), but is preserved in all other recent crinoids.

Insofar as known, the column is a truly primary organ which develops very early in crinoid embryology. The first stem joint (columnal) is formed directly after the left somatocoel has assumed its aboral position by rotation of the internal organs. This first columnal is located aborally to the basals. As a rule, every new columnal is introduced by becoming inserted between

the basals (or infrabasals) and the next preceding stem joint. Insertion of new columnals occurs regularly one after another, so that each individual columnal assumes a more distal position in the stalk as it grows.

Mature development of the stalk may produce quite different products. Among recent stalked crinoids two types of stalks are distinguished and discussed below: 1) a very simple type, present in the Bourgueticrinida, and 2) a much more complex one in the Isocrinida.

The simple type of stalk observed in the Bourgueticrinida, an order containing primitive, delicate, and simple-stalked crinoids, consists of simple elements, all more or less alike. They become introduced in the stalk as described above. The newly formed columnals in the proximal part of the stalk, adjacent to the calyx, have undifferentiated

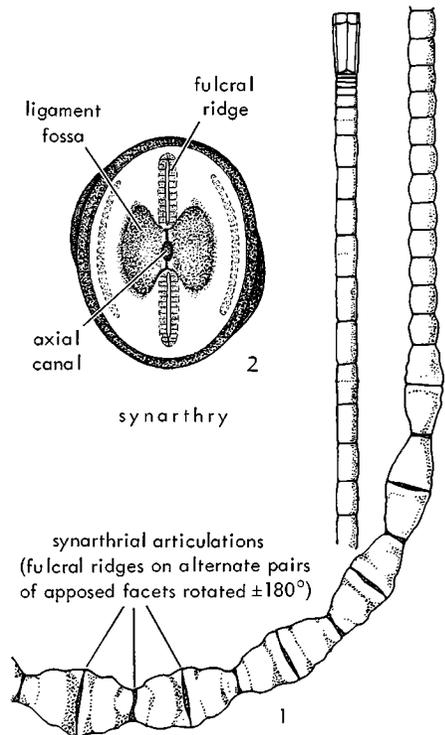


FIG. 9. Growth and scheme of columnar synarthries.—1. Column of *Naumachocrinus hawaiiensis*, with columnals united by synarthries (after Clark, 1915).—2. Synarthrial joint face (schematic) (after Carpenter, 1884a).

cylindrical forms. The full-grown columnals in the distal part of the stalk have undergone a certain differentiation in form. During its individual growth each columnal adapts its form to the relatively enormous development of the elliptical articular surfaces (Fig. 9). The stem growth is confined to insertion of more columnals if needed. The stem does not expand very much in diameter during growth. Its distal part is produced in radicular cirri or it terminates in a calcareous plate. The bourgueticrinid type of stalk normally lacks differentiation into nodals and internodals and is generally devoid of cirri.

Columnal articulation in the Bourgueticrinida is entirely ligamentary and non-muscular. Some proximal columnals may have closely fitting interfaces, connected with very short and few ligament fibers. Such elements are said to be united by **synostosis**. The regularly occurring type of articulation in the Bourgueticrinida is named **synarthry**. Columnals united by synarthrial ligamentary articulation have typically elliptical articular surfaces, the longer axes of which are placed at different angles to one another on the proximal and distal faces of each individual columnal. The articular surface itself is **bifascial**, for a median fulcral ridge separates two fossae that lodge the ligament bundles. Synarthrial articulation allows differential movement of the columnals in two directions. The stem of the Bourgueticrinida is able to accommodate to almost every passive and horizontal movement to which it is exposed, especially in such cases where the synarthrial articulations are placed at various different angles along the length of the stalk.

Exceptionally, nodals occur in the stems of some Bourgueticrinina (e.g., *Monachocrinus*). Where present, they display no regular distribution along the stalk and the cirri which they bear may be deciduous.

A complex type of stem is developed in the Isocrinida (e.g., *Neocrinus*). The complication consists in differentiation of the columnals into nodals and internodals and in their different mode of growth. The nodal columnals are placed at regular intervals along the stalk, closely spaced near the crown but more distant from one another away from the crown. The distances be-

tween successive pairs of nodals in mature parts of the column may be subequal or they may increase distally. The stem may attain great length, with nodals normally bearing a cirlet of five cirri, but some with cirri reduced to two, or three, as in *Endoxocrinus alternicirrus*. The cirri fit movably into sockets on sides of the nodals. They are composed of 20 to 50 cirrals, all more or less alike, cylindrical or elliptical in section and connected by simple ligamentary articulations. Cirri of the Isocrinida are known to assist in attachment of the crinoid. Unlike some comatulid cirri, they are smooth sided. Fixation to the bottom in isocrinids takes place in juvenile specimens through a terminal attachment disc (Fig. 8).

The growth of the isocrinid stem is more complex than in stalks of bourgueticrinid type. Nodals are introduced in the stem just below the lowermost plate cirlet of the theca. Series of internodals are intercalated between the nodals. This occurs as follows. Between two cirrus-bearing columnals, which thus are recognizable as nodals, one internodal is introduced as a primary internodal (Fig. 10). Soon, secondary internodals are introduced between the nodals and the primary internodal. Tertiary internodals then are inserted next above and below the secondary internodals, quaternary internodals above and below each of the tertiary internodals, and so on until a characteristic number of internodals is formed. The nodal and contiguous suc-

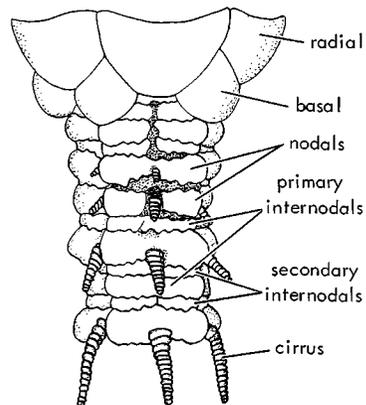


FIG. 10. Growth zone in proximal part of column of *Neocrinus decorus* (Breimer, n).

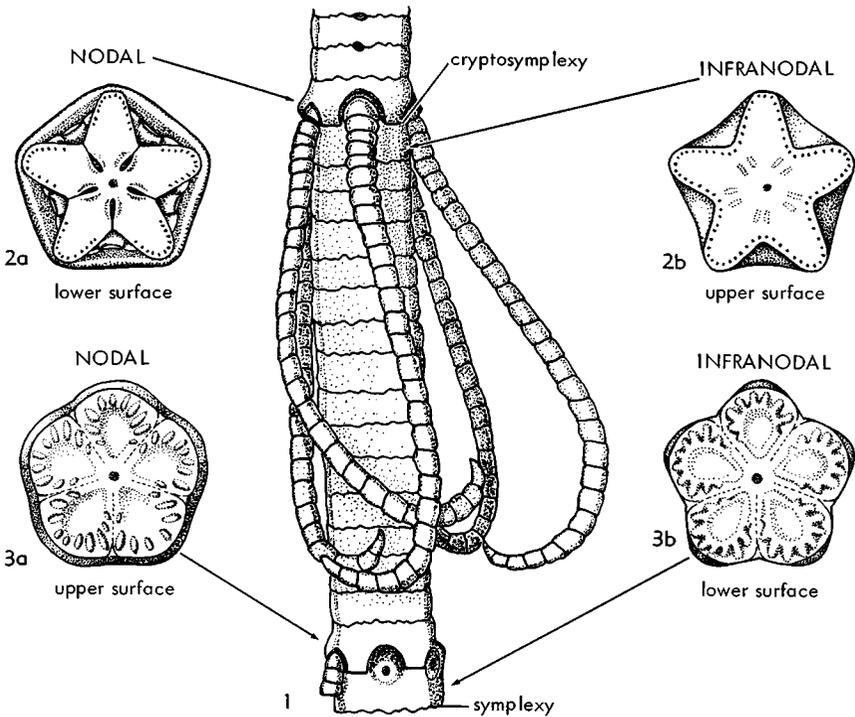


FIG. 11. Portion of adult column of *Neocrinus decorus* with schematic enlargements of columnal articular facets (Breimer, n).

1. Complete noditaxis consisting of nodal with attached cirri (3rd columnal from top) and 15 subjacent internodals, uppermost of which is classed as infranodal.
2. Cryptosymplexy between nodal (2a) and infranodal (2b).
3. Symplexy at upper surface of nodal (3a) and lower surface of infranodal (3b).

cession of internodals on the proximal side of the nodal are defined as a **noditaxis**. The number of columnals in successive noditaxes is a constant character in most isocrinid species, among which all internodals in a full-grown noditaxis are similarly pentagonal in transverse outline and subequal in size. In still incomplete noditaxes in the proximal part of the stem the internodals show readily seen differences in height, and to some extent in diameter, indicating their order of appearance between the nodals.

The articular facets of isocrinid-type columnals are all nonmuscular and ligamentary. Two types exist (Fig. 11). 1) One type of ligamentary articulation occurs between a nodal and the internodal next above it, and between internodals; they are of a type called **symplexy**. On one joint face culmina (ridges) interlock with crenel-

lar grooves on the opposite joint face, marked externally by crenulate sutures. This type of articulation allows very little movement between the columnals so united. Consequently the stem in the isocrinids is rather stiff and only capable of gentle bending. 2) The other ligamentary joint faces between a nodal and the internodal next below it, called **infranodal**, articulate as a synostosis, frequently, but incorrectly, indicated as a **syzygy**. Externally the synostosis is marked by a straight suture between nodal and infranodal. The synostosal connection allows nodal and infranodal to have moderately flexible differential movement in all directions.

A very special type of ligamentary articulation between columnals is found in *Ptilocrinus brucei*. Its cylindrical columnals are united by ten ligament bundles, located in

niches in the intercolumnar sutures (Fig. 12). These bundles are not situated between the joint faces, but are located near the outer edge of the columnals and, hence, fully exposed to the exterior. They provide the stem a considerable degree of flexibility. The columnals of *Ptilocrinus* are formed by five to ten different segments (according to the species) and in further growth these merge into a single plate as they assume positions in the distal part of the stalk.

### PROXIMALE AND CENTRODORSAL

It was a hypothesis of CLARK (1915a) that the stem of all recent and Mesozoic crinoids possesses a skeletal element known as the **proximale**, or a structure strictly homologous to it. The proximale normally is the last columnal to be formed and, as no further columnal formation occurs, it becomes intimately attached to the calyx by a union exactly similar to that between basals and radials (synostosis). The proximale primarily denotes maturity of the column and the completion of stem growth. It takes the shape of the dorsal part of the calyx and assumes the function of a centro-dorsal plate. The enlargement of the proximale affects also the columnal just below it, the proximal face of which, becomes closely approximated to the distal face of the proximale, uniting with it in exactly the same way as the proximale unites with calyx plates. This union is known in zoological literature as the "stem syzygy," but the union between the plates in reality is a synostosis. The nodal plates of the Isocrinida are interpreted by CLARK as reduplicated proximales, having the same synostosomal connections with the infranodals as the proximales have with the underlying columnals.

Though interesting, CLARK's hypothesis is conjectural. The proximale may indeed denote the end of column formation, itself being the last columnal formed (as is said of *Phrynocrinus*). In the Isocrinida no end of growth in the stem seems ever to occur. No single specimen of an isocrinid, to my knowledge, has ever been found with a fully developed noditaxis immediately beneath the lowermost thecal circlet. If CLARK's hypothesis were right, a single isocrinid noditaxis would be homologous to a complete stem in the Millericrinida, and

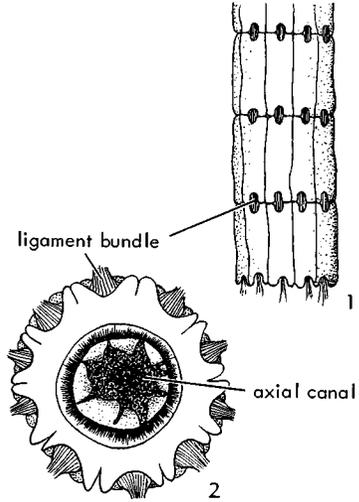


FIG. 12. Column of *Ptilocrinus brucei* (Breimer, n).—1. External aspect of few columnals, showing ligament bundles.—2. Interarticular face of columnal with axial canal and ten peripheral ligament bundles, enl.

Bourgueticrinida, which remains to be seen. Theoretically, it is also possible that the proximale is ontogenetically not the last but the first columnal to be formed, retaining its original contact with the basals and after it all other columnals are formed successively.

Adult comatulids, after shedding their juvenile stalks, are characterized by the presence of a skeletal element called **centrodorsal**: a huge hemispherical or conical plate at the aboral pole of the skeleton commonly provided with a high number of cirri. Ontogenetic evidence from *Antedon* seems to suggest that it originates as a single element and is the modified topmost columnal of the juvenile pentacrinoid stalk, no other elements from the column entering its construction. In this interpretation the centrodorsal is supposed to be homologous with the proximale of other crinoids. However, phylogenetic evidence from fossil comatulids (see RASMUSSEN's section on Evolution of Comatulida, this *Treatise* volume) seems to suggest that the conical centrodorsal may be composite and formed by several nodals, which are articulated and not fused. The continued formation of new parts with cirrus sockets and cirri at the upper edge of the centro-

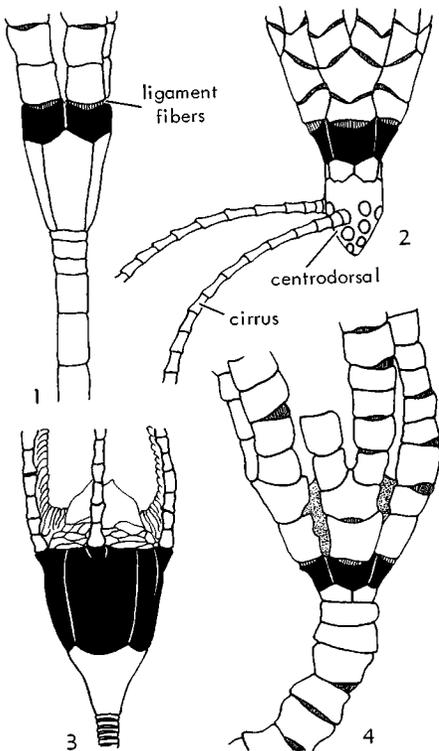


FIG. 13. Radial and basal circlets in various recent crinoids (radials solid black).—1. *Democrinus conifer* (Breimer, n).—2. *Atelecrinus anomalous* (after Clark, 1915a).—3. *Hyocrinus bethellianus* (after Carpenter, 1884a).—4. Presumed *Zeuctocrinus* from Antarctic (Breimer, n).

dorsal seems to correspond to the normal proximal insertion of new nodals at the top of the column, although these parts in most recent comatulids are fused with the centrodorsal.

LUDWIG (1877) showed that on the upper or adoral surface of intact centrodorsals of *Antedon* there are five radial depressions lodging the ends of five blind, radial, coelomic sacs extending from the coelom. A. M. CLARK (1973a) found for some fossil and recent comatulids that these coelomic extensions may completely penetrate the centrodorsal.

### INFRABASALS

In the fossil crinoids the proximal cycles of plates in the aboral skeleton—*infrabasals*, *basals* and *radials*—are involved in the for-

mation of a well-defined aboral cup or calyx. Contrary to most fossil crinoids, recent forms only exceptionally develop an aboral cup. It is well defined in some primitive genera (e.g., *Calamocrinus*; *Holopus*; *Hyocrinus*, Fig. 13,3; *Ptilocrinus*) and of sufficient extent to enclose the entire visceral mass. Among isocrinids the aboral cup (Fig. 10) is nothing but a platform supporting only the central portion of the visceral mass. In the comatulids an aboral cup is altogether absent. The visceral mass is supported by the centrodorsal and by the proximal parts of the arms, rather than by the radial and basal circlets.

The *infrabasals* of crinoids normally form a closed circlet of five small plates at the aboral pole of the theca. They are disposed in radial position and rest upon the top-most columnal. In later fossil and recent crinoids the *infrabasals* are greatly reduced and functionless, or altogether absent. By application of the Law of WACHSMUTH and SPRINGER the recent crinoids are shown to be *dicyclic* and it is assumed that *infrabasals* are normally present in juvenile growth stages but become resorbed during later ontogeny. For this reason the recent crinoids lacking *infrabasals* are termed *cryptodicyclic* or *pseudomonocyclic*.

*Infrabasals* have been conclusively demonstrated to occur in some Comatulida (e.g., *Antedon*, *Promachocrinus*) but only as transitory skeletal elements in the juvenile growth stages. *Promachocrinus kerguelensis* has five *infrabasals*, which for some time in the ontogeny are large and well developed. In postmetamorphic growth stages the greatly reduced *infrabasals* become concealed by the proximale and finally either fuse with it or atrophy. This condition occurs in all recent comatulids in which *infrabasals* have been observed. The large plate formed by the coalition of *infrabasals* with the proximale therefore in reality might be a double structure.

Among the Isocrinida *infrabasals* are present in some Mesozoic forms, but as a rule, they are absent in recent adult isocrinids. They are stated (CLARK, 1908a) to be rudimentary in *Metacrinus*. In the extant Millericrinida, Bourgueticrinida, and Cyrtocrinida no evidence whatever of the presence of *infrabasals* is found and also

no evidence that they ever existed in any of their ancestors. Since these crinoids have stems with circular outlines, without nodals and nodal cirri, application to them of the Law of WACHSMUTH and SPRINGER is impossible. Strictly speaking, these crinoids can only be called **monocyclic**, rather than pseudomonocyclic or cryptocyclic.

### BASALS

The basals are primarily five in number, forming a cirlet near the aboral pole of the theca between the cirlet of infrabasals and the cirlet of radials, with both of which they alternate, being interradial in position. The basals have synostosomal sutural contacts with both infrabasals and radials. In nearly all recent crinoids the basals are modified in some way. In some genera they are well developed, in lateral contact with one another all around the basal cirlet, forming a fair portion of the calyx (Fig. 13,1,3). In *Hyocrinus* and *Ptilocrinus* their number is reduced to three. In *Democrinus* (Fig. 13, 1) the basals may be greatly elongated, forming the largest part of the calyx; they may be more or less fused together showing irregular or weakly defined interbasal sutures. The recent isocrinids generally have an interrupted basal cirlet, the basals are externally visible only as five swollen triangular plates between the aboral parts of the radials (Fig. 10). Only a few isocrinid genera possess a laterally uninterrupted basal cirlet (e.g., *Annacrinus*, *Hypalocrinus*).

Among recent comatulids the Atelecrinidae are the only ones in which the basals persist as normal basals instead of becoming modified. They are visible externally (Fig. 13,2). In all other recent comatulids the basals in the adult become metamorphosed into a peculiar plate, termed the **rosette** (Fig. 14,3). This element is an internal centrally perforated calcareous disc or diaphragm covering the cavity of the centrodorsal. The structure is decagonal in outline and has five triangular processes directed to the sutures between the five radials, interradial in position; also, it bears five spoutlike processes in radial position. The interradial processes of the rosette may connect with five rodlike structures, known as **basal rays** (Fig. 14,1), lying on the oral

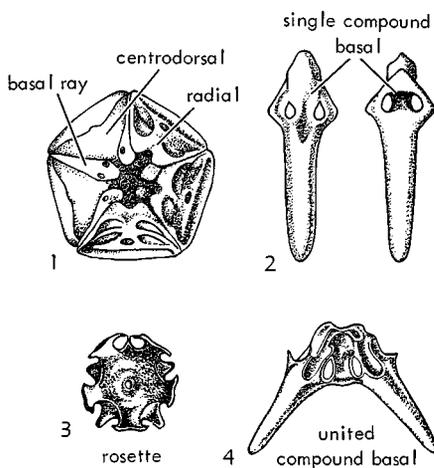


FIG. 14. Basal structures of comatulids (after Carpenter, 1884a).—1. Ventral view of centrodorsal with basal rays and three radials in place. —2. Two single compound basals.—3. Ventral view of rosette.—4. Side view of united compound basal.

surface of the centrodorsal in interradial position. In some genera the rosette can be seen at the external surface between the radials and the centrodorsal. If a basal ray unites with an interradial process of the rosette a single compound basal may be formed (Fig. 14,2). Two basal rays may fuse with two interradial processes from the rosette to form a united compound basal (Fig. 14,4).

### RADIALS

Regularly crinoids have five **radials** arranged in a circle in the cup. The radial cirlet may be interrupted by primary interradials and by an anal plate, as in *Thaumatoocrinus*. The radials alternate with the basals and are connected to them with sutural contacts of synostosomal type. Each radial is followed by a series of brachial plates, with the first of which it has a muscular articulation. Traditionally the radials have been considered as first brachial plates, but in modern work they are more frequently regarded as calyx plates. Probably, they are both. In stalked crinoids they may indeed be very large (e.g., *Hyocrinus*, Fig. 13,3) and substantially contribute to the formation of an aboral cup. In the comatulids the radials compose the

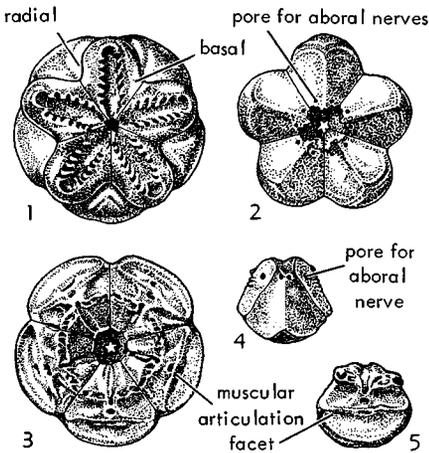


FIG. 15. Structure of the radials in *Neocrinus decorus* (after Carpenter, 1884a).—1. Lower surface of radial and basal circlets showing stem impression.—2. Upper surface of basal circllet showing basal-radial facets.—3. Upper surface of radial circllet showing straight muscular articulation on distal facet of radials.—4. Lower facets of radial.—5. Upper face of radial.

only circllet of plates forming an aboral cup in the adult stage. As the basals are modified into a rosette, the radials are in contact with the centrodorsal; this contact is also a synostosis.

In two genera of the comatulids, *Pro-machocrinus* and *Thaumatocrinus*, multiplication of radials occurs; besides the five regular radials an extra set of five radials is formed, giving the adult crinoid ten radials, all of which are alike and each bearing one arm. In the early larval stages of these crinoids only five regular radials occur in the usual radial position. At a later stage in ontogeny narrow, linear inter-radial plates are introduced between the "radial radials." These elements develop into plates morphologically indistinguishable from the five regular radials. They are "interradial radials" or **pararadials**.

The internal surfaces of each radial typically shows five small, rounded openings leading to the interior and serving for passage of the chief cords of the aboral nervous system (Fig. 15,2,4). A pair of openings is present also on the lower sides of the radials for reception of the interradian nerve trunks from the basals; the lateral sides of

the radials have one opening for passage of the radial nerve commissure to the adjoining radials and the upper articular surface of the radial has a large central canal, just oral to the transverse ridge, for passage of the radial nerve trunk to the brachials.

The upper facets of the radials bear complicated articular facets to which the lower ends of the first brachials are joined (Fig. 15,3,5). These facets may have different positions on the radial. They may be inclined at an angle of  $45^\circ$  to the polar axis of the animal, being trapezoidal or even triangular in shape. In comatulids they may even be parallel to the polar axis and become practically oblong. The articular facets of the radials represent what is known as **straight muscular articulation**. This may serve as a basis for consideration of all articulations between the brachials.

The articular facets are divided by a more or less prominent ridge, which extends transversely across the joint face. It serves as the fulcrum upon which the motion at the articulation is accommodated. The ridge is known as the **fulcral ridge**. Just adoral to it the **central canal** is found. Aboral to the fulcral ridge is an unpaired **aboral ligament fossa** lodging the extensor ligament bundle, which in articulation antagonizes the flexor muscles. Near the adoral margin of the articular facet a pair of **adoral muscle scars** is located, lodging the flexor muscles. Between the adoral muscle scars and aboral ligament fossa a pair of **interarticular ligament fossae** is present. The straight muscular articulation is chiefly characterized by its internal bilateral symmetry. Marked asymmetries may occur in the muscular articulations, mainly due to unevenness of the interarticular ligaments.

#### ANALS AND "INTERRADIALS"

Adult recent crinoids normally lack any plate or plates in the posterior interradius or other interradii. The pentagonal symmetry is not disturbed by differentiation of the posterior interradius. In exceptional cases interradianly disposed skeletal elements are found separating the radials; these are not true perisomic plates, but probably belong to the aboral skeleton. In juvenile growth stages of various comatulids anal plates are known to occur. Gen-

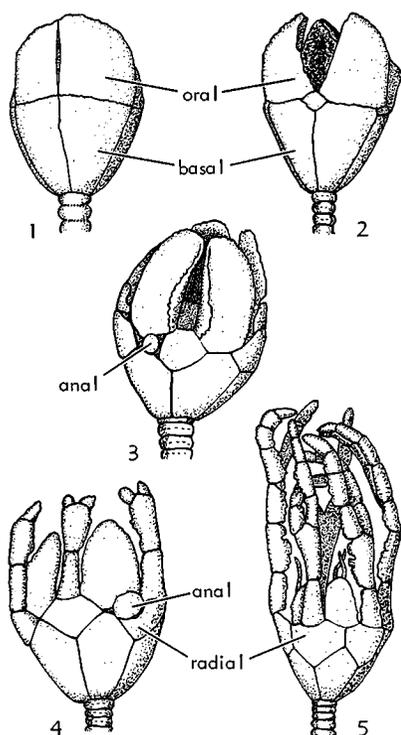


FIG. 16. Transitory development of anal plates in early ontogeny of *Hathrometra proluxa* (after Clark, 1915a).—1-3. Successive early to late cystidean stages.—4-5. Early and subsequent pentacrinoïd juvenile stages.

erally they never persist, but are resorbed before maturity.

In the pentacrinoïd stage of comatulids (e.g., *Antedon*, *Comaculia*, *Comactinia*, *Promachocrinus*, *Thaumatocrinus*) an anal plate occurs for some time in the posterior interradius between the *C* and *D* radials (Fig. 16,1-5). From the ontogenetic development of *Promachocrinus kerguelensis* it is known that this anal plate appears before any of the radials is introduced. The *C* radial appears soon after the anal plate at its right side. The radial grows much faster than the anal plate so as to extend partly beneath it. The anal plate then is pushed out of the radial circlet as the *C* and *D* radials establish lateral contacts. After extrusion the anal plate is resorbed.

CLARK (1915a) concluded that the first-

formed anal plate is homologous to the radial of fossil crinoids and not to anal *X*, as was the traditional interpretation of his days. BATHER (1915) and MORTENSEN (1920), however, interpreted the first-formed anal plate as the true *C* radial pushed leftward. Eventually this was replaced by a secondarily formed new plate which, in their view, took the form and place of a true right posterior (= *C*) radial and assumed its functions. Such a horizontal replacement of one radial by another is entirely unknown from crinoid paleontology. In a modern interpretation of fossil inadunates (PHILIP, 1965), however, the *C* radial and adjoining radial are interpreted as superradial and inferradial, respectively. In a phylogenetic succession of inadunate genera the *C* inferradial may become entirely excluded from the aboral cup. It seems reasonable to explain the two plates successively formed in the posterior interradius of the comatulids as homologues of the infer- and superradials of fossil crinoids.

If the first-formed anal plate of some extant crinoids is to be interpreted as the morphological equivalent of an inferradial (radial), an anal *X* should be expected to occur also. CLARK (1915a) found the anal *X* and the radial side by side between the *C* and *D* radials in juvenile pentacrinoïd growth stages of *Promachocrinus kerguelensis*. A large, modified, posterior interradius (anal *X*) does not exist in adult recent crinoids. Interradial plates are known, however. These may occur in all five interrays with exactly the same degree of development, or all five are absent; a plate in the posterior (*CD*) interrays alone never occurs.

In the juvenile pentacrinoïd growth stage of *Antedon bifida* five interradians develop between the orals and the basals, separating the radials from each other all around the aboral cup. The one in the posterior interradius may be the homologue of the anal *X* of fossil crinoids. Interradial plates ordinarily do not develop, but if they appear, are soon resorbed. In *Promachocrinus* and *Thaumatocrinus*, however, they increase in size as the radials move farther and farther apart and ultimately they assume the characters of radials adjoining them. These interradians develop into pararadials and

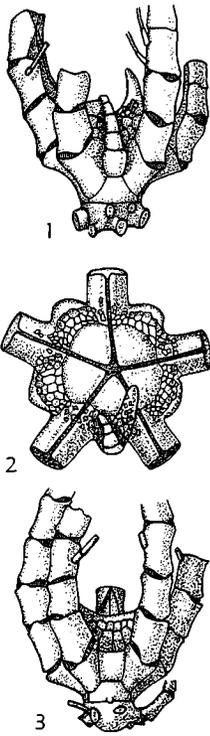


FIG. 17. Interrupted radial circling in six-ray juvenile stage of *Promachocrinus abyssorum* (after Carpenter, 1884a).—1. Side view of CD interray with posterior armlet (center).—2. Oral aspect of calyx.—3. Interradial aspect showing primary interradials in contact with basals.

give rise to a series of plates which form arms in no way distinguishable from those arising from the true radials. In these ten-rayed genera, however, armless interradials may occur and such plates appear as simple interradials separating the radials. Commonly six-rayed forms are found among representatives of these otherwise ten-armed genera. Moderately numerous individuals of *P. kerguelensis* are six-rayed, the extra ray being located between *C* and *D* rays, resting on an anal *X*. The other interradials either have been resorbed or suppressed, as in five-rayed genera. The interesting crinoid described by CARPENTER (1884a) as *Thaumatoocrinus renovatus* (Fig. 17,1-3) was reinterpreted by CLARK (1915a) as such a six-rayed form of the ten-armed species *P. abyssorum*, with which it was found associated. The posterior "arm" is the first

to be formed among the pararadial arms, but apparently development sometimes does not proceed beyond this stage.

## ARMS

### NUMBER AND COMPONENTS

Normally, the arms of recent crinoids are densely pinnulated complex structures that primarily serve the function of feeding. For this purpose a structure of ambulacral grooves is developed on the adoral sides of the arms and pinnules. The microorganisms on which crinoids feed are caught by podia bordering the ambulacra. Only secondarily have the arms assumed other functions than feeding and then special means for carrying out the other functions have been adopted.

An important secondary function of the arms in recent crinoids, found exclusively in the nonstalked feather stars, is locomotion, either by swimming or creeping. Antedontid comatulids have reasonable swimming capacities, in which the arms play a main role. In the comasterid comatulids cirri are absent and the rather clumsy arm structure is specially adapted for their creeping mode of locomotion. In temporary fixation, the posterior arms are used; these are devoid of an ambulacral groove, but do have genital pinnules.

The number of arms in extant crinoids is extremely variable. Some forms have only five simple arms, whereas multibrachiate forms may possess no less than 200 free arm ends. No matter what may be the number of free arm ends, the arm bases are practically always laterally in contact because of their incorporation in the theca. The tegmen is situated at a fairly high level above the radials. Since the tegmen is flexible and the arm bases themselves have flexible connections, the arm bases are not included into a rigid calyx, as in the camerates.

Arms of crinoids are supported by skeletal elements located in longitudinal series all along the arm, such elements being termed *brachials*. Inasmuch as the arms commonly divide in several places, the brachials constituting various division series (called *brachitaxes*) are given ranking designations (e.g., **primibrachs**, **secundibrachs**, **tertibrachs**, etc.). The number of

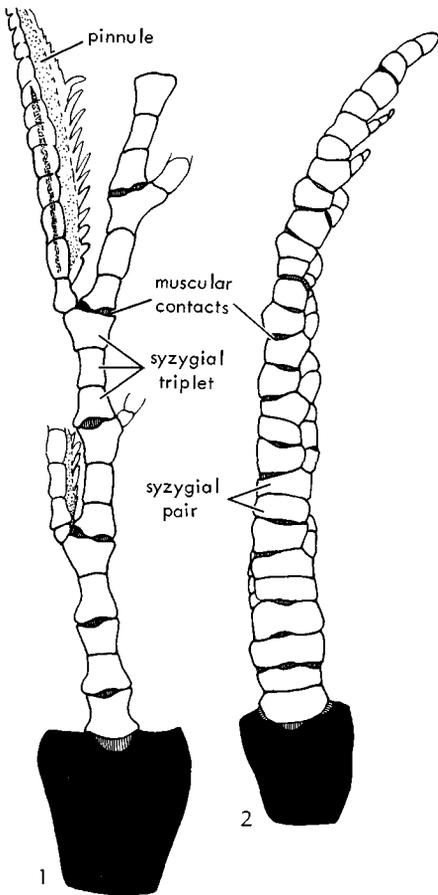


FIG. 18. Arm structures in primitive five-armed crinoids (Breimer, n).—1. *Hyocrinus betheliani* showing muscular and syzygial articulations of brachials.—2. *Ptilocrinus pinnatus*.

plates in a brachitaxis is variable. The most proximal brachitaxis is composed of a primibrach or primibrachs and the radial, which for this purpose may be regarded as an arm plate (although most paleontologists exclude the radial because undoubtedly, it is a cup plate). The plates terminating a brachitaxis distally are either the last-formed brachials of the free arm ends or axillary brachials upon which the arms divide. They are ranked like the brachials proximal to them as **primaxils**, **secundaxils**, **tertaxils**, and so on.

Primitively, crinoids have only five unbranched arms. Among recent crinoids this five-armed condition is preserved in such

stalked forms as *Rhizocrinus*, *Ptilocrinus*, and *Hyocrinus* (Fig. 18). Normally, the five arms in five-armed forms are all alike, and have the same development on the five radial sides of the body. *Holopus* (Fig. 19), which is adapted to life in reef environments where it is cemented at its base to hard rocky bottoms, has the most peculiar

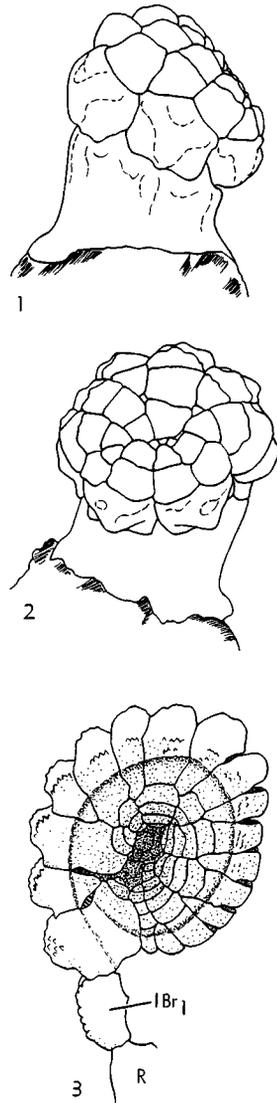


FIG. 19. Organization and arm structure in *Holopus rangi* (Breimer, n).—1,2. Side views showing undivided peduncle beneath radials and incurved short arms.—3. Side view of single inwardly coiled arm, enl.

arms of any recent crinoid. The ten arms are divisible into smaller arms called a **bivium** and larger ones called a **trivium**.

Ten-armed crinoids very strongly tend to have only two primibrachs, the second one axillary and called a **primaxil**. This condition is exclusive in the comatulids. Only in isocrinid genera, such as *Metacrinus*, are more than two primibrachs seen in each ray. In most multibrachiate comatulids the brachitaxes between the first and the last have either two or four brachials. Multibrachiate isocrinids (e.g., *Cenocrinus*) may have more than four elements in brachitaxes between the first and the last.

#### ARM GROWTH

Growth of the arms in extant crinoids has been studied and described especially by CLARK (1915a, 1921) and GISLÉN (1924). Early in crinoid ontogeny the arms are formed as radial extrusions of the body on five different sides of the embryological theca, shortly after the radial plates have been introduced. The brachial elements are formed in line with the radials; they are the product of terminal growth and skeletal secretion at the tip of the growing arm. In five-armed crinoids such terminal growth is the only mode of arm formation observed. It is known in literature as the **direct or continuous mode of arm formation**. The ten-armed stage in crinoids, whether transitory or ultimate, is brought about in the same direct way. Two primibrachs in each ray are produced by terminal secretion, the second being axillary and called the primaxil. In direct arm growth the primaxil is thus a primarily formed plate. After secretion of a primaxil, two growth sectors appear distally from it. These start to produce a pair of separate arms equal to each other in form and size. The resultant ten-armed pentacrinoid larval stage is so widespread among recent crinoids as to be almost universal. It occurs in all pentacrinoid growth stages of the recent crinoids as far as known. To be remembered here is discussion of such ten-armed comatulids as *Promachocrinus* and *Thaumatocrinus*, which developed their ten arms without the intervention of primaxils, but with intercalation of five pararadials. No ten-armed crinoids are known to possess prim-

axils formed in other than the direct mode of growth.

Crinoids with more than ten free arm ends are termed **multibrachiate**. Several different ways of bringing about a multibrachiate condition are observed in recent crinoids. One is by direct or continuous growth, just described. It is supposed to occur in the isocrinid *Neocrinus*. Studies by CARPENTER (1884a) have led me to conclude that the secundaxils and tertaxils of this genus are formed by terminal growth. If so, *Neocrinus* is the only genus with any indication of reaching a multibrachiate arm structure in this way.

A second way of producing a multibrachiate arm pattern is also direct and continuous but not by terminal growth of arms. Instead, it involves **differentiation of pinnules**. This mode of growth is found in some isocrinids (e.g., *Metacrinus*, Fig. 20, 1) and millericrinids (e.g., *Calamocrinus*). The best observations have been made by GISLÉN (1924), who observed that the formation of secundaxils to quartaxils in *Metacrinus* is accomplished as follows. At the free arm ends of the ten-armed pentacrinoid growth stage, certain pinnules begin to gain strength and become larger. New small pinnules then arise on the sides of the enlarged pinnules, which gradually attain the same length and girth as the main arm. The place for thickening of pinnules in this way is found in the region between immature and mature pinnules of the arm. Since this region is rather near the distal extremity of the arm, it is clear that the arm ramification at a secundaxil will occur fairly near the tip of the growing arm. Therefore, a moderately large number of brachials is always included in successive, different brachitaxes. The secundaxils, tertaxils, and so on, hence are formed by modification of a preexisting normal brachial plate. It is unknown whether the primaxil in *Metacrinus* is formed in the same way. The large number of primibrachs (7), which in part are pinnulated, makes one suspect that it is. GISLÉN counted the number of plates in the secundibrach-to-quartibrach series in several different species of *Metacrinus* and found that an overwhelming majority of the brachitaxes contained even numbers of brachials (taking syzygial pairs as units). He ex-

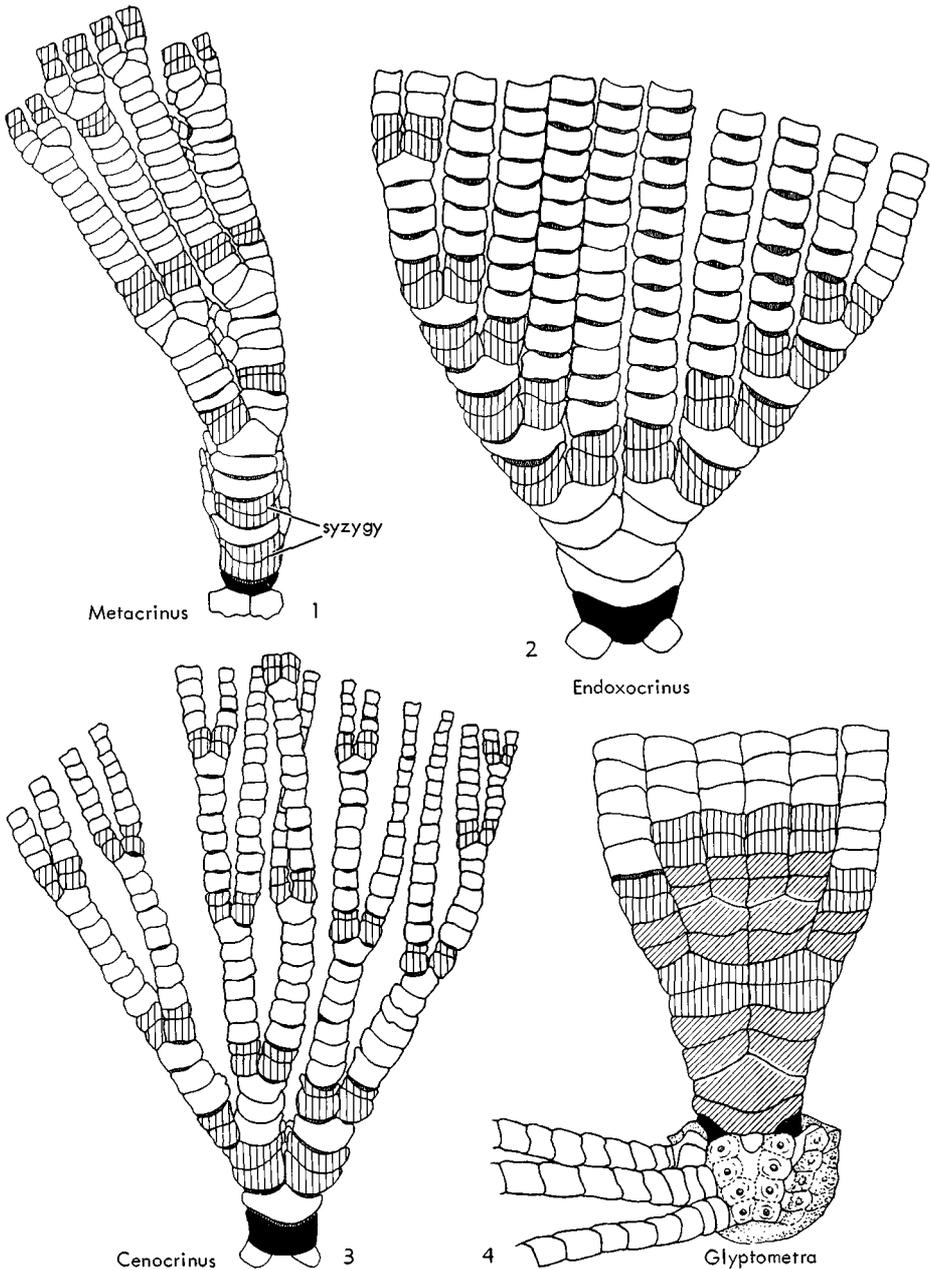


FIG. 20. Types of arm ramification in recent crinoids with distribution of synarthrial (oblique ruled) and syzygial (vertical ruled) brachial pairs.

1. Dichotomy (or isotomy) in *Metacrinus wyvillei* (Breimer, n).  
 2. Endotomy in *Endoxocrinus parvae* (Breimer, n).  
 3. Heterotomy in *Cenocrinus asteria* (Breimer, n).  
 4. Exotomy in *Glyptometra investigatoris* (after Clark, 1921).

plained this satisfactorily by noting that the first pinnule is always borne by the first brachial unit on the abmedial side of the arm, so that the new arm is formed from a pinnule on the admedial side of the arm, where it is more protected during its further growth than on the outer side.

Among comatulids still another method of developing the multibrachiate condition exists. This was discovered by MINCKERT (1905a) and is now known as the **indirect or discontinuous mode** of arm ramification. During ontogeny of the comatulids the ten-armed stage is reached by continuous terminal growth. One or more of the ten arms may be shed by **autotomy** at a proximal syzygial interface, probably by degeneration of the elastic fibers connecting the brachials, for syzygies are articulations of low resistance where arms may break easily. At this level the autotomy is exclusively produced. The hypozygal segment is prepared for **regeneration** of the shed arm. It may happen that the hypozygal regenerates an axillary plate and two arms, instead of a new epizygal and single arm. When an axillary brachial is generated, it provides a new arm ramification and augments the number of free arms; hence it is called **augmentative regeneration**. When a non-axillary brachial is generated, it introduces no arm-pattern change, and this is termed **reproductive regeneration**. Discontinuous arm duplication is also reported to exist in the isocrinid genera *Endoxocrinus* and *Teliocrinus*.

In all types of arm ramification described so far, the arm divisions borne by a given axillary plate are equal as compared to one another. In *Calamocrinus*, however, the arms borne by the axillaries are unequal, smaller lateral arms or **ramules** being formed alternately toward left and right on the asymmetrical axillary plates. Both the main arm and the ramules are pinnulated. In this genus the arms are probably formed in the manner described for *Metacrinus*, except that as a rule the first pinnule and first ramule come off toward the left in *Calamocrinus*.

#### MATURE PATTERNS OF RAY STRUCTURES

The different ways of forming arm ramifications which have been described produce various patterns of ray structures

in mature crinoids. The number of free arm ends and the branching pattern may be characteristic for species or for genera. In some this pattern is highly stable but in others extremely variable.

In *Metacrinus* (Fig. 20,1) a regular dichotomous branching is achieved on relatively prominent axillaries, each brachitaxis containing relatively numerous elements. This is an isotomy, producing two equal arms on each axillary plate, with no arms undivided.

Quite another pattern of branching is displayed by *Endoxocrinus* (Fig. 20,2) in which regularly the admedial brachitaxis remains undivided and the abmedial one forks again, leaving very short brachitaxes behind. This produces an endotomous pattern of branching, which is highly typical for the genus. Without exception the axillaries following the primaxil are located in the abmedial brachitaxes.

An irregular pattern of branching, which could be indicated as bilateral heterotomous is found in *Cenocrinus* (Fig. 20,3), in which some brachitaxes may remain unbranched, while their fellows on the same axillary plate give rise to another ramification. The distribution of the undivided brachitaxes is irregular, for either the admedial or abmedial brachitaxis may remain undivided. In parts of the total ray structure a bilateral symmetry may be produced, though by no means do the two half-rays necessarily display a bilateral symmetry.

The opposite of the endotomous pattern of *Endoxocrinus* is theoretically conceivable and would give an exotomous pattern of ray structure. Actually, however, it scarcely exists among recent crinoids. Only in the comatulid family Charitometridae are several genera (e.g., *Glyptometa*, *Pachylo-metra*, *Zygometa*) that have six-armed rays, with secundaxils on the admedial brachitaxis, whereas the abmedial one remains undivided (Fig. 20,4). Unlike *Endoxocrinus*, the axillary brachials above the primaxil have an admedial position in the half ray.

The arm structure of *Calamocrinus* as described above could be called a holotomous pattern, because a pinnule grows out alternately to left and right into a ramule, which never gains the same strength and size as the original arm.

## BRACHIAL ARTICULATIONS

All recent crinoids are grouped in the subclass named Articulata because of the elaborate articular faces of their brachials. The articulations between brachial plates are of two types, designated respectively as muscular and ligamentary. The first of these is most common and the second less so. In recent crinoids musculature is confined to the arms and pinnules, for the stalks and the cirri lack any musculature. Slight indications that some ligament fibers in stalks and cirri may have contractile power are found, however. The collagenous nature of problematical ligaments is described by MEYER (1971). The emphasis on musculature and its development in the recent crinoids is quite variable. Sessile stalked forms have weakly developed musculature, as have creeping forms among the comatulids. Antedontacean comatulids, especially the swimming antedontids, have very powerful muscles. Strength and effect of musculature is also determined by the number of ligamentary connections between the brachials; stiff arms may be produced where many ligamentary connections are present in such arms. This is particularly strong in some stalked crinoids. In *Hyocrinus*, for instance, the number of ligamentary articulations may exceed the muscular ones. No examples are found among the recent crinoids of arms fully devoid of muscular articulations, such crinoids being represented only by fossil forms. The opposite, however, occurs in the recent crinoids. The undivided arms of the specialized reef crinoid *Holopus* have exclusively muscular articulations, ligamentary ones being altogether absent.

**Muscular Articulations.** Most articulations between the brachials of recent crinoids are of muscular type, for in addition to the presence of ligaments, muscles importantly aid arm movements. As stated previously, musculature is confined to the arms, which function primarily for feeding. Since the arms extend outward while feeding and flex inward while resting, a mechanism for effecting these movements is required. Therefore, the brachials are provided with paired flexor muscles located on the inner (adoral) parts of their articular facets and an extensor ligament on the outer (aboral) parts of the facets. The muscles

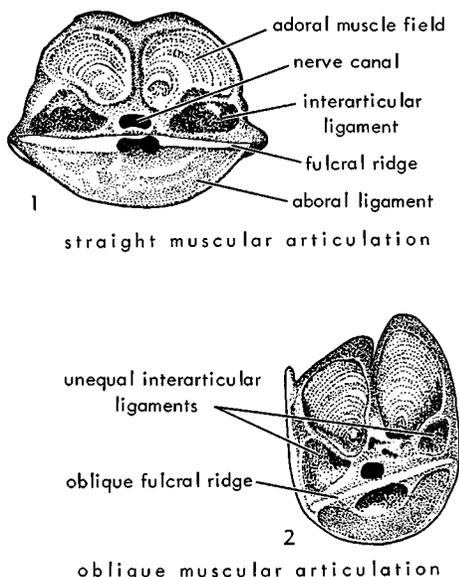


FIG. 21. Muscular brachial articulations.—1. Straight muscular articulation in radial of *Endocrinus alternicirrus* (after Carpenter, 1884a).—2. Oblique muscular articulation on brachial of *Neocrinus decorus* (Breimer, n).

and ligament are on opposite sides of a transverse fulcral ridge that serves as a fulcrum when the antagonizing muscles and ligament induce differential movement of contiguous pairs of brachials. Between the fulcral ridge and the adorally placed muscle areas is a pair of interarticular ligaments attached to the facets on opposite sides of a crest or groove running from the transverse ridge to the inner (adoral) margin of each facet.

When the described features of the articular facets are subequal on left and right sides, they display bilateral symmetry of the halves divided by the crest or groove running normal to the transverse ridge. The plane of such facets is disposed at a right angle to the longitudinal axis of the arm and its edge, seen either from the outer (aboral) or inner (adoral) side of the brachials, runs transversely straight across the arm. Articulation of this type is known as **straight muscular articulation** (Fig. 21, 1).

In many recent crinoids, features of the brachial articular facets lack bilateral symmetry and their planes are more or less oblique to the arm's longitudinal axis. The

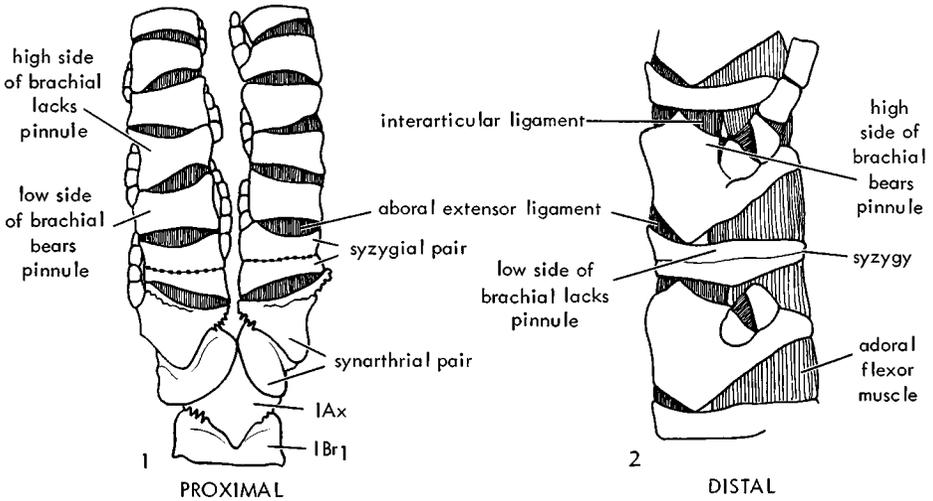


FIG. 22. External obliqueness of brachials and the reversion phenomenon in *Florometra serratissima* (Breimer, n).

1. Proximal parts of free arms with pinnules given off from lower side of brachial.

2. Distal parts of free arms with pinnules given off from higher side of brachial.

articulation then is designated as **oblique muscular articulation** (Fig. 21,2) and from different aspects can be characterized as possessing **external obliquity** and **internal obliquity**. The former refers to the oblique disposition of the facetal planes as viewed from either the outer (aboral) or inner (adoral) sides of the arm. The latter takes account of inequality of size and asymmetry in arrangement of paired muscle and ligament areas of the facets, features which cannot be observed without disarticulating successive brachials from their neighbors. The nature of both external and internal obliquity needs to be studied in relation to pinnule sockets located alternately on left and right upper edges of successive brachials. If one observes the adoral side of the arms from which all soft tissues except the ligaments have been removed, he finds the inner terminations of the facetal grooves or crests between the two muscle fields perfectly aligned with the longitudinal axis of the arm. Therefore, it is proper to account for features of internal obliquity in oblique muscular articulations by stating that the enlarged muscle and interarticular ligament fields on the left or right sides of the facets have differentially displaced the transverse ridge toward the outer (aboral) margin of the

facet more than the opposite smaller muscle and interarticular ligament areas adjacent to them beyond the median groove or crest. The ligament on the aboral side of the transverse ridge and the enlarged one on the adoral side may operate as a sort of bifascial or synarthrial articulation (explained in discussing ligamentary articulation, below) disposed more or less obliquely.

External obliquity seen in oblique muscular articulations is marked by inclined attitudes of the outer (aboral) and inner (adoral) margins of the facetal planes with respect to the longitudinal axis of the arm. The distal articular facet of each brachial slopes gently to somewhat strongly upward to left or right sides of the arm, with greatest height of each brachial on the side which bears a pinnule socket and least height opposite to this. Thus, along either the left or right sides of an arm, viewed from its aboral or adoral side, successive brachials alternately are taller and lower. Usually the sockets for attachment of pinnules are located on the higher side of the brachials, at least in middle and distal portions of the arms. In some crinoids (e.g., *Florometra serratissima*, Fig. 22) the opposite may be true of proximal brachials, pinnules being given off from the lower

side of each brachial. External obliquity of this sort has been termed **reversion** by GISELÉN (1924). It is known only in comatulids, among which such swimmers as the antedontids display reversion most clearly and some creeping comasterids only moderately or very little. The phenomenon has not yet been explained satisfactorily but probably it has to do with the “synarthrial capacities” of the oblique muscular articulations. By reversion of the articulations at least two different longer axes of oblique synarthrial articulation are superposed in the arm. This tends to increase the flexibility of the arm when it is exposed to lateral pressure.

Internal obliquity of the oblique muscular articulations is mainly caused by pinnulation. Forms with defective pinnulation (e.g., *Atelecrinus*), which lack pinnules on proximal brachials of the free arms, have straight articular musculations on such pinnuleless brachials. Proximal brachials of the free arms by invasion of the pinnule socket, which lies either between the muscle and the interarticular ligament or adorally from the muscle fields. Distal brachials of the free arms may have the pinnule sockets situated either on their lateral or on their adoral surfaces, completely separated from the articular facet, but still causing obliquity of that face.

It should be kept in mind that no sharp distinction may be found between straight and oblique muscular articulations, for the two types intergrade with one another. Perhaps the only perfect straight muscular articulation is to be found in the interface between radials and the first primibrachs. As a rule, oblique muscular articulation is most strongly developed immediately after the axillaries; in distal direction they first tend to become straight but farther on they become somewhat more oblique again.

**Ligamentary Articulations.** Ligamentary articulations known to occur in the arms of articulate crinoids are chiefly of three types: synostosomal, syzygial, and synarthrial.

Ligamentary contacts in the arms of *Calamocrinus* and *Ptilocrinus* are of such a simple type that they are best indicated as **synostosomal**. The brachials so united have practically flat interfaces held together by short ligament fibers rather evenly distributed over the joint face.

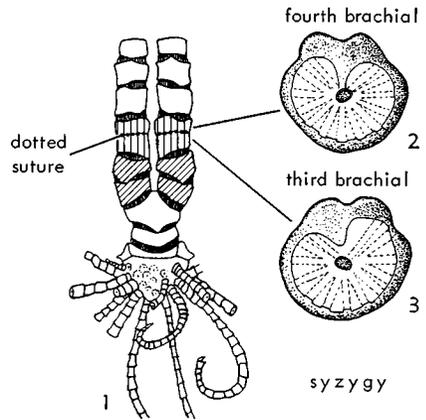


FIG. 23. Proximal arm portions (1) of *Eumorphometra hirsuta*, showing synarthrial articulations (obliquely ruled) between 1st and 2nd secundibrachs and syzygial ones (vertical ruled) between 3rd and 4th secundibrachs; schematic views of distal facet of 3rd secundibrach (3) and proximal facet of 4th secundibrach (2), enl. (after Carpenter, 1888).

**Syzygial** articulations are confined to the arms and are even specially developed to serve the mobility of arms in vagile crinoids. What is known in the literature as stem syzygy is in fact a synostosis or cryptosynostosis. On the other hand, synarthries are not confined to crinoid arms for they occur in the stalks of Bourgueticrinida.

The sort of ligamentary articulation most frequently found in the arms of recent crinoids, but typically developed only in the comatulids, is syzygial. It may be defined as a ligamentary articulation in which the opposed joint faces bear a number of culmina that radiate from the axial canal, the culmina of apposed faces meeting one another instead of being interlocked by fitting into crenellae. When the syzygial suture is observed from the outer (aboral) side of the arm, it appears as a characteristically dotted line. The ligament fibers at the syzygial contact are very short and located mainly in the depressions (crenellae) in between the radiating culmina and therefore appear externally as dots along the suture (Fig. 23). The syzygial contact allows the plates so connected slight mobility in all directions. The syzygy may be regarded as an extremely helpful articulation since it may prevent extended arms

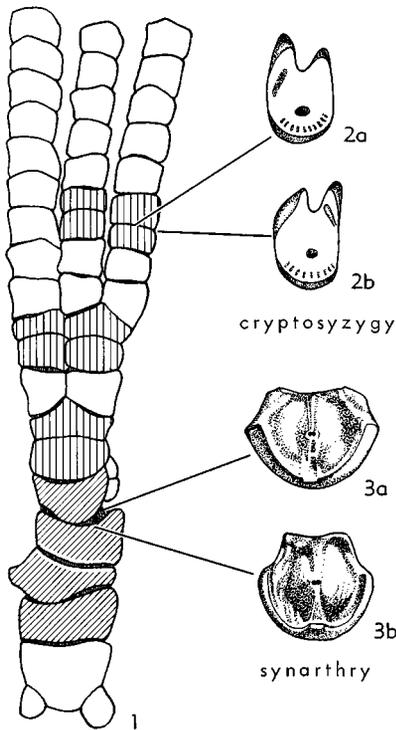


FIG. 24. Ligamentary articulations in arms of *Neocrinus decorus* (Breimer, n).—1. Outer (aboral) face of arm showing distribution of brachials united by synarthrial (oblique ruled) and syzygial (vertical ruled) articulations.—2. Facing articular facets of tertibrach syzygial brachial pair (cryptosyzygy); 2a, proximal facet of 4th tertibrach; 2b, distal facet of 3rd tertibrach.—3. Facing articular facets of synarthrial brachial pair; 3a, proximal facet of 4th primibrach; 3b, distal facet of 3rd primibrach.

from breaking when exposed to torsion. The plates united by syzygy are sometimes indicated as a syzygial pair. It is stressed however, that the term syzygy is introduced to designate the type of ligamentary articulation, in order to discriminate it from other such articulations. The plate below the syzygial contact is called **hypozygal** and the one above it **epizygal**. Very commonly axillary brachials are joined to plates next preceding them by syzygy.

In stalked crinoids syzygies are far less developed than in the comatulids. The radiating culmina of their articular facets are very short and may even be interrupted to form rows of tubercles; they fail to

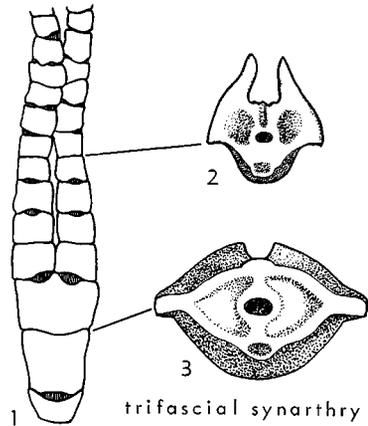


FIG. 25. Trifascial synarthrial brachial articulation in *Bathycrinus aldrichianus*.—1. Outer (aboral) side of arm showing locations of facets illustrated (Breimer, n).—2. Distal facet of 4th secundi-brach (after Carpenter, 1884a).—3. Distal facet of 1st primibrach (after Carpenter, 1884a).

reach the aboral surface of the brachials and do not show a dotted suture. Such weakly developed syzygies, known as **cryptosyzygies**, occur in the isocrinids (Fig. 24). The mobility allowed by such contacts is probably very low.

A third type of ligamentary articulation, known as **synarthrial**, evidently developed to allow the brachials so united a differential flexible movement in two directions. Brachial synarthries are fundamentally of the same kind as are found in the stalks of some crinoids (compare Fig. 24 with Fig. 9), inasmuch as two larger ligament bundles are present on either side of an articular bar or fulcral ridge running in adoral-aboral direction. The central nerve canal is located on this ridge. Traditionally—and rightly—this type of synarthry has been called a **bifascial articulation**. Another type of synarthry possessing three ligament bundles has been termed **trifascial articulation**. It occurs in certain ten-armed Bourgueticrinida (e.g., *Bathycrinus*; see Fig. 25). In *Bathycrinus* such synarthrial pairs fully replace syzygial pairs.

Synarthries, like syzygies, may be weakly developed and these are indicated as **cryptosynarthries**. They occur in creeping types of comatulid crinoids (Comasteridae). The power of flexibility is practically reduced to nil.

A rather special type of ligamentary articulation is found in *Neocrinus blakei* and *Hypalocrinus naresianus* (Fig. 26). This is known as **symmorphial**, a ligamentary contact in which a prominent transverse culmination of the epizygal brachial fits into a corresponding depression of the hypozygal; peripheral culmina and crenulae may occur near the aboral margins of the symmorphic joint faces, just as in cryptosyzygies. For this reason the symmorph may be considered as a modified sort of syzygy. Symmorphial contacts allow only very slight possibility of differential movement of the brachials in two directions, if any at all.

Among all ligamentary contacts the synostosis is morphologically the most simple and phylogenetically the oldest type. Cryptosynarthries, cryptosyzygies, and cryptosymplexies are all very close to synostosis and sometimes in literature are indicated as such. It seems logical to think that synarthries, syzygies, and symplexies are derived from synostoses. Indeed, as soon as a concentration of ligament fibers into bundles occurs and the remaining spots are filled in with calcareous ridges, striae, or culmina, we get tendencies toward synarthries, syzygies, and symplexies, which might be called cryptosynarthry, cryptosyzygy and cryptosymplexy, respectively.

The distribution of synarthrial and syzygial contacts in recent crinoid arms has been an object of study by CLARK (1908e). His conclusions have been criticized by GISLÉN (1924). From observations of these workers some regularities in distribution of the ligamentary articulation types are known. The most regular occurrence of synarthrial and syzygial pairs throughout the arms is found in the comatulids. These crinoids develop only two primibrachs in each ray, with articulation between them of synarthrial type (except in the Zygommetridae where it is a syzygial). All brachitaxes between the primaxil and most distal axillary include either two or four brachials. In case only two brachials are present in a brachitaxis, they are united by synarthry. If, on the contrary, four brachials constitute the brachitaxis, numbers 1 and 2 are united by synarthry, whereas 3 and 4 are joined by syzygy. The free-

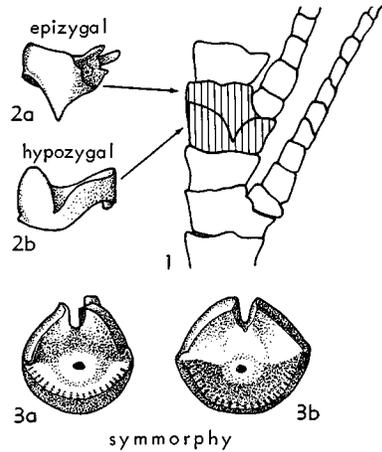


FIG. 26. Symmorphic brachial articulations in *Neocrinus blakei* (after Carpenter, 1884a).—1. Side view of part of arm with pinnules at right, showing location of symmorphically articulated brachials (vertical ruled).—2. Side views of distal (2a) and proximal (2b) units of brachial pair.—3. Facetal views of symmorphial brachial pair illustrated in 2; 3a, distal facet of hypozygal; 3b, proximal facet of epizygal, enl.

ending arms (or terminal brachitaxes) invariably start with a synarthrial pair followed by a syzygial pair. This so-called distal synarthrial pair in comatulids very generally is more elaborate, larger than the following plates, and not uncommonly ornamented (see Fig. 22, *Florometra serratisima*). Syzygies may be repeated at regular intervals in the free arms. The extent of such intervals is characteristic of genera or species. Synarthries are not repeated in the free arms.

In Isocrinida the distribution patterns or synarthries and syzygies are less regular than in comatulids. Isocrinids with two primibrachs show them usually united by syzygy, but in *Neocrinus* and *Hypalocrinus* by synarthry. Isocrinids may have more than two primibrachs. For example, *Metacrinus* has either four primibrachs: a synarthrial pair followed by a syzygial pair, just as in comatulids; or seven primibrachs, with first a synarthrial pair and then a syzygial pair midway in the brachitaxis. The composition of the free-ending arms is different from the comatulids (except for *Hypalocrinus*). As a rule, synarthries do not occur in the free-ending arms, and even

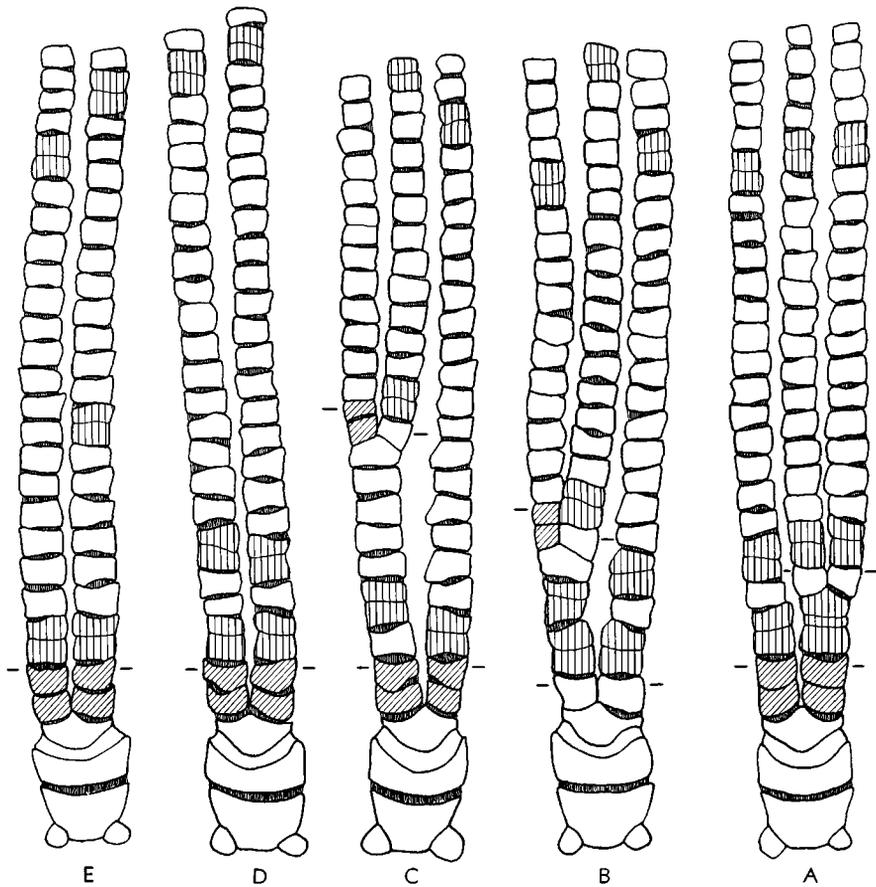


FIG. 27. Semidiagrammatic representation of arm ramification and distribution of synarthrial (oblique ruled) and syzygial (vertical ruled) pairs of brachials in a specimen of *Neocrinus decorus* (Breimer, n).

syzygies may be altogether absent there (e.g., *Endoxocrinus*). The distribution of ligamentary articulations in *Neocrinus* is shown in Figure 27. Brachitaxes between the primaxil and last axillaries have four elements as a rule: a synarthrial pair and a syzygial pair. Exceptionally, the number of such brachitaxes may be three or five. Free-ending arms invariably begin with a synarthrial pair followed by a syzygial pair if they arise from the primaxil. If they arise from a higher-rank axil, the synarthrial pair is commonly suppressed to a single plate, which is followed by syzygy, or it is present but not followed by a syzygy. In many cases it is also observed that the first two brachials do not form a synarthrial pair,

but brachials 3 and 4 form a syzygial pair. Compared to the comatulids, this means a strong reduction of synarthries in the free-arm ends, and, consequently a lower degree of lateral flexibility in the arms.

In five-armed Bourgueticrinida (e.g., *Rhizocrinus*, *Democrinus*) synarthries are absent. The arms are composed of regularly alternating syzygial pairs. In ten-armed bourgueticrinids (e.g., *Bathycrinus*, Fig. 25) syzygies are absent, being replaced by synarthries of trifascial type; only secundi-brachs 3, 6, and 9 have muscular articulations at both ends, which means that the arms are formed mostly by synarthrial pairs.

In the Cyrtocrinida, synarthries are altogether absent, but syzygies are widespread.

In *Hyocrinus*, for instance, syzygial triplets (Fig. 18, I) regularly follow one another in the distal parts of the arms. A very peculiar flexible arm occurs in *Holopus*, for all of its brachial articulations are of muscular type.

#### PINNULATION

Modern crinoid arms are densely pinnulated structures. A **pinnule** is a lateral appendage of the arm supported by serially arranged skeletal segments called **pinnulars**. The pinnulars are interconnected by ligament and muscle fibers, as are the brachials. Parts of the coelomic, water-vascular and nervous systems penetrate into the pinnules. On their adoral sides pinnules bear ambulacra. The morphology and function of the pinnules is largely the same as that of the main arms.

As a rule, pinnules are distributed alternately along left and right sides of the arm, with a single pinnule to each brachial. More precisely, each pinnule is given off by a **pinnular arm unit**, for this may be composed of more than one brachial. Pinnulation is subject to several strict rules. Normally, every brachial with muscular articulations on its proximal and distal facets comprises a pinnular arm unit, but this may consist of brachial pairs or even triplets united together by syzygy or synarthry. Such multiple-brachial pinnular arm units invariably give rise to a pinnule from their distal component, and never from their proximal or intermediate brachial. Thus epizygals are pinnule-bearing, whereas hypozygals lack pinnules. No axillary arm plate of a recent crinoid is known to give rise to a pinnule, even when muscular articulations characterize both its proximal and distal facets.

Absence of pinnules other than as just mentioned constitutes **defective pinnulation**. This is known in many species of both stalked and stalkless recent crinoids. Defective pinnulation occurs when pinnules are absent at the base of a brachitaxis in places where they could be expected. In the hyocrinid genera *Calamocrinus* and *Ptilocrinus* the first pinnule is to be found on the left side of the fourth brachial viewed aborally, while pinnules on more proximal brachials are missing. In the five-armed bourgueticrinid genera *Democrinus* and *Rhizocrinus*, the first pinnule is found

on the left side of the fourth pinnular arm unit, more proximal pinnular arm units lacking pinnules. In these genera up to nine brachials may constitute these four pinnular arm units (e.g., *Democrinus campbellianus*). Ten-armed bourgueticrinids, such as *Bathycrinus*, have even more defective pinnulations; the first pinnule is developed on the admedial sides of the sixth pinnular arm units (which may include up to nine brachials) in the secundibrachitaxis.

The only known case of **complete pinnulation** is found in the ten-armed cyrtocrinid *Holopus*. Each of its secundibrachs is a pinnular arm unit because ligamentary connections between the brachials are absent. The first pinnule occurs on the first secundibrach.

Isocrinida and Comatulida tend to have more complete pinnulation than most millericrinids, bourgueticrinids, and cyrtocrinids. Even forms with many primibrachs (e.g., *Metacrinus*) have the pinnulation as complete as possible. The first pinnule is located on the second primibrach on the right side of the basal synarthrial pair. The first three or four pinnules on the primibrachs are entirely or at least partly fixed to the thecal wall; such pinnules are known as **fixed pinnules**.

Multibrachiate isocrinids have brachitaxes (apart from the free arms) made up of two to four brachials, but in no case is more than one pinnule present. If only two plates form a brachitaxis, these are invariably interconnected with ligaments; hence the proximal brachial has no pinnule and the second has none either, because it is axillary. If four plates form a brachitaxis, it contains a synarthrial pair with one pinnule and a syzygial pair without a pinnule, for the fourth brachial again is axillary.

The free-arm ends of isocrinids generally have no basal synarthrial pair. Commonly, as in *Annacrinus*, *Cenocrinus*, and *Endoxocrinus*, the free arms begin with a syzygial pair of brachials. The first pinnule is on the abmedial side of this basal syzygy. Accordingly, pinnulation of the free arms borne by any one axil is **symmetrical**. In *Teliocrinus* the basal syzygy of the free arms may occur between either the second and third or third and fourth brachials. The first pinnule is always located on the first brachial and uniformly

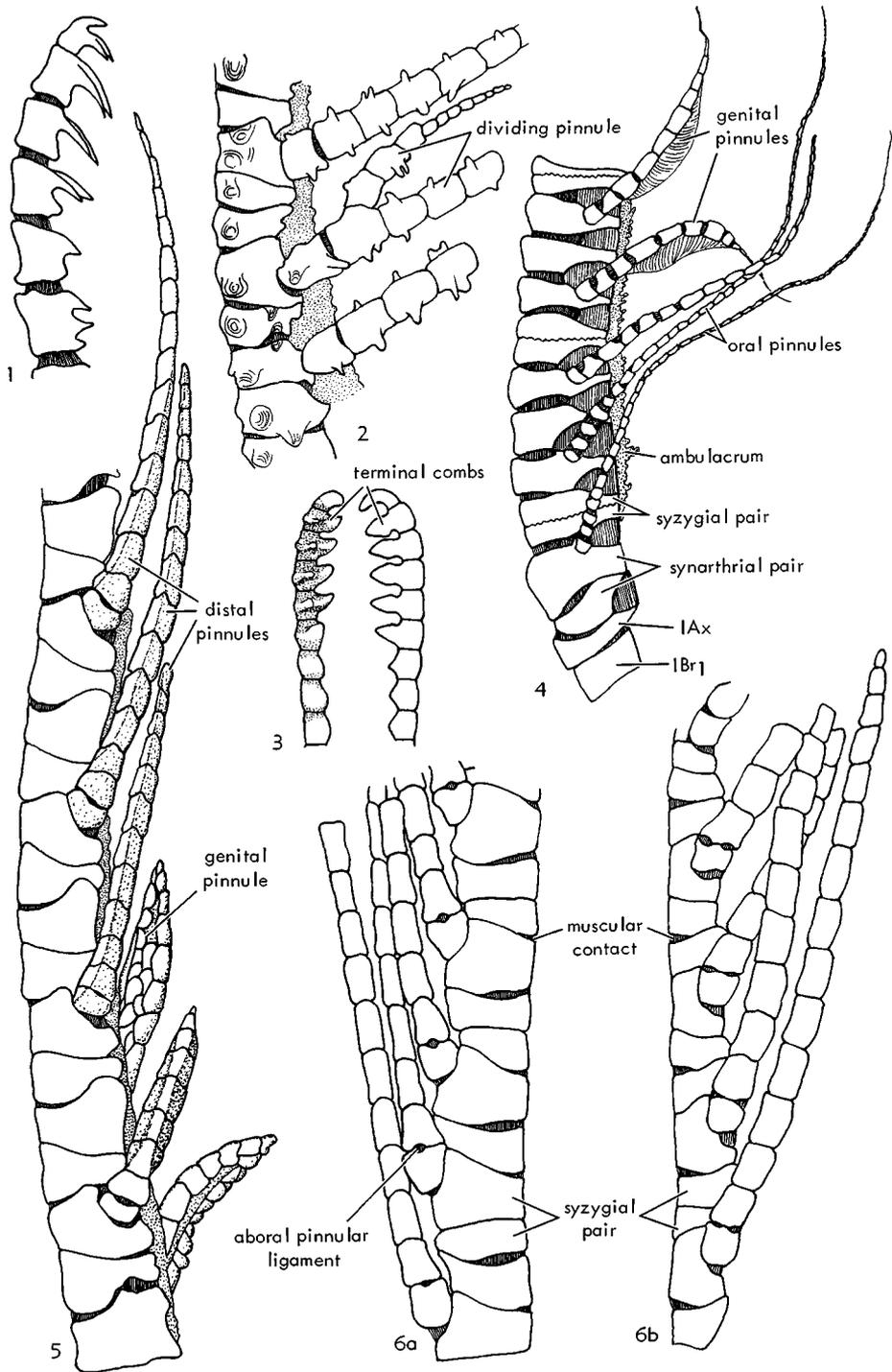


FIG. 28. Pinnulation and pinnular structures. (Explanation on facing page.)

either abmedial or admedial in direction. This makes pinnulation of the free arms arising from any given axil **identical**.

The free arms of the isocrinid *Hypalocrinus* and all comatulids begin with a synarthrial pair of brachials followed by a symmorphial pair. The first pinnule is found on the abmedial side of the synarthrial pair and the second pinnule on the admedial side of the syzygial pair. The pinnulation pattern is mostly symmetrical.

The form and organization of pinnules is variable according to specialized functions which they may assume. Very generally those of comatulids are differentiated into oral, distal, and genital pinnules.

The **oral pinnules** (Fig. 28,4) typically have become transformed into tactile organs or modified for defense of the naked, non-calcified tegmen of the comatulids. These pinnules are associated with the first synarthrial and syzygial pairs of brachials in the free arms on which they invariably occur. Several additional oral pinnules may follow, however. For effective performance of their function the oral pinnules have been developed as long, slender structures composed of many small pinnulars, which give them enormous flexibility. Ambulacra are absent on these pinnules.

Oral pinnules are restricted to the comatulids, those of comasterids being curiously specialized. Their distal pinnulars, which may be produced into arrowhead- or spade-like shapes, form the terminal comb (Fig. 28,3). Probably they serve to aid in fixation. Comasterids may use their posterior arms to curve around objects (see Fig. 41) for fixation; the terminal combs of the oral pinnules are helpful, since comasterids have few or no cirri.

Stalked crinoids with armored tegmens do not seem to need defensive organs to protect the vulnerable ambulacral ducts on the tegmen.

Following the oral pinnules are several **genital pinnules** (Fig. 28,4,5) which bear the gonads. In the spawning and breeding

season these pinnules appear as swollen structures, for the gonads are packed with mature gametes. Genital pinnules are generally very much shorter than oral ones, being composed of only about ten pinnulars. An ambulacral groove that may be present on them is functional for food-collecting outside of the breeding season when the pinnule is not swollen.

The **distal pinnules** (Fig. 28,5), including all beyond the oral and genital pinnules, serve in gathering food particles, and hence their ambulacral grooves are particularly well developed. Throughout the recent crinoids they are very uniformly composed of about 20 segments. The total length of functional ambulacra of individuals is determined mainly by the number and length of their distal pinnules and by the number of their free arms. CLARK (1921) has observed that ten-armed crinoids possess longer distal pinnules than multibrachiate species, and that relative length of the pinnules decreases in direct correlation with increase in the number of arms.

The growth and development of pinnules is known from the ontogeny of several different genera of comatulids. Pinnulation develops only very late in ontogeny. Juvenile comatulids of the ten-armed growth stage may have free-arm ends built of as many as 20 secundibrachs without a single pinnule present. Pinnules seem to become introduced in a distal-proximal sequence. The first oral pinnule is formed only after about half a dozen distal pinnules are well developed. This distal-proximal order of pinnule development may be understood by bearing in mind that the distal pinnules serve as food-collecting appendages, and as such apparently precede reproductive and tactile pinnules in order of appearance. The delay in development of oral pinnules may become appreciable enough to cause defective pinnulation.

In multibrachiate species that have surpassed the ten-armed growth stage, a terminal growth of pinnules is observed at

- 
1. Side view of spiny pinnular tips in *Comatella nigra* (after Clark, 1921).
  2. Dividing pinnules of *Ptilocrinus antarcticus* seen from side (Breimer, n).
  3. Terminal combs on comasterid pinnules (after Clark, 1921).
  4. Oral and genital pinnules of *Promachocrinus* in side view (Breimer, n).
  5. Genital and distal pinnules of *Democrinus rawsoni* in side view (Breimer, n).
  6. Pinnulation in two proximal fragments (6a,b) of *Ptilocrinus brucei* (Breimer, n).

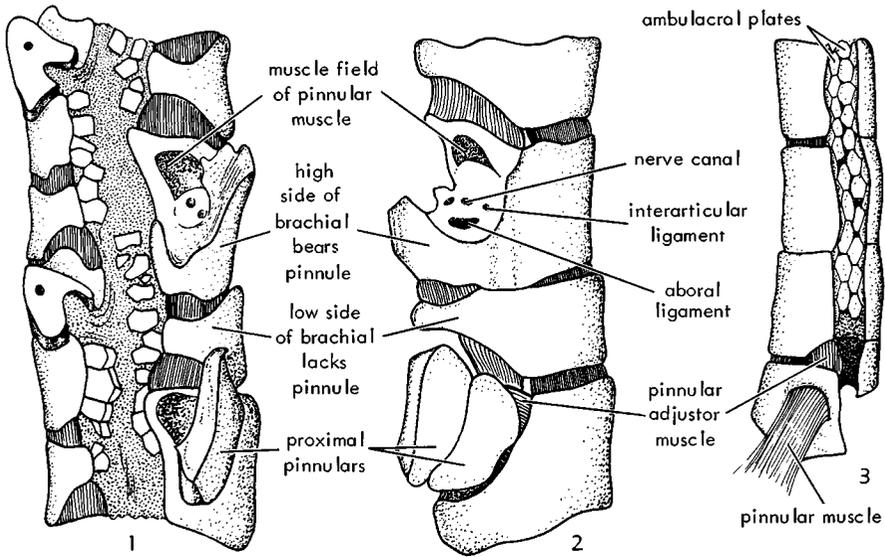


FIG. 29. Pinnular articular structures in *Neocrinus decorus* (Breimer, n).

1. Adoral side of arm fragment showing proximal pinnulars joined to alternating brachials on opposite sides of arm.
2. Side view of same fragment corresponding to right side of 1.
3. Four proximal pinnulars with ambulacral covering plates.

the growing arm tips. The order of introducing new elements at the growth tip is: 1) a brachial, 2) a first pinnular, 3) another brachial, and 4) a first pinnular on the opposite side as the latter. This means that in multibrachiate crinoids pinnules are introduced in alternating order directly after appearance of the brachial to which they belong.

As mentioned previously, pinnules may contain a variable number of pinnulars, which generally are all alike, apart from the proximal two pinnulars. In the genital and distal pinnules these two pinnulars are always shorter than succeeding ones. The first pinnular is usually two or three times wider than high and more or less crescentic in outline; second pinnular is trapezoidal in shape, with width about equal to height. The two pinnulars are specialized in form because they serve special functions in movement of the pinnules and are provided with well-developed muscular-articulation facets.

The contacts between brachial and first pinnular, and also between first and second pinnulars are of a straight muscular type, with a large aboral ligament, and on the

opposite side of the transverse ridge two equal interarticular ligaments and a pair of equal adoral muscles on either side of a crest or groove running normal to the transverse ridge.

The articulation between the first pinnular and the brachial to which it is attached is a straight muscular one, with the transverse ridge of the facet placed at an angle of about  $45^\circ$  to the longitudinal axis of the arm. The muscles connecting the first pinnular to its brachial may be displaced to the lateral side of the first pinnular (see Fig. 29,3). These muscles serve for adjusting the position of the pinnule with respect to the arm, moving the pinnule toward or away from the arm. The muscles may be regarded as **pinnular adjustor muscles**.

The articulation between the first and second pinnulars is a strongly developed muscular articulation, with the transverse ridge at right angles to the preceding one. The transverse ridge separates two strongly beveled sides of the articular surface. Contraction of the adoral muscles between the two pinnulars causes flexion of the pinnule.

The articulation between all pinnulars beyond the first pair is of a specialized type,

entirely confined to the pinnular interfaces; it is termed **pinnular articulation**. It is very uniformly constructed throughout recent crinoids, consisting of a pair of small adoral muscles and a pair of large aboral ligaments on either side of a fulcral ridge running in adoral-aboral direction. It is therefore no longer a true transverse ridge. The pinnular fulcral ridges are oriented at right angles to the transverse ridge between the first and second pinnulars and all have the same orientation throughout the pinnule. The pinnular articulation allows mobility in lateral direction only. The pinnular muscles are unable to contribute either to adjustment or to flexion of the pinnule. Musculation in the pinnules is mostly rather weak and consequently these appendages have a degree of rigidity. Musculation is better developed in the oral pinnules, which may even have extreme flexibility.

## ADORAL SKELETON

### COMPONENT PARTS

The **adoral or perisomic skeleton** has been topologically defined (p. T19) as including every skeletal element which may be present in the adoral body wall. This wall has a main central part around the mouth, formerly referred to as the disc, but presently indicated as the **tegmen**. In forms with an advanced ontogeny the adoral body wall extends between the arm bases, so as to assist in forming lateral parts of the theca. The wall is mainly devoted to the functions of food-gathering, food-conveying, and food-receiving. Accordingly, the organ systems involved in these functions largely determine its form and shape. The water-vascular system also is involved in food-gathering. Its entrances, the **hydropores**, are distributed over the central and interradial parts of the adoral body wall and its terminal parts, the **podia or tube feet**, accompany the ambulacra all along their course. The ambulacral system is involved in food-conveying. Its main elements are the **ambulacra**, descending from the pinnules and arms and leading over the tegmen toward the mouth. The entrance to the digestive system and the exit from it invariably are located in the adoral body wall.

### DEVELOPMENT

The degree of calcification of the adoral body wall is far smaller than in the aboral body wall. Consequently, the adoral skeleton contains much less definite and characteristic elements than the aboral skeleton. Unlike the latter, it does not contribute substantially to overall body form. A function of skeleton-secretion in the adoral wall is to provide internal coherence. This may lead to quite different products. In some comatulids the adoral wall appears to be a leathery integument entirely devoid of skeletal plates. But even such apparent leathery walls actually possess microscopic carbonate deposits in the form of rods, spicules, and smaller meshworks. In some isocrinids (e.g., *Neocrinus decorus*, Fig. 30) the tegmen is wholly calcified and plated. The need for calcification of the adoral body wall, and especially of structures bordering the ambulacra, depends on the requirement for protection of the food-conveying system, which is vital to the crinoid organism. In comatulids with naked tegmens the proximal pinnules are differentiated either into long and slender, very flexible, tactile structures or rigid, spinelike structures that serve for defense of the vulnerable tegmen. In isocrinids, however, the proximal pinnules are not differentiated, necessary protection of the ambulacra on the tegmen being provided by strong calcification of structures bordering the ambulacra.

Ontogenetically the adoral body wall becomes individualized only after rotation of the coelomic compartments. Just before this rotation a part of the lateral body wall of the crinoid embryo invaginates so as to form the vestibule, which later is cut off as a separate cavity and assumes an oral position after rotation. The roof of the vestibular cavity is the embryologic adoral body wall. It is supported by five large skeletal elements called **orals**, and these are the first elements to be formed in the skeleton of the adoral body wall. The orals correspond in interradial position to the basals in the aboral skeleton and are formed at about the same time. The floor of the vestibular cavity is primitively situated at the upper level of the radial cirlet as soon as the radials have been secreted. The roof

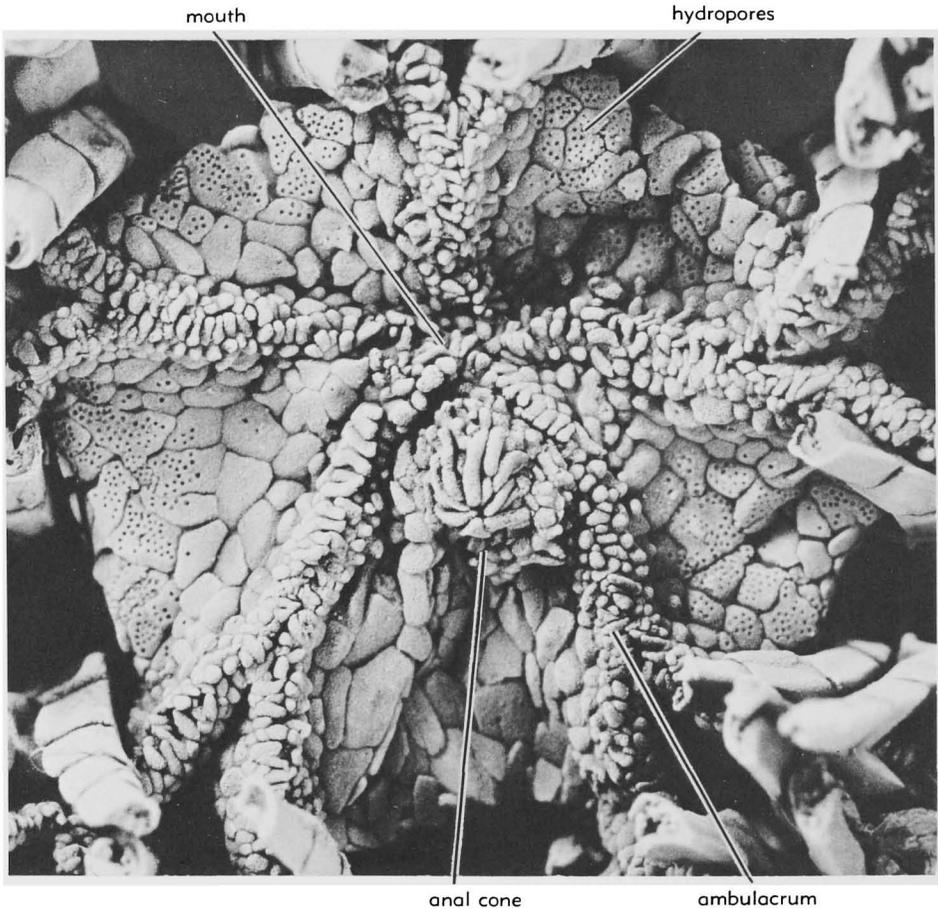


FIG. 30. Tegmen of *Neocrinus decorus*, showing hydropores on interambulacral plates except in *CD* interray (Breimer, n, through courtesy of Dr. Porter M. Kier, Washington).

of the cavity opens by formation of slits between the orals. The circllet of oral plates is split up into five lappets, which give them the appearance of five large valves. Shortly before opening of the roof of the vestibular cavity, the mouth has been formed in the bottom of this cavity. It is functional immediately after opening of the vestibular cavity and the orals are preserved for some time as protection for the juvenile mouth. In some forms with primitive ontogenetic development the orals persist during maturity and the mouth retains its position beneath them. The orals are fully preserved in *Hyocrinus* and *Holopus* (Fig. 31), in which the ambulacra run beneath

edges of the orals. These five plates clearly protect the ambulacra. In the ontogeny of most comatulids, however, the orals are resorbed and the roof of the vestibular cavity disappears entirely. The bottom of the cavity forms the tegmen and during further life assumes the role of the adoral body wall. It is perhaps not justified to define the position of the mouth in crinoids with large valvate orals as subtegminal, since the tegmen may be recognized as an outgrowth of the bottom of the vestibular cavity.

#### TEGMEN

In mature crinoids the location of the

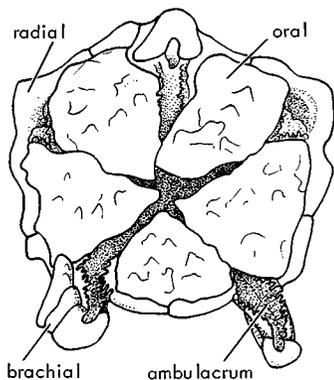


FIG. 31. Tegmen of *Hyocrinus* sp., roofed over by five large oral valves (Breimer, n).

tegmen is variable. Primitively, it is developed as a flat-lying structure at the upper edge of the radial cirlet. This position is retained in *Hyocrinus* and *Holopus*, whereas in *Calamocrinus* and *Ptilocrinus* a series of small scales becomes intercalated between edges of the radials and orals. Here the tegmen is a much inflated structure standing on the calyx. In all other recent crinoids the tegmen is elevated to a much higher level. In the bourgueticrininids it is located at the level of the fourth brachial element beyond the radial cirlet; in five-armed forms above four primibrachs and in ten-armed crinoids above the two primibrachs and the proximal two secundibrachs. In the isocrinids, which generally are multibrachiata (except *Hypalocrinus*), the tegmen may be so elevated as to reach the bases of the free arm ends. Generally, the lower tertibrachs are in contact with the tegmen. In comatulids the tegmen is raised also. Commonly it is above the two primibrachs and may even be higher than the fourth secundibrach.

Elevation of the tegmen beyond the upper edge of the radial cirlet provides extension of the central body cavity and hence enlargement of the theca. To maintain the theca as a closed space, the bases of the arms must contribute to its formation. This may be achieved by lateral abutment of the proximal brachials, as in bourgueticrininids, or by further expansion of the body wall in regions between the arms, as in isocrinids. The body wall in these places may be reinforced with perisomic plates or scales

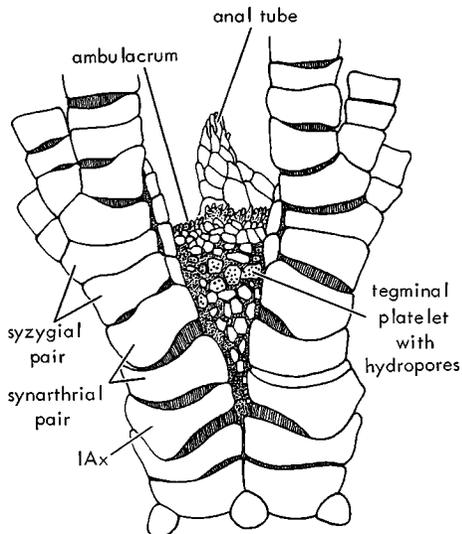


FIG. 32. DE interray of *Neocrinus decorus*, showing perisomic plates with hydropores (Breimer, n).

known as **interbrachial plates** (Fig. 32). These plates merge with others developed in the interradian parts of the tegmen.

Extension of the central body cavity is caused entirely by marked increase in volume of the gut as the animal grows. To provide the necessary space for it, the adoral body wall migrates upward between the arm bases. The ultimate location of the tegmen is determined by the volume of the gut, which in turn is determined by the length and efficiency of the ambulacral grooves. This length depends on such factors as richness of food and feeding mechanism. Valuable remarks on this subject have been made by GISLÉN (1924).

The mature tegmen evidently and naturally is divided into **ambulacral and interambulacral areas**. The ambulacra converge on the mouth in a perradial position. The alternate intervening regions are indicated as interambulacral areas. Perhaps it would be better to indicate these regions simply as the **interradial areas of the tegmen**, since they may be occupied almost completely by the ambulacral grooves from fixed pinnules. This is particularly evident in *Metacrinus*, which has as many as eight primibrachs, four of which bear pinnules. These four pinnules are fixed to the theca and have their ambulacral tracts running independ-

ently over the tegmen toward the mouth (CARPENTER, 1884a, pl. 39, fig. 2).

The interradial parts of the tegmen commonly are calcified in some degree. A strong development of interradial plates in the tegmen occurs in the isocrinids, where a complete pavement of small, irregularly arranged plates forms interrays of the tegmen. The presence of these scaly plates allows observation of **hydropores** in the tegmen, at least in dried specimens. The hydropores do not show up when submerged in alcohol. In naked tegmens they are only observable in anatomical sections of the body wall (Fig. 32). They are present in interradial areas of the tegmen, but may be absent from the posterior interray, as in *Neocrinus*, *Endoxocrinus*, and *Calamocrinus*. In *Metacrinus* posterior hydropores occur only in narrow zones bordering the C and D ambulacra. In crinoids with orals preserved in mature growth stages, the hydropores may perforate the orals. Up to 20 hydropores can be seen in each of the five orals of *Holopus*, whereas orals of *Hyo-crinus*, on the contrary, lack any hydropores. In this genus the orals are valvate structures, the hydropores may pierce the tegmental wall below the orals, whereas in *Holopus* the orals closely abut each other and apparently are not capable of much movement. CUÉNOT (1948) stated that *Rhizocrinus* preserves five orals, each of which is pierced by a single hydropore. If this is true, the posterior one should be interpreted as the primary hydropore.

The radial parts of the tegmen are formed by the ambulacra. These extend from arm bases to the mouth and distally follow all divisions of the arms, running to the very tips of the pinnules. **Ambulacra** may be absent in the oral pinnules of comatulids and in the posterior arms of some comasterids. The structure of the ambulacra is rather simple. Their bottom is the ambulacral groove, formed out of the ambulacral epithelium. It never seems to be calcified and is perhaps the only part of the crinoid body wall entirely devoid of calcareous deposits. The sides of the ambulacra are produced into series of lappets, at the internal sides of which are groups of three podia or tube feet. These are terminal extensions of the water-vascular system. The podia may eventually contain one or

more calcareous spicules, but calcite secretion in them is hardly worthy of mention. It would be contrary to their food-gathering function to stiffen them with much calcite secretion. The lappets bordering and in some crinoids covering the ambulacra commonly are calcified, however.

The plates deposited in the lappets are of two sorts: **ambulacral plates** and **adambulacral plates**. The ambulacral plates are present in the top of the lappets or occupy all the lappet in case adambulacral plates are absent. In most stalked crinoids four series of plates are developed along the ambulacra: two rows of adambulacral plates and two rows of ambulacral plates (Fig. 33,1,2). In case adambulacral plates are present, these are mostly notched for the reception of saccules, which may be seen to alternate with the adambulacral plates. The latter commonly are observed in terminal parts of the pinnules. Toward the bases of pinnules they may be absent, even if present at the pinnule tips. The lateral body wall of pinnules may be so much extended, especially in genital ones during the breeding season, that the distance between the ambulacral plates and pinnulars becomes large enough to break up the series of adambulacral plates, with replacement of them by a lateral pinnule wall reinforced with many irregularly distributed scales and plates of calcite. The genital pinnules of *Poecilometra acoela* are very short and swollen structures with a complete adoral armor of abutting adambulacral plates. Ambulacra are absent (Fig. 33,4).

In *Neocrinus decorus* (Fig. 33,1) the ambulacra are confined to the narrow strip on the adoral side of pinnules, with ambulacral plates, adambulacral plates, and pinnulars in contact along the entire length of the pinnule. In many comatulids (e.g., *Glyptometra*, Fig. 33,3) the ambulacral plates are very large, rounded valvate structures imbricating on one another. They act as a shield below which the podial groups hide. Down along the arms and on the tegmen the arrangement of adambulacral and ambulacral plates may be less regular than on the pinnules (Fig. 30). It is questionable whether the ambulacral plates on the tegmen of *Neocrinus decorus* ever open. These have become much elongated

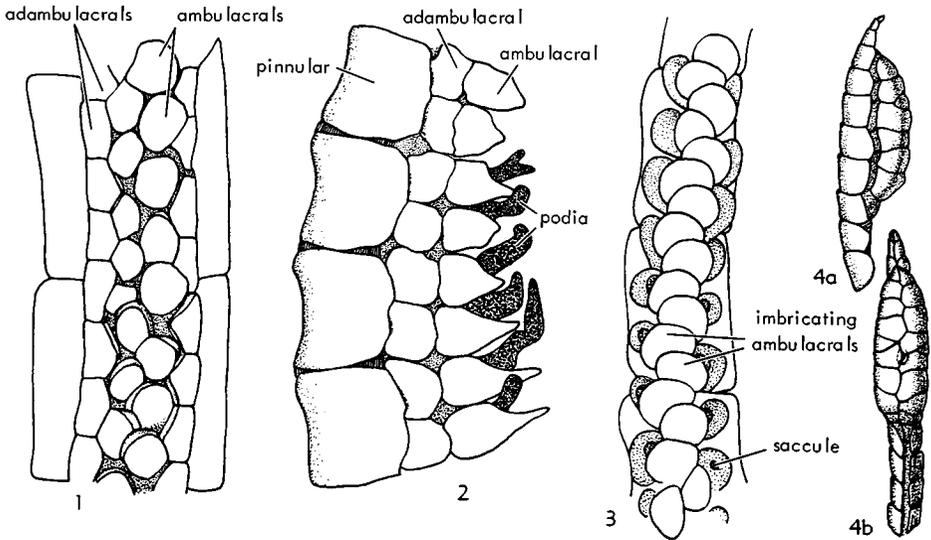


FIG. 33. Ambulacral and adambulacral plates.

1. Adoral aspect of two pinnulars of *Neocrinus decorus* with ambulacral plates closed (Breimer, n).
2. Lateral aspect of four pinnulars of *Ptilocrinus antarcticus* with ambulacral plates opened and podia exposed (Breimer, n).
3. Adoral aspect of three pinnulars of *Glyptometra selena* with imbricating ambulacral plates (Breimer, n).
4. Genital pinnule of *Poecilometra acoela* in lateral (4a) and adoral (4b) aspects where elements of adoral skeleton contribute to form complete harness around the swollen gonads (after Carpenter, 1888).

and form a sort of palisade roof over the tegminal ambulacra for protection of the rich food stream. The palisade appears to be rather permanent.

The area immediately surrounding the mouth is never fully calcified. This part of the tegmen is kept flexible for opening and closing the mouth. The ambulacral lappets form a five-sided area around the mouth called the **peristome**, in which groups of labial podia are observed in naked tegmens of the comatulids; the ring canal of the water-vascular system is located directly underneath the peristome. The anus very commonly is situated on a protuberance of the posterior part of the adoral body wall. This structure, known as the **anal tube**, commonly is supported by elongated skeletal pieces, which form a sort of cone (Fig. 30).

### VISCERAL SKELETON

The **visceral skeleton** is not formed of definite and coherent plates or scales, as in the adoral and aboral skeletons. It is mainly composed of numerous calcareous

rods, spicules, and small meshwork platelets distributed more or less plentifully in strands and webs of connective tissue. It is to be remembered that especially the aboral or perivisceral coelom has a spongy structure characterized by the presence of numerous strands and webs of connective tissue (Fig. 1, anatomical section *Antedon*). These structures may be calcified to a greater or lesser extent. Calcification may also occur in the membrane separating the adoral and aboral coelomic canals in the arms. Complete calcification of such internal and intercoelomic membranes as known in some fossil crinoids (e.g., *Teleocrinus*, Miss., N.Am.) is not known in recent crinoids. In some articulate (e.g., *Bathycrinus*, *Rhizocrinus*) the visceral mass may be so extended that it suppresses the perivisceral coelom and comes into contact with the body wall (CARPENTER, 1884a, pl. VIIIb, fig. 6-8; pl. VIIIA, fig. 8). The suppressed coelom may be traced as a calcified film of connective tissue connecting the body wall with the wall of the visceral mass.

## MORPHOGENESIS

The oldest information on morphogenesis of living crinoids, quite incomplete, has been derived from the studies of the North Atlantic species *Antedon bifida*, found along the coasts of France and England. More comprehensive and detailed work has been done by European authors (W. B. CARPENTER, 1866; PERRIER, 1886-90; BARROIS, 1888; and BURY, 1888) during the latter half of the last century on the Mediterranean species *A. adriatica* and *A. morroccana*. An exhaustively precise description of the development of *A. adriatica* was published by SEELIGER (1892), and his paper is still basic for our knowledge in the field. General echinoderm and crinoid literature (CLARK, 1921; CUÉNOT, 1948; HYMAN, 1955) has always been guided by his description.

Complete description of a crinoid ontogeny is available only for *Antedon*. Information on the ontogeny of other comatulid genera is very scattered and incomplete. During the first half of the present century, a series of papers by MORTENSEN included data on growth and development of many comatulid genera. JOHN (1938) provided information on the development of Antarctic crinoids. Our knowledge on the morphogenesis of the stalked crinoids is so inadequate as to be practically nil. A few, but valuable, remarks have been made by SARS (1868) on juvenile growth stages of *Rhizocrinus lofotensis*. His description has attracted little attention, however.

Main stages in the life history of comatulid crinoids are 1) the **embryonic stage**, lasting about five days in the egg membrane, either lying on the sea bottom, attached to the mother crinoid, or kept in a special brood pouch. Rupture from the egg membrane then initiates the second life stage, which is 2) the free-swimming **larval stage**. It is very short, lasting only a few hours or days. The larva settles and now **metamorphosis** will lead to 3) a stalked juvenile **cystidean stage**. In this life stage the organism quickly learns how to feed and to perform other essential functions and it develops the necessary organ systems for them. The definite body form is only gradually assumed during 4) the juvenile

**pentacrinoïd stage**, during which the arms grow out. The pentacrinoïd stage may last for several months, terminating when the young animal sheds its stalk and becomes free-moving again. The juvenile crinoid reaches sexual maturity shortly before the breeding season. When it first spawns it is about one year old. Upon spawning it attains 5) the **adult** life stage, which may last four or five years.

## EMBRYO

The life span during which the crinoid is called an embryo starts with fertilization of the oögametes and ends with escape of the developing crinoid from the egg membrane. The embryonic period is variable in duration, in *Antedon* lasting five days.

Crinoids are normally oviparous animals. Egg production usually is very prolific. The eggs are yolky and thus the embryo is able to develop for a considerable period without feeding. FELL (1945, 1948) considered the production of a yolky egg to be a primitive condition, which has ever been retained by crinoids. Fertilization normally is external and takes place immediately after discharge of the oögametes by rupture of the ovarian wall, stimulated by the male spawning products. The zygote may fall to the sea bottom and become attached to some substrate, but usually pinnules of the mother crinoid serve for attachment. Partly this may be explained by ready availability of the pinnules for anchorage of the embryos and partly by the fact that the external pinnular walls may be provided with cement glands for fixation of the eggs. The fertilized egg is enclosed in a definite membrane, probably a fertilization membrane, the fine structure of which is described by HOLLAND (1973). In most crinoids development takes place inside the membrane until the free-swimming larval stage is reached.

Some crinoids are known to diverge from the normal pattern. For example, various Antarctic species (e.g., *Isometra vivipara*, *Notocrinus* sp., *Phryxometra nutrix*) are viviparous. In such forms egg production is low, for usually only a few of them are

yielded by individuals. Fertilization is internal in *I. vivipara*; sperm have been observed in the genital tube of the ovary, but it is unexplained how they work their way into the ovary. The eggs of viviparous crinoids develop in a **brood chamber** or **marsupium** located in the pinnules or in the arm at the pinnule bases. The marsupium is an extension of the adoral body wall adjacent to the gonad. The eggs get into the marsupium by rupture of the wall separating the ovary from the marsupium and the embryo escapes by an external opening in the marsupium.

Embryologic development begins with a short period of cleavage of the zygote. The blastomeres are subequal in size and placed in line with one another; denoting that the cleavage is holoblastic and radial. The result of cleavage is production of an 128-celled blastula of coeloblastula type. The *Antedon* egg reaches this stage in about seven hours after fertilization.

Gastrulation begins as an invagination at one pole of the blastula, but gradually it becomes embolic. The invagination forms the anlage of the entomesoderm. Cells at the far end of the invagination opposite the blastopore proliferate to give off numerous cells into the blastocoel. The cells wander about and assume the functions of mesenchyme. The invagination is cut off as a closed sac at one side of the blastocoel. The axis through the blastopore may be regarded as the anteroposterior axis. The archenteral sac lies in the posterior part of the embryo, which otherwise is filled with the entodermal mesenchyme. Gastrulation is completed when the blastopore has become closed off completely. In *Antedon* this takes place after 36 hours.

The stage in embryonic development during the next 48 hours is mainly characterized by repeated division of the archenteral sac, in which several different coelomic compartments are formed as anlagen of the main internal organ systems to be developed later in ontogeny. The divisions of the archenteral sac are shown schematically in Fig. 34.

The archenteral sac first divides into two equal parts called **somatocoel** and **enterohydrocoel** (Fig. 34, 1a, b). The somatocoel, which has an elongated form, is located at

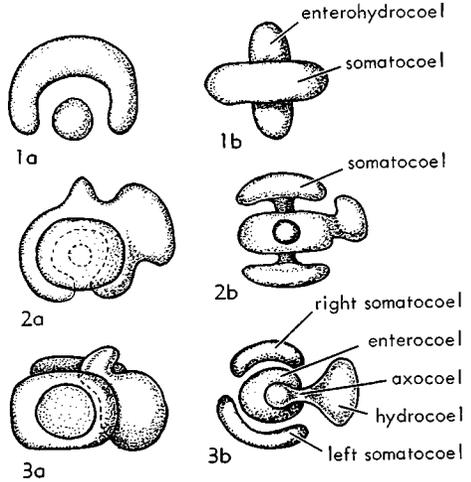


FIG. 34. Coelomic divisions in embryo of *Antedon* (after Heider, 1912).—1-3. Early, intermediate, and late larval stages (1a, 2a, 3a, side views; 1b, 2b, 3b, dorsal views).

the posterior side of the embryo and is embraced by the crescentic enterohydrocoel, located in an anterior position. The somatocoel prepares for a further division, expanding its left and right extremities into the form of a dumbbell with constricted central portion (Fig. 34, 2a, b). Soon the somatocoel divides into two parts: the left and right somatocoels. The enterohydrocoel also prepares for further division by evaginating its ventral and dorsal extremities. The ventral evagination which has considerable size and volume is separated as the **hydrocoel**. The much smaller dorsal evagination becomes the **axocoel**. The remainder of the enterohydrocoel is the **enterocoel** (Fig. 34, 3a, b). It will develop as the future digestive system, but for quite awhile it remains a closed sac without entrance or exit to the external world. The axocoel and the hydrocoel both contribute to formation of the water-vascular system later in ontogeny. For this purpose the hydrocoel assumes a crescentic form and evaginates in five primary lobes. The crinoid axocoel and hydrocoel represent the left first and second coelomic compartments as compared to general echinoderm embryology. The right first and second compartments do not develop in crinoids.

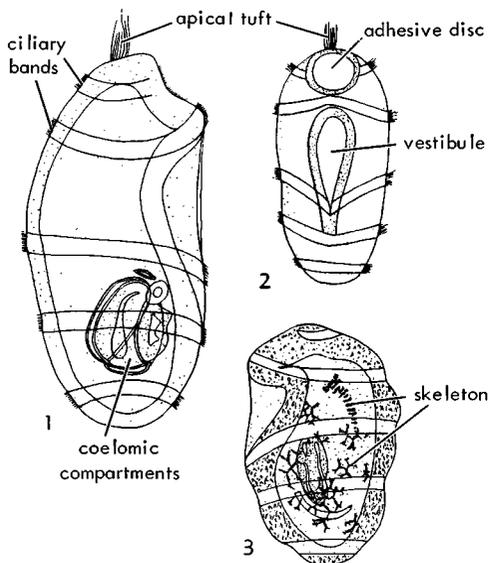


FIG. 35. *Doliolaria* of *Antedon* (after Seeliger, 1892).—1. Position of coelomic compartments in posterior part of larva.—2. Exterior ventral aspect of larva.—3. Skeleton of larva.

Through divisions of the archenteral sac the crinoid embryo assumes its primary bilateral symmetry and primary orientation. It now has well-defined anterior, posterior, ventral, and dorsal sides. The anteroposterior axis runs through the site of the former blastopore located posteriorly. The ventral and dorsal sides are indicated by the positions of the hydrocoel and axocoel, respectively. Left and right sides are indicated by the left and right somatocoels (Fig. 35).

Figure 35 shows that the coelomic compartments occupy only a rather small area in the posterior part of the embryo, exactly the same in position as the original archenteral sac. The larva now has assumed a much more elongated form, the external appearance of which is determined by further development of the ectoderm and mesenchyme. Part of the ectoderm is differentiated into nervous tissue, occurring in several different bands along the embryo. Accompanying them are four external bands of cilia and an apical tuft of cilia at the anterior extremity of the embryo (Fig. 35, 1,2). In part, the ectoderm also differenti-

ates into glandular tissue, mainly concentrated in a small spot near the anterior pole of the embryo, forming there the adhesive pit. Elongation of the embryo is also caused by the further development of wandering mesenchyme cells, formation of which continues in this stage of development. The ventral side of the embryo is determinable externally by the placement of an elongated depression of the body wall, known as the vestibule (Fig. 35,2). This important feature in further development of the crinoid is situated between the first and second ciliary bands.

At the end of its embryonic life the crinoid differentiates some of its mesenchyme into skeleton-secreting cells. Larval-skeleton secretion in echinoderms has been described by OKAZAKI (1960) and others from the developing sea urchin larva. This seems pertinent to the mode of secreting skeletal elements in crinoids, for development of crinoid hard parts is believed to proceed in essentially the same way as in echinoids. If this is true, formation of the crinoid skeleton is intracellular, deposition of calcium carbonate occurring in syncytial cell-masses and being initiated simultaneously in several different spots of the embryonic body wall. Two-dimensional meshworks of the carbonate are thus formed, arranged in two circles, protecting the coelomic compartments at the posterior extremity of the embryo (Fig. 35,3). These circles each contain five future skeletal plates, five to be developed as basals and five others as orals; they are longitudinally in line with one another. A columnar pile of circular carbonate meshes is formed in the anterior half of the embryo. These represent future stem segments or columnals. The embryo now has completed its development and is ready to escape from the egg membrane. It takes a developing *Antedon* larva five days to reach this moment.

## LARVA

The embryonic part of crinoid development is completed in about five days. The embryo ruptures the egg membrane and begins a short life span as a free-swimming larva. The larva, commonly described as a *doliolaria*, has a length of about 0.25 mm.

when it emerges from the membrane. Its free-swimming period is variable in length, known to vary from five to 108 hours. Free-swimming larval stages are more or less suppressed in crinoids that breed their young. In *Phrixometra nutrix* the free-swimming larval stage is even completely suppressed. The embryos develop directly into the stalked pentacrinoid stage and attach themselves to the mother animal (Fig. 36).

Throughout its entire larval life the crinoid is unable to feed, for it still lacks a mouth. The larva is autotrophic. For its supplies of energy it must depend completely on its built-in food reserve, which contains many vitelline substances. The enteric sac is observed to be crowded with cells, interpreted (MORTENSEN, 1920; HYMAN, 1955) as mesenchyme cells wandering into the enteric sac as amoeboid cells, which may have acquired food by phagocytizing degenerated tissues elsewhere in the larva.

During the free-swimming larval period no further development of internal organs occurs. The larva only grows in size and volume, with continuous increase in size and weight. Skeletal plates on the posterior side of the larva develop further. The larva swims with its anterior pole in front and is able to rotate along its longer axis.

At the end of its free-swimming larval life the crinoid prepares to become attached by selecting a suitable spot for fixation with the help of its anterior apical tuft. When such a spot is detected, the larva settles on its adhesive disc, which directly underlies a calcitic attachment disc at the end of the pile of columnal plates. Attachment sites for crinoids with calcite attachment discs generally are stony and firm substrates.

## METAMORPHOSIS

Directly upon settlement of the larva a short period (about 5 days) of accelerated development sets in, introducing radical change in total organization of the larva and in its life habits. The fundamental phenomena dominating the metamorphosis are 1) loss of original bilateral symmetry of the larva by a temporary shift in the position of internal organs and by preponderant growth of the left side of the larva as com-

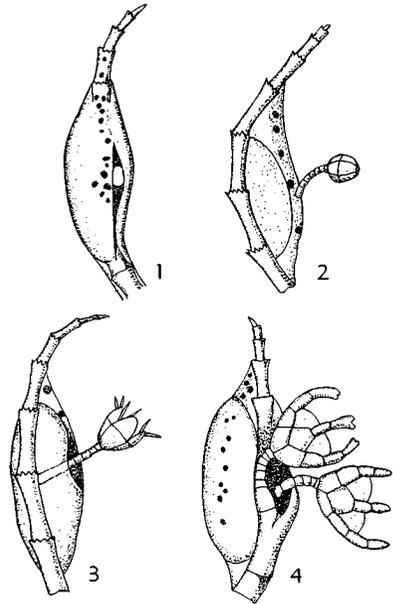


FIG. 36. Genital pinnules of viviparous comatulid *Phrixometra nutrix* (after Mortensen, 1920).—1. Egg in marsupium.—2. Early cystidean stage.—3. Late cystidean stage.—4. Pentacrinoid growth stage, attached to marsupium.

pared to its right side; 2) a rotation of the internal organs amounting to 90 degrees introduces a pentaradial symmetry with its own new orientation; and 3) physiological loss of autotrophic feeding and preparation for heterotrophic feeding, which implies further development of the organ systems that function in feeding.

When just settled, the larva is about 1 mm. long. After settlement, the vestibule—up to now a simple depression of the ventral body wall—becomes invaginated and constricted into a large internal sac, which is destined to play an important role in metamorphosis. Some of the internal organs have temporarily shifted their position. The enteric sac still lies in the posterior part of the larva, and the hydrocoel in ventral position between the vestibule and enteric sac. The axocoel temporarily has an anterior location; it has produced an elongated evagination that opens to the exterior as the hydropore in the ventral part of the body wall. The right somatocoel, developed into a bowl-shaped vesicle partly

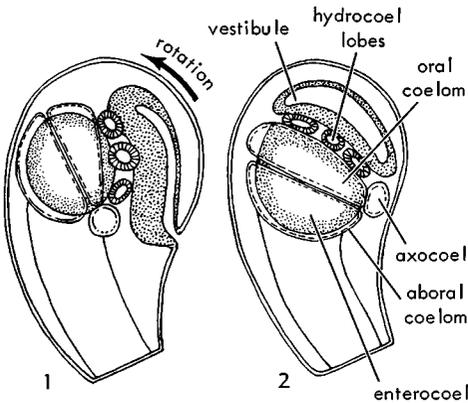


FIG. 37. Rotation of internal organs in *Antedon* larva (after Barrois, 1888).—1. Before rotation. —2. After rotation.

surrounding the enteric sac, has temporarily assumed a position on the dorsal side of the enteric sac. The left somatocoel is located between the right somatocoel and hydrocoel. It is crescentic in shape, embracing part of the enteric sac with blind ends meeting on its anterior side.

Soon after constriction of the vestibule, a rotation of the internal organs completely changes orientation of the larva (Fig. 37, 1,2). A 90-degree rotation brings the vestibule to the free end of the larva opposite the attachment disc. The other organs rotate with the vestibule, retaining their prerotation mutual positions. The former posterior side of the larva now becomes its top and develops as the free oral pole of the animal. The left somatocoel becomes the adoral coelom and the right somatocoel the aboral coelomic compartment. The position of the hydropore denotes the future posterior side. The elongated fixed part of the larva, formerly anterior, now develops as a stalk and the former posterior part of the larva develops as a theca. The theca is completely closed, with its body wall supported by closely abutting circles of five basals and five orals. The basals are aligned longitudinally with the orals, which cover the roof of the vestibule, the basals supporting the lower part of the theca, which includes the enteric sac.

The next step taken by the larva in metamorphosis is to prepare for heterotrophic feeding. Previously, the enteric sac of the

larva has possessed no external openings, the mouth and anus still being absent. For feeding the larva needs to develop primitive food-catching organs and a mouth for receiving the food. In order to achieve this, the central part of the bottom of the vestibule begins to form an evagination that connects with the enteric sac, thus providing a passageway from the sac to the vestibule; these are the future esophagus and mouth. The esophagus is embraced by the five-lobed crescentic hydrocoel, which previously had formed a projection to meet the axocoel and unite with it as the primary stone canal. The central part of the hydrocoel now completely surrounds the esophagus as the future ring canal of the water-vascular system. The five lobes of the hydrocoel first form five primary podia and later on develop as the ring canal of the water-vascular system. The hydrocoel lobes then develop so as to push themselves upward through the bottom of the vestibule, thus forming five primary podia, which are lined with ectodermal epithelium. The larva now prepares to give the external world access to the just-formed mouth and podia. To this end the roof of the vestibule ruptures between the five oral plates, which now open as large valves, giving access to the just-formed mouth and podia. The bottom of the vestibule grows out as the tegmen with the mouth at its center as located originally. The posterior end of the enteric sac makes an evagination located near the primary hydropore on the posterior side. This opens to the exterior as the anus.

Opening of the vestibule occurs about five days after attachment of the larva. During the accelerated development of these days it has not grown very much, for its length is only 1.25 mm. as the vestibule opens.

## CYSTIDEAN STAGE

The stalked crinoid possessing five oral valves and feeding with the help of primary podia is the oldest crinoid growth stage with definite pentaradial symmetry. This is termed the **cystidean growth stage** in zoological literature for some quite obscure reason (no cystoid being known to have the same organization as this crinoid de-

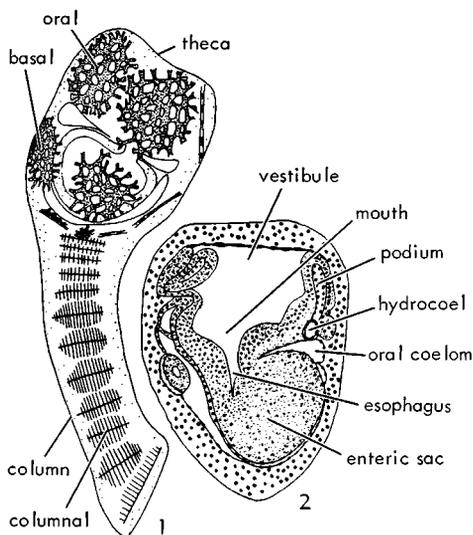


FIG. 38. Cystidean growth stage of *Antedon* (after Seeliger, 1892).—1. External form and skeleton. —2. Anatomical section through anterior free end of larva.

velopmental stage). The juvenile crinoid, morphologically characterized by the presence of a stalk and a theca, and by the absence of arms, remains for about six weeks in the so-called cystidean growth stage (Fig. 38). Physiologically it is characterized by its primitive feeding mechanism of primary podia. During the cystidean stage the development of internal organs goes on but remains incomplete. The genital system and aboral nervous system develop only in later growth stages.

The skeleton of the cystidean crinoid still consists mainly of large basals and orals (Fig. 39,1). Eventually infrabasals and anal plates may become introduced but radial plates do not make appearance until shortly before the pentacrinoid stage.

The podia, once formed, elongate further and divide into groups of three podia situated in alternation with the oral valves (Fig. 39,2). In line with the orals the hydrocoel extends five paired evaginations that develop into five short interradial podia. This brings the total podia up to 25. Each of the longer ones in the triads of radial podia has conspicuous sensory papillae, which in part have a tactile function, serving for the detection and capture

of food particles. They contain some very tiny nerve fibrils, a large muscle fiber, and some mucus-secreting gland cells. The nerve fibrils connect with the ectoneural nervous system, which is the only nervous system active in this growth stage of the crinoid. The ectoneural nervous system follows the course of the hydrocoel and the podia and is well developed there.

The enteric sac grows out into a curved stomach after it has been provided with mouth and anus. The main part of the aboral somatocoel still surrounds the enteric sac and is still crescentic in shape. A small part of the aboral somatocoel is cut off from the main somatocoel mass after its five extensions have been sent off into the stem, where they form the chambered organ and axial canal of the stalk. The remaining part of the aboral somatocoel develops further into the perivisceral coelom. The oral coelom is modified in essentially the

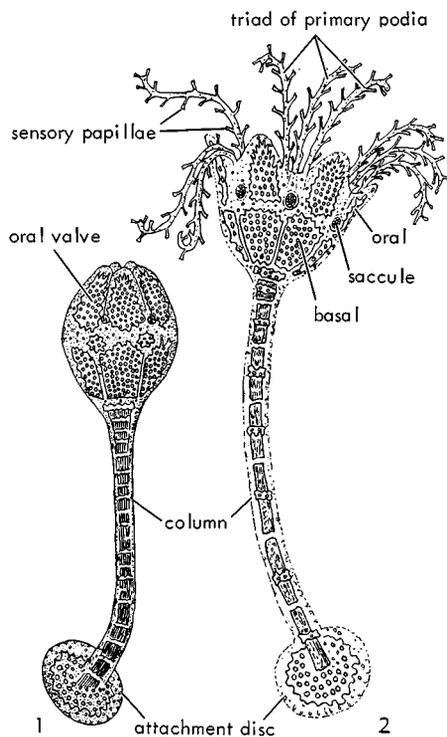


FIG. 39. Morphogenesis of cystidean stages in *Antedon*.—1. Early growth stage (after Thomson, 1865).—2. Late growth stage (after Clark, 1921).

same way as the hydrocoel and its future development everywhere follows the course of the hydrocoel, underlying it as the sub-ambulacral coelom. Both of the coelomic compartments are now crescentic in form with their blind ends meeting on the posterior side to form a vertical membrane, which is thought to play an important role in the anlage of several different internal organ systems. The two coelomic compartments also meet in an equatorial plane so as to produce a horizontal mesentery at the place of their junction.

The axial organ is introduced shortly after separation of the chambered organ from the aboral somatocoel. This gland is reported to develop from the aboral part of the mesentery, which connects with the center of the chambered organ. The traditional opinion is that the primary gonad originates from the axial gland. This may be erroneous, however, since DAWYDOFF (1948) has stated that the definitive gonad originates as an elongated strand of compact cells located in the aboral part of the vertical mesentery. This strand is closely associated with the axial gland. The primary gonad seems to be transitory only, since it is reported to disappear after some time in the developing crinoid.

### PENTACRINOID STAGE

After six weeks in the cystidean growth stage, the juvenile crinoid reaches what is called the **pentacrinoïd stage**, so named for its resemblance to stalked pentacrinoïds. The pentacrinoïd stage is characterized by its development of arms and pinnules (Fig. 40), with consequent adaptational outgrowth of the hydrocoel as the water-vascular system. During all of this stage the crinoid remains attached by its stalk. In comatulids the pentacrinoïd stage ends when the crinoid breaks away from its stalk and starts a free-swimming life. Comatulids may remain for several months in the pentacrinoïd stage. It is doubtful whether one should distinguish a pentacrinoïd stage in the development of stalked crinoids, since they do not break free but remain attached by the stem throughout their life span.

The first sign of a crinoid's arrival at the pentacrinoïd stage is appearance in the

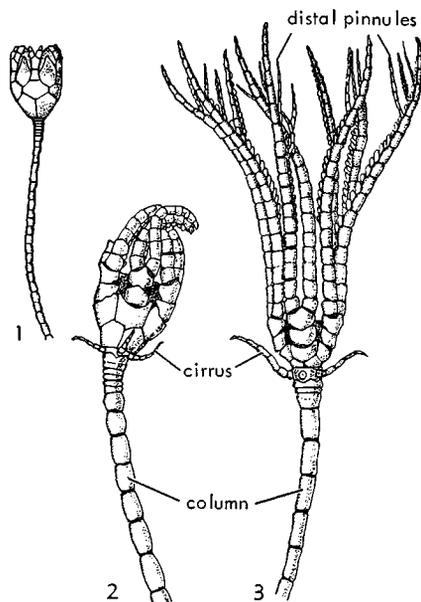


FIG. 40. Morphogenesis of pentacrinoïd stages in *Antedon* (Breimer, n).—1-3. Early, middle, and late growth stages showing (3) absence of pinnules in proximal arm portions of late pentacrinoïd stage, shortly before take-off from column.

theca of five **radial plates** arranged in alternation with the basals (Fig. 40,1). Once the radials are introduced, the theca starts formation of the arms as five large radial extensions. Each radial extension soon becomes supported by skeletal pieces called **brachials**. The internal organization of the radial extensions or arms requires a rather drastic change in the further outgrowth of the internal organs. Inasmuch as the arms are radial extensions of the body, all internal organs of the body must prepare for extending themselves into the arms. This implies a partial reduction of morphologic organization realized in the cystidean growth stage.

Feeding of the pentacrinoïd larva is effected by the arms, which bear ambulacra and podia for this purpose. Hence, the most drastic changes are made in the hydrocoel and its evaginating podia. Most of the original 25 podia disappear and only the five radially disposed primary podia persist. The arms are initiated as radial evaginations of the bottom of the former vestibule, which comprises the five primary

podia (Fig. 40,2). These now grow out as radial canals of the water-vascular system. The adoral and aboral coeloms also form five radial extensions which penetrate into the growing arms as the adoral and aboral coelomic canals. Their contact is the horizontal membrane, which is continuous with the horizontal membrane in the central body cavity. In this mesentery parts of the blood-lacunar and genital systems eventually will be lodged. The vertical mesentery atrophies.

Definite podia are formed on the adoral surface of the arms in groups of three as terminal extensions of the water-vascular system. These triads of podia are placed in alternating order on both sides of a band of differentiated ectoderm, which now develops as the ambulacral epithelium. It differentiates some of its cells into mucus-secreting gland cells and others into attenuated supporting cells provided with cilia. The ectoneural nervous system everywhere underlies the ambulacrum.

Internally the water-vascular system changes its organization also. Up to now the hydrocoel ring has had only one opening to the exterior, obtained by its fusion with the elongated axocoel, which opened outward by means of the primary hydro-pore. Four other such stone canals are added to the original one, one in each interradius. They are formed by fusion of ingrowing canals from the bottom of the former vestibule, and by outgrowing canals from the hydrocoel ring. The five stone canals connect five hydropores in the tegmen with the five interradial sides of the ring canal. Normally these tubular connections are broken and the primary hydropores disappear, but in *Rhizocrinus* a stage with five hydropores seems to be definitive. The small tubes hanging from the ring canal persist. To these free hanging stone canals many others are added in the four regular interradial sides of the ring canal. In the interradial parts of the tegmen many more hydropores may be formed, however, but without direct tubular connections with the stone canals and without a direct correlation in number between pores and stone canals.

When arms grow out, the orals are resorbed, the oral valves atrophy, and the vestibule bottom becomes an adoral mem-

brane or tegmen in which mouth and anus are located. The final stages in the development of the pentacrinoid are reached by further development of the arms and the first appearance of **pinnules**. The five- and ten-armed crinoids all develop these numbers of arms by direct terminal growth of the radial extrusions of the theca. In comatulids the arms have terminal growth sectors that divide after two primibrachs have been formed at the base of the growing arm. Ten arms are now developed, provided with ambulacra and groups of podia on the adoral side. The ambulacra become flanked by a fringed border giving rise to lappets under which the podial triads may hide. Saccules alternate with the lappets. The lappets may be reinforced with skeleton deposition. For a long time the arms remain devoid of pinnules. Up to 20 or 30 brachials may be formed in the free-arm ends before the first pinnule develops. The first pinnules to make appearance are distal ones which provide additional possibilities for food-gathering as the crinoid increases in volume (Fig. 40,3).

At end of the pentacrinoid stage the organism may be a few centimeters long, including the length of its stalk. The top-most columnal or **proximale** has been differentiated with accompanying development of one or more circles of cirri. The proximale unites with the infrabasals as the **centrodorsal**. When its time has come, the pentacrinoid breaks from the stalk and starts swimming around.

## ADULT STAGE

When the juvenile crinoid has left its stalk it is not yet a mature and adult animal. Its juvenile status is easily recognized by the absence of genital pinnules. The **adult stage** is reached when genital pinnules have become differentiated and packed with ripe gametes. The animal is now prepared to take part actively in the reproduction of its species. As most crinoids have only short breeding seasons once every year, it is inferred that juvenile crinoids reach sexual maturity in their first breeding season after birth, hence at an age of about one year old.

The anlage and development of the genital system of crinoids is insufficiently

known. As already stated, the primordial sex cells are probably formed in the vertical mesentery in what could be called a primary gonad. This vanishes, however, as does the entire vertical membrane later in ontogeny. Ripening sex cells appear in the horizontal membrane of mature crinoids. It is believed that the cells are formed in genital cords of the genital tubes and are transported toward the genital pinnules when ripening. The genital pinnules serve

only for storage of the gametes. They are not true ovaries and testes.

Almost nothing is known about the first appearance and development of the aboral nerve system in crinoids. This is surprising, for the aboral nerve system is the main nervous system of crinoids and very conspicuous, present in such well-studied places as the base and arms. All one may speculate is to say that apparently the aboral nervous system develops very late in morphogenesis.

## SKELETAL MORPHOLOGY OF FOSSIL CRINOIDS

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## GENERAL FEATURES

The body of most crinoids consists of two main parts: the **crown** (corona) and the **pelma** (Fig. 41). The pelma comprises the **stem** (column or stalk), its appendages or **cirri** (if any), and the anchorage structures or **holdfast**. The crown is formed by a central mass that contains the main bulk of the viscera, and by five (simple or branched) **arms** (brachia), which are radial extensions of the central mass and are continuous skeletally with its supporting skeleton, or **theca**.

The theca consists of the **cup** or **calyx**, below the free arms, and the **tegmen**, which extends inward from bases of the free arms and forms a roof over the body cavity. The cup is joined to the topmost segment (**columnal**) of the stem and is primarily composed of lowest ray plates (**radials**) accompanied below by a cirlet of interradially disposed plates designated as **basals**. Such cups are termed **monocyclic** because the radials overlie a single cirlet of plates. All other crinoid cups possess a second plate cirlet (named **infrabasals**) beneath the radials and consequently are classed as **dicyclic**.

All these plates, primary components of the cup, may combine with overlying plates, which are suturally joined more or less firmly together. These latter are identifiable as arm segments (**fixed brachials**) and in many crinoids between-arm plates (**interbrachials**). Supplementary plates in the posterior interray are classed as **anals**. The boundary between lower cup plates of the calyx and higher fixed plates is not prominent, since it is determinable only by the recognition of plates belonging to the radial cirlet, the summits of which are not accentuated.

The tegmen may contain relatively large interradially placed plates named **orals** and associated with them **ambulacral plates** that cover the ambulacra and plates that lay between the ambulacra. In addition, part of the tegmen may be elevated as an **anal pyramid**, **anal sac**, or **anal tube**.

Each of these features, which taken together characterize the crinoids, can show extraordinary modifications or even be lacking. For instance, many fossil crinoids have

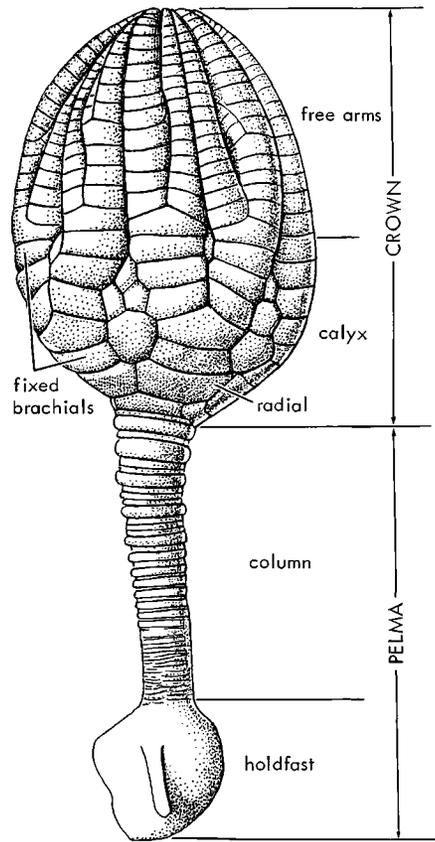


FIG. 41. *Calpiocrinus intermedius* SPRINGER, M. Sil., Eng., complete specimen of flexible crinoid,  $\times 3$  (Springer, 1920).

no holdfast, the stem itself assuming the function of a root. Some have no stem at all, their crown being entirely free or attached directly to the substratum. Others have lost infrabasals or radials and arms, or have retained only one or two brachia. Some have a body comprised of less than a dozen plates, whereas others have several hundred thousand and possibly even more than two million skeletal elements. In size, these echinoderms range from microcrinoids with a theca only one or two millimeters in diameter to relative giants with a theca ten centimeters or more in height and breadth. The arms of some crinoids are as much as one meter in length and

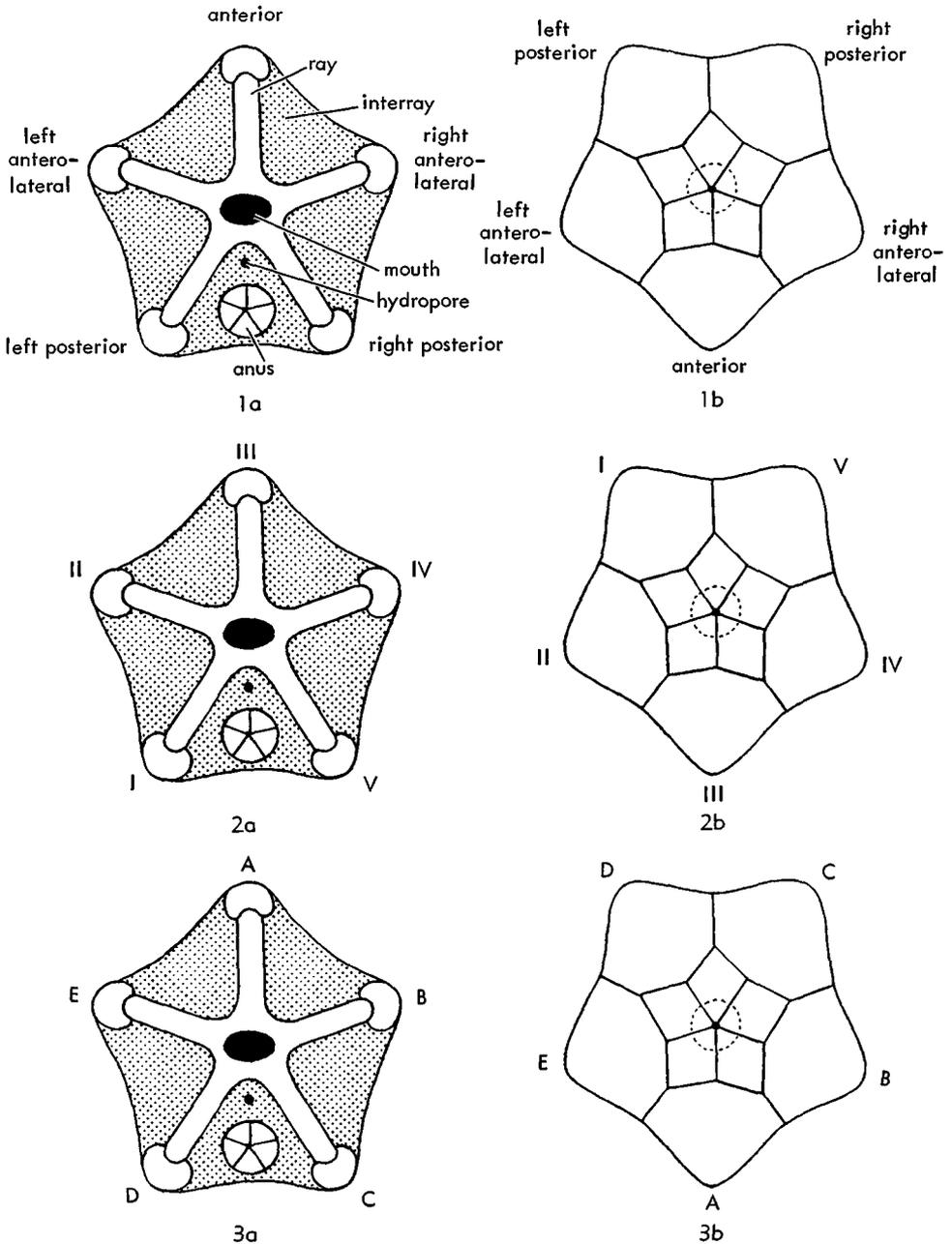


FIG. 42. Orientation of the theca in Crinoidea, in adoral and aboral views according to the systems of: 1a,b, BATHER; 2a,b, JAEKEL; 3a,b, CARPENTER (Ubaghs, n).

crinoid columns 20 meters or more in length have been recorded. When account is taken of all these variations, one must judge that crinoids are an extraordinarily

plastic group of invertebrates, and this diversity itself is certainly not the least of their most distinctive features.

In the course of time the crinoids evolved

in many directions and inhabited diverse marine environments. Because they include many distinctive short-lived forms and are widely distributed in marine deposits of the world, they may be useful, at least in some cases, for age determination and stratigraphic correlation.

## ORIENTATION AND SYMMETRY

The position of the mouth in or near the center of the tegmen in typical crinoids allows recognition of an **adoral** (ventral or actinal) side and an **aboral** (dorsal, abactinal, or adapical) side of the organism. One may therefore distinguish an **adoral skeleton** essentially pertaining to the adoral side, and an **aboral skeleton** located on the aboral side. Such a distinction, although purely topological, is more convenient for descriptive purpose than a distinction between a **primary** skeleton, first developed in ontogeny, and a **secondary** or **supplementary** skeleton, the elements of which are added to or intercalated between primary plates.

For any structure located on the aboral side of the body, the terms proximal and distal refer to directions respectively toward the aboral pole of the cup or away from it. Thus plates of the first (lowest) circlet in the cup or calyx are the proximal elements of the crown, and the top ossicle of the stem is the proximal element of the stem. For adoral elements of the theca, however, it is the center of the tegmen that is considered to be the proximal point.

As in most radiate echinoderms, the skeletal individual elements, termed **ossicles**, of most crinoids have a quinquerradiate arrangement. Thus, the crown may be divided into five **rays** alternating with five **interrays**. The rays consist of the radials and all structures (mainly arm plates) supported by them. The midline of each ray is a **radius**; it corresponds to the trace of a plane passing through the oral-aboral axis of the body and dividing the ray into two equal parts. The body elements bisected by such a plane are **radial**, or more precisely **perradial**, in position. In similar manner, the interrays, that is to say the five sectors comprised between the five rays, are bi-

sected by five **interradii**, and the structures located between the rays are said to be **interradial** in position.

For designating individual radii and interradii (or rays and interrays) most workers on fossil crinoids have used a method initiated by WACHSMUTH & SPRINGER (1889b), though generally attributed to BATHER (1890a, 1900a), or directly derived from it (Fig. 42, *1a,b*). The key for use of this method is furnished by position of the anus, which is usually situated on the tegmen in one of the interrays. Accordingly this interray is conventionally designated as **posterior** and the opposite ray as **anterior**. Now with the crinoid in its natural position, the mouth directed upward and the anal side toward the observer, it is possible to distinguish right and left sides, which respectively correspond to the right and left sides of the observer. To preserve this orientation when the crinoid is viewed from above, the anal side must be nearest the observer (downward in a figure); when viewed from below, the anal side must be away from the observer (upward in a figure). According to their position, the rays are respectively called **anterior, right anterolateral, right posterior, left posterior, and left anterolateral**; similarly, the interrays are designated as **right anterior, right posterolateral, posterior, left posterolateral, and left anterior** (Fig. 42, *1a,b*) or, as suggested by MOORE (1952a), **anteroright, posteroright, posterior, posteroleft, and anteroleft**. However, many authors, including BATHER in his first works, have used a more simple nomenclature and called both lateral rays and interrays respectively **right anterior, right posterior, left posterior, and left anterior**.

An alternative method of orientation, judged more natural and less confusing by its author, was proposed by JAEKEL (1918) (Fig. 42, *2a,b*). Starting from the interray which in cystoids contains the hydropore and gonopore and which corresponds generally to the anal interray of crinoids, he designated the ray at left of the pores by the Roman numeral I and the remaining rays counted in clockwise direction (in adoral view) by the four succeeding numerals II-V, so that the hydropore and gonopore (and in crinoids the anus) come to

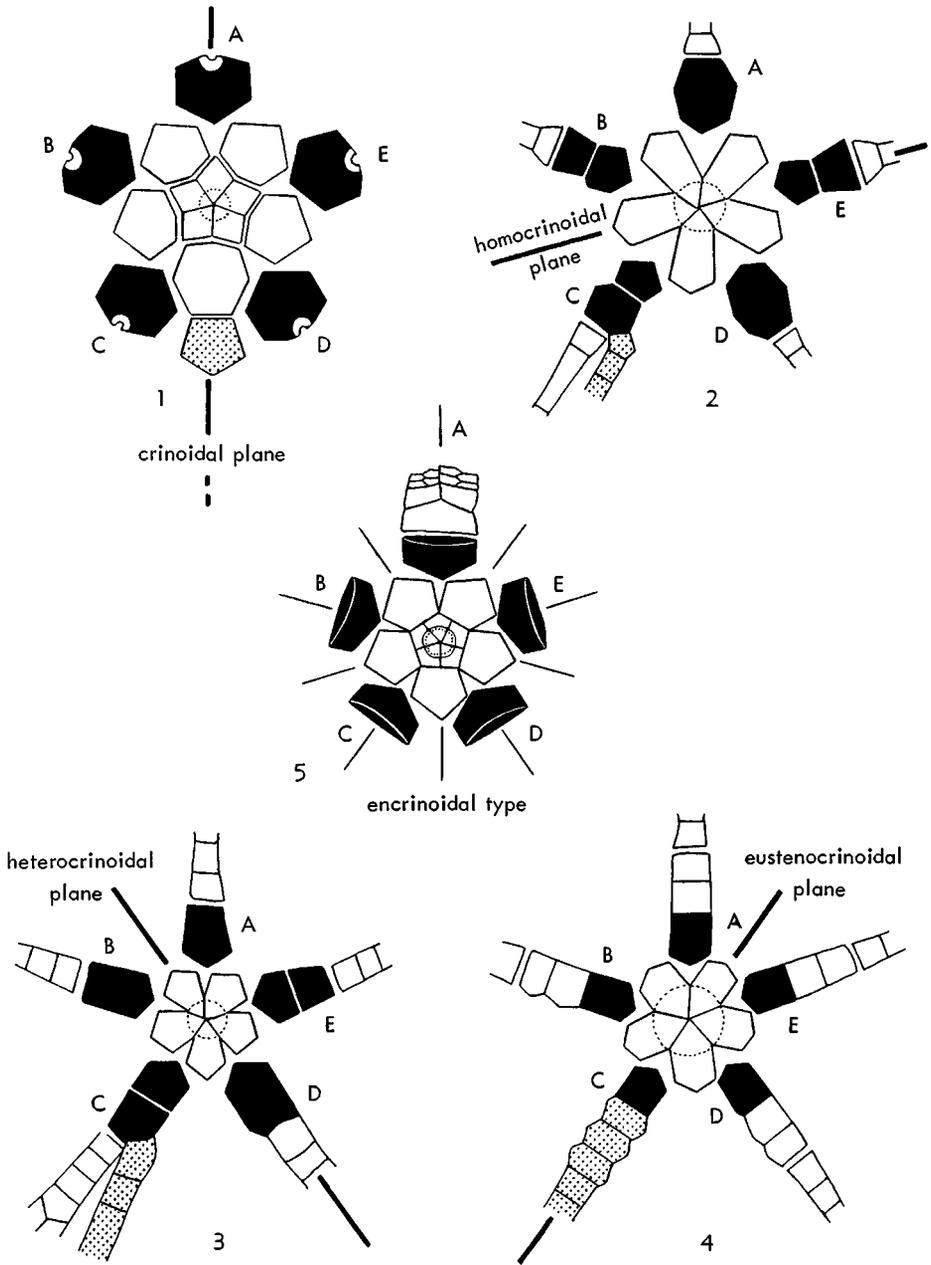


FIG. 43. Orientation of bilateral symmetry plane in some inadunate crinoids (mod. from Moore, 1962b).  
 1. Crinoidal plane, *Cyathocrinites*.  
 2. Homocrinoidal plane, *Homocrinus*.  
 3. Heterocrinoidal plane, *Heterocrinus*.  
 4. Eustenocrinoidal plane, *Eustenocrinus*.  
 5. Encrinoidal planes, *Sinocrinus*.

lie in V-I interray. This system, in spite of simplicity and suitability for the purpose

of comparison among echinoderms, has practically never been applied to crinoids.

In this *Treatise* the nomenclature introduced by P. H. CARPENTER (1884a) has been accepted (Fig. 42,3a,b). The letter *A* is assigned to the ray opposite the interray containing the anus, and *B*, *C*, *D*, and *E* to other rays, in clockwise succession in adoral view, and counter-clockwise sequence in aboral view. The interrays are designated by the letters of rays that bound them (*AB*, *BC*, *CD*, *DE* and *EA*).

Quinqueradial symmetry is rarely perfect in crinoids, for usually it is disturbed by a bilateral symmetry, which is determined typically by position of the anus in one of the interrays of the tegmen and generally associated with this in most Paleozoic forms by the presence of additional plates and other distinctive features in one of the interrays of the cup. The plane of bilateral symmetry passing through the oral-aboral axis, the anus and hydropore (if present), is called the **crinoidal plane of symmetry** (Fig. 43,1). It is particularly obvious in Paleozoic crinoids, and may be considered as the normal crinoid plane of bilateral symmetry.

Other more or less dominant planes of bilateral symmetry may exist in crinoids. One is exemplified by the recent comatulid family Comasteridae (see above, p. T20). Others are illustrated by disparid inadunates, in which the structure of the body and particularly the presence and arrangement of undivided and compound radials allow recognition of three different planes

of bilateral symmetry: 1) **homocrinoidal plane**, which passes through the *E* ray and *BC* interray (Fig. 43,2); 2) **heterocrinoidal plane**, which coincides with the *D* ray and *AB* interray (Fig. 43,3); 3) **eustenocrinoidal plane**, which bisects the *C* ray and *EA* interray (Fig. 43,4). According to LANE & WEBSTER (1967), the homocrinoidal plane corresponds to the larval dorsoventral symmetry plane.

These alterations from normal pentamer symmetry are not the only ones found among crinoids. Some others may be mentioned, such as produced by: 1) **reduplication of rays**, as in recent *Promachocrinus*, which has ten radials and ten arms at the adult stage; 2) **reduction of rays** from the normal five to four, three, two, or even a single ray; 3) **inequality of rays** in size; 4) **grouping of rays** into a **bivium** and **trivium**, as in the recent *Holopus*; and 5) **torsion of rays**, as in the flexible *Mespilocrinus*. Some of these modifications may depend on ecology, for instance, in rheophilic species, which may lose their radial symmetry and acquire a purely adaptive bilateral symmetry.

Finally, in what has been called the **encrinoidal type** of bilateral symmetry (MOORE, 1962b) the cup may show perfect pentamer symmetry, so that none of the rays can be distinguished from others and each one coincides with a plane of bilateral symmetry (Fig. 43,5).

## ABORAL SKELETON

The **aboral skeleton** includes every skeletal element located in the teguments that form the surface of the body opposite to that containing the mouth and ambulacra. It comprises 1) all the ossicles of the column, with its appendages and anchorage structures, 2) the plates that compose the aboral cup or calyx (except interbranchials), and 3) the ossicles that support the arms and the pinnules. Morphologically the interbranchials belong to the adoral skeleton, but since they are an important component of the calyx of many Paleozoic crinoids, it has been judged convenient to treat them along with the other elements that form this part of the theca.

## STEM

### GENERAL FEATURES

Most adult fossil crinoids possessed a stem. Only in a few species the stem became more or less atrophied or lacking altogether in the adult growth stage. Generally, the stem was well developed, and displayed wide diversity in size and shape. Its characters are diagnostic for some Paleozoic species and genera, and for a large percentage of Mesozoic and Cenozoic species.

The diameter of the stem in fossil crinoids ranges from less than 1 mm. to more than 10 cm. According to BOUŠKA (1946), a stem fragment composed of several col-

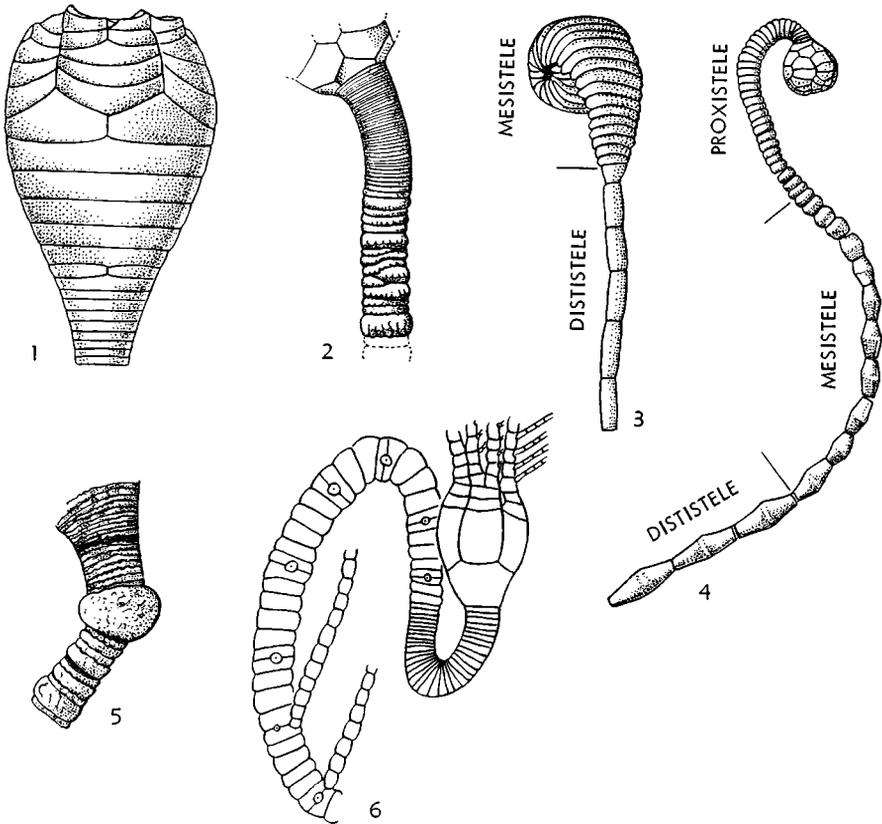


FIG. 44. Xenomorphic crinoid columns.

1. *Apiocrinites parkinsoni* (VON SCHLOTHEIM), M. Jur., France, with enlarged proxistele,  $\times 0.7$  (de Loriol, 1882-84).
2. *Onychocrinus diversus* MEEK & WORTHEN, Miss., USA (Iowa), proxistele and part of mesistele,  $\times 1$  (Springer, 1920).
3. *Ammonicrinus doliiformis* WOLBURG, M.Dev., Ger., with abrupt change between coiled mesistele and dististele, ca.  $\times 1$  (mod. from Wolburg, 1938b).
4. *Mespilocrinus konincki* HALL, L.Miss., USA (Iowa), with well-differentiated proxistele, mesistele, and dististele,  $\times 1$  (Springer, 1920).
5. *Nevadacrinus geniculatus* LANE & WEBSTER, Perm., Nevada, with bent column and greatly enlarged columnal between proxistele and mesistele,  $\times 2$  (Lane & Webster, 1966).
6. *Camptocrinus crawfordvillensis* SPRINGER, Miss., USA (Ind.), diagrammatic representation of part of crown, proxistele, and portion of mesistele,  $\times 3$  (Van Sant in Van Sant & Lane, 1964).

uminals (doubtfully attributed to *Pernocrinus*) from the Lower Devonian of Bohemia has a maximum diameter of 11.5 cm. In many crinoids the stem tapers or expands distally or remains essentially constant in width throughout most of its length.

The total length of crinoid stems belonging to different species is rarely known. It must have been enormous (more than 20 m.) in some Mesozoic pentacrinids, but

this is exceptional. Most species had columns probably not exceeding 1 m. and generally much shorter. For instance, in the famous Crawfordville fauna (Mississippian) found in Indiana it appears that one group of crinoids lived with crowns raised 20 to 25 cm. above the sea floor and another group had stems 60 to 100 cm. long (LANE, 1963b).

In cross section, the majority of fossil crinoid stems are circular, many are pen-

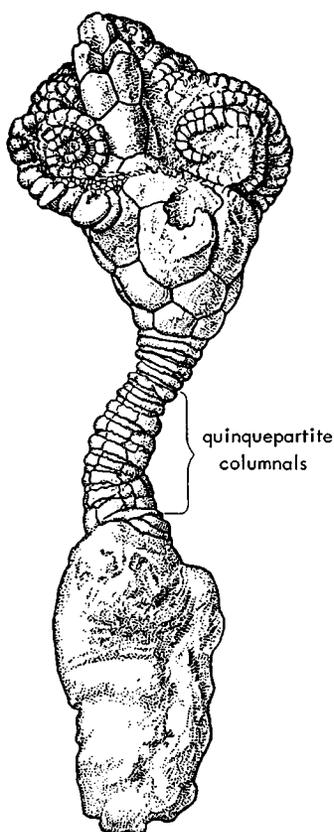


FIG. 45. *Euspirocrinus spiralis* ANGELIN, Sil., Gotl., with partially quinquepartite column,  $\times 2$  (Bather, 1893a).

tagonal, stelliform or elliptical, and a few are quadrangular or crescentic.

In longitudinal aspects, the stem may be uniform or almost uniform from end to end (**homeomorphic**), but it may also be more or less differentiated into distinct regions (**xenomorph**, Fig. 44), according to shape, size, proportions, arrangement and ornamentation of its component **ossicles (columnals)**. Frequently, a proximal part (**proxistele**) may be distinguished from an intermediate part (**mesistele**) and a distal part (**dististele**); in some stems more than three regions are recognizable. Differences between these parts have an ontogenetic significance, since in any crinoid column the proxistele is last-formed and the dististele, earliest-formed.

Any part of a stem comprising two or more columnals in anatomical connection is termed a **pluricolumnal**.

Each columnal generally is composed of a single ossicle. In some Paleozoic crinoids, however, it consists of five separate pieces (**pentameres**). Ordinarily the pentameres of successive columnals do not alternate, so that the stem is quinquepartite, that is, divided into five sectors by five longitudinal sutures (Fig. 45). All known species provided with quinquepartite stems belong to inadunate genera or to the camerate genus *Cleiocrinus*. Very different in origin is the secondary fragmentation of columnals into more or less irregular pieces, as illustrated, for example, by a highly specialized representative of the Crotalocrinitidae (*Pernero-crinus*).

The stem is pierced by a longitudinal, usually central, **axial canal**, which in recent crinoids contains coelomic and nervous extensions from each of the five lobes of the chambered organ. It is possible that in some Paleozoic crinoids with an extremely wide canal, the axial canal lodged other organs or served other functions also, but what organs or functions is not known.

A relation occurs between orientation of the stem and that of the proximal cup plates (Fig. 46). This relation is expressed by the so-called "law of WACHSMUTH & SPRINGER" (1885, p. 229), which in fact is an empirical rule, liable to exceptions, and applicable only to quinquepartite or pentagonal stems or axial canals. According to this rule, in dicyclic crinoids (Fig. 46,1) the columnal pentameres and outer angles of the stem are directed interradially and therefore alternate with the infrabasals, whereas the longitudinal sutures, sides of the stem, angles of the axial canal, and attachments of cirri are located perradially. On the contrary, in monocyclic crinoids (Fig. 46,2) the columnal pentameres and outer angles of the stem are perradial, whereas the longitudinal sutures, sides of the stem, angles of the axial canal, and placement of cirri are interradial.

Exceptions are known in regard to all of these features. Some are only apparent and result from the fact that in some crinoids the infrabasals, which are present in

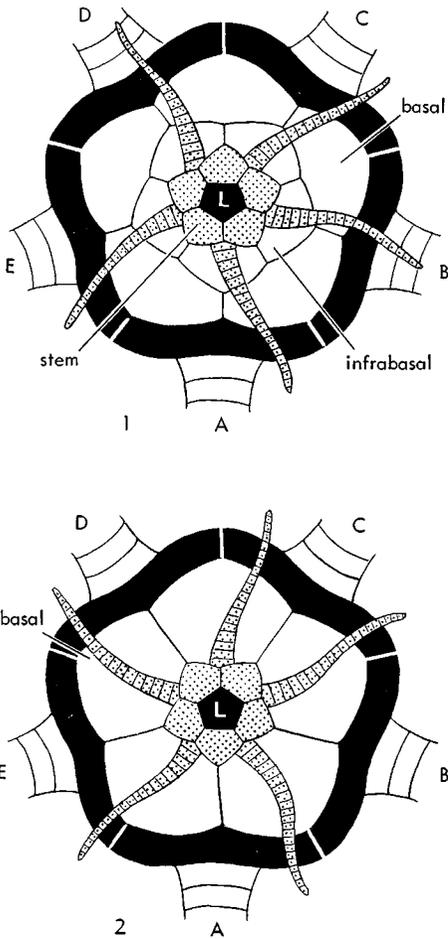


FIG. 46. Diagrammatic aboral views of dicyclic (1) and monocyclic (2) crinoids, showing orientation of various columnal features with reference to "law" of WACHSMUTH & SPRINGER (Ubaghs, n). [Explanation: Rays identified by letter symbols of CARPENTER system. Basals, infrabasals and arm-plates unshaded; radials and lumen (L) of axial canal of stem black; transverse section of column and cirri stippled.]

juveniles or near ancestors, are invisible or absent in adults. Such crinoids, monocyclic in appearance, are really dicyclic, and for them consideration of stem orientation allows recognition of concealed or former presence of infrabasals. But other exceptions cannot be explained in this way. For instance, positions of the pentameres generally alternate with those of the axial

canal angles (Fig. 47,1). Some Ordovician species, however, including *Aethocrinus moorei* and *Grenprisia billingsi*, differ from all other species by having both pentameres and axial canal angles identically directed (Fig. 47,2). Moreover, in the first-mentioned species, the pentameres, instead of alternating with proximal thecal plates<sup>1</sup> in accordance with general rule, are identical with them in orientation (Fig. 48,1,3). The reasons of such differences may have a phylogenetic significance, but they are still obscure. Other exceptions concern the exterior angles of the stem, which usually correspond with pentameres but in some crinoids do not. The axial canal angles may be differently oriented as they ought to be according to "law." BATHER (1893a, p. 44) reported that a stem occurring in the Upper Silurian of Gotland has angles of both stem and axial canal and the longitudinal sutures all with the same orientation. In the recent comatulid *Antedon bifida*, the first-formed cirri are radial, but second-formed cirri are interradial. These diversities of plan suggest that actual changes of orientation can take place or secondary structures can obscure primitive arrangements.

It is generally agreed that the crinoid stalk originated from either an aboral evagination of a more or less globose theca (BATHER, 1900a) or a constriction of the posterior part of an elongated wormlike body (JAEKEL, 1918).<sup>2</sup> In either case, it is supposed that the primitive stem included a spacious cavity surrounded by an integument of numerous irregularly arranged skeletal pieces. Such a primitive stage has not been found among crinoids, but it occurs in several Cambrian Crinozoa, such as the eocrinoid *Gogia*, the lepidocystoid *Lepidocystis*, and the crinozoan *Echmatocrinus* discovered by SPRINKLE in 1967 in

<sup>1</sup> According to PHILIP & STRIMPLE (1971), these plates (herein called infrabasals) should be considered as homologous with proximal pentameres. Reasons for rejecting this alternative interpretation have been given by UBAGHS (1969, 1972).

<sup>2</sup> Another origin of the crinoid stem has been postulated by A. H. CLARK (1910c, p. 213), who supposed the columns of the recent and most fossil crinoids to be homologous to the central plate of the presumed common ancestor of crinoids and echinoids; this plate would have gradually become thickened and elongated and developed transverse fractures which later would have been modified into definite articulations.

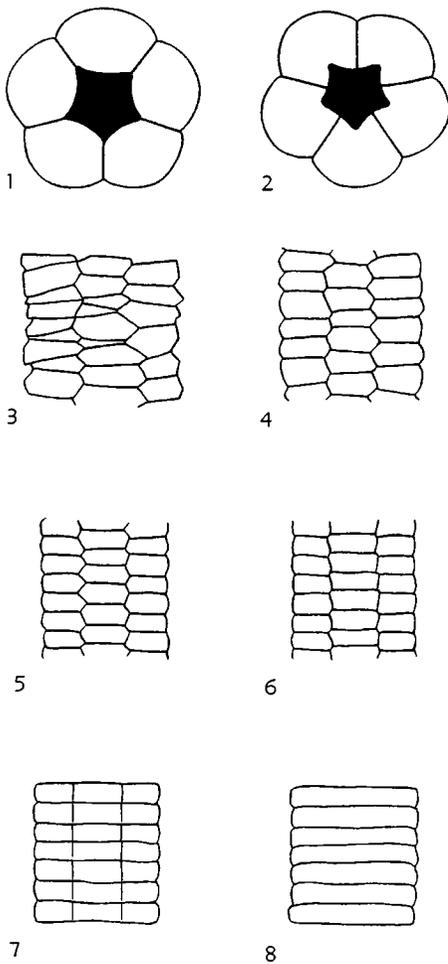


FIG. 47. Orientation and evolution of pentamerism in the column (Stukalina, 1967).—1. Diagrammatic transverse section, with angles of axial canal (black) alternating with pentameres.—2. Diagrammatic transverse section, with angles of axial canal having same orientation as pentameres.—3-8. Diagrammatic morphological series of pluricolumnals showing how the pentameres, originally irregular and alternating (3,4), presumably were arranged in horizontal rows (6,7), and eventually fused to form solid columnals (8).

the Burgess Shale, Middle Cambrian of British Columbia (SPRINKLE, 1973a). Moreover, its former existence in crinoid ancestors is suggested by features of some primitive inadunates, particularly *Aethocri-nus moorei* from the Lower Ordovician of

France (Fig. 48). These features are: 1) irregular interlocking of plates forming the skeletal support of the stem, 2) similar and apparently correlative irregular arrangement of thecal plates and columnals, 3) merging in outer form of the cup into the stem, 4) merging of the thecal cavity into the very large axial canal of the stem, 5) similar ornamentation of the stem and cup plates, 6) presence of numerous irregular pieces in the distal region of the stem, that is to say, in the earliest formed part of the stem during development.

The next stage in evolution of the crinoid stem probably was characterized by progressive introduction of pentamerism (Fig. 47,3-8). At some time the individual hexagonal plates were supposedly arranged in alternating circlets of five around a very wide axial canal. Then the plates or pentameres no longer alternated, but were arranged in horizontal rows divided by five longitudinal sutures. Finally the pentameres of each row became fused to form monolithic columnals, at first still retaining wide axial canals or a quinquereadial arrangement of markings on the joint faces, or both. Such an evolution is not entirely hypothetical, for it may be traced in the limits of single stems in which the quinquepartite columnals of the distal region are replaced by monolithic columnals in a proximal direction (Fig. 45).

In most crinoid groups, the changes described above were accomplished before Ordovician time or during the first part of this period, for in Ordovician rocks the number of columnals with pentameres placed at different levels was already very small compared with that of monolithic columnals or with columnals composed of pentameres placed at same levels. During the following periods, the quinquepartite columnals disappeared progressively: seven genera with such columnals have been reported from the Silurian, three from the Devonian, two from the Mississippian, and only one from the Permian (SIEVERTS-DORECK, 1957b).

#### NODALS AND INTERNODALS

Columnals may be all alike throughout a crinoid stem or most of it in xenomorphic stems, or they may differ in shape

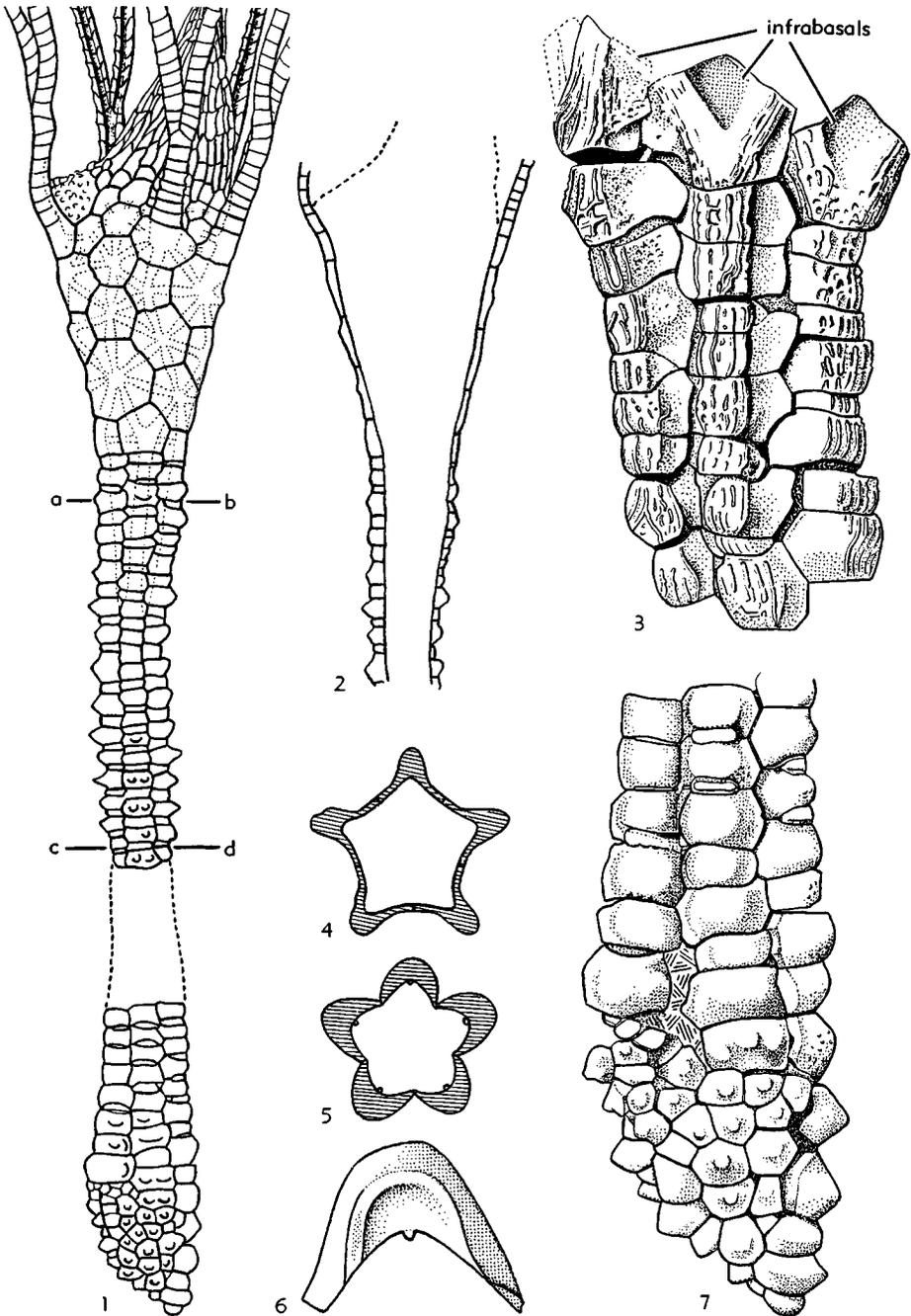


FIG. 48. *Aethocrinus moorei* UBAGHS, L.Ord., France (Ubaghs, 1969).

- 1. Reconstruction of an almost complete specimen, CD-interray view,  $\times 1.5$ .
- 2. Diagrammatic sagittal section showing how the thecal cavity progressively merges into the large axial canal of the column,  $\times 1.5$  (Ubaghs, n).
- 3. Proximal portion of column and infrabasals,  $\times 10$ .
- 4, 5. Transverse sections of column at levels marked a-b and c-d in Fig. 1,  $\times 3$ .
- 6. Distal face of a columbal pentamere,  $\times 10$ .
- 7. Distal end of column,  $\times 3$ .

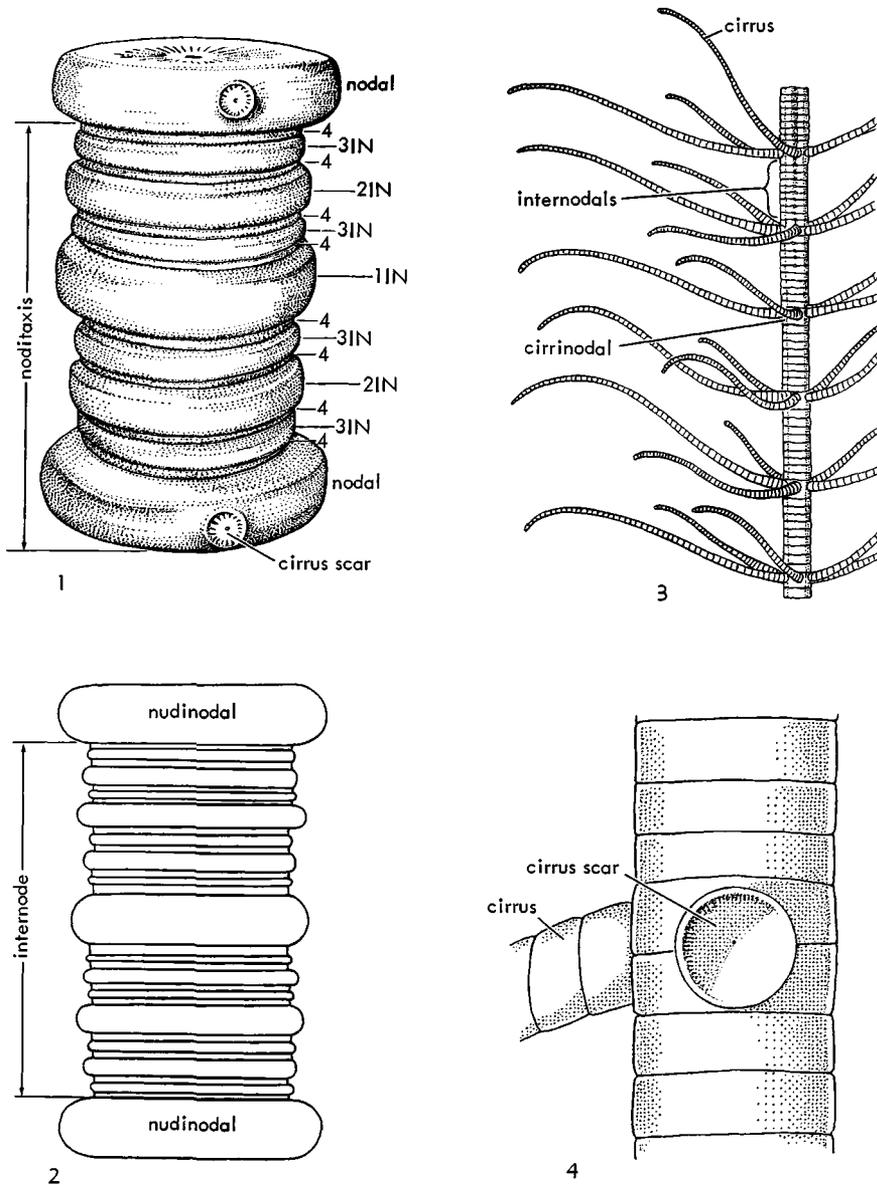


FIG. 49. Morphology of heteromorphic column.

1. Complete noditaxis and additional cirrinodal, 15 internodals (IN) divisible into four orders (Moore, Jeffords, & Miller, 1968).
2. Complete internode and two nudinodals, 31 internodals divisible into five orders (Ubaghs, n).
3. *Teliocrinus springeri* (A. H. CLARK), recent,

- India, part of column, with long cirri arranged in whorls of five,  $\times 2$  (Clark, 1915a).
4. *Austinocrinus mexicanus* (SPRINGER), U.Cret., Mexico, part of column and cirrus, with cirrus scar on two nodals (compound nodals),  $\times 2.5$  (Springer, 1922b).

and height at various levels. In the first case, the column (or parts of it in a xeno-

morphic stem) is said to be **homeomorphic**, in the second, **heteromorphic**. Notice must

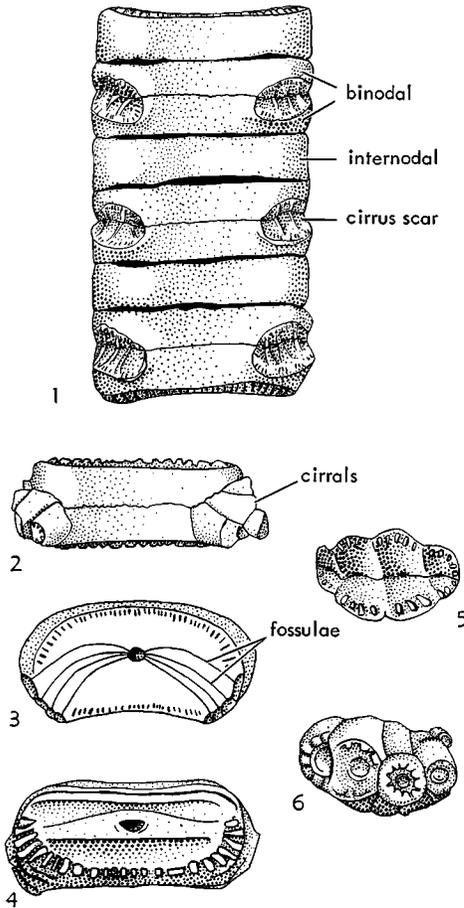


FIG. 50. *Campptocrinus compressus* WRIGHT, L. Carb., Scot. (Ubaghs, n).—1. Portion of column seen from cirrus-bearing side,  $\times 6.5$ .—2. Binodal, with proximal cirrals still attached to them,  $\times 6.5$ .—3. Synostiosal articulation between binodals,  $\times 6.5$ .—4. Synarthrial articulation between binodal and internodal,  $\times 6.5$ .—5. Compound cirrus scar,  $\times 13$ .—6. Distal aspect of proximal cirrals showing articula,  $\times 13$ .

be made of apparently homeomorphic, but actually heteromorphic, stems in which longitudinal sections reveal the existence of thin and narrow columnals, which are not visible externally.

In heteromorphic stems the largest and most conspicuous columnals are called **nodals** and the smaller columnals between them are termed **internodals**. All internodals between a pair of sequent nodals form an **internode**, and a nodal plus the

internode on its proximal side is a **noditaxis** (Fig. 49,1-3).

In recent crinoids, each nodal is characterized by bearing a whorl of generally five articulated appendages, or cirri (Fig. 49,3). Many fossil crinoids have the same arrangement, or their nodals are provided with a smaller number of cirri down to a single one. On the other hand, many fossil species have no cirri. One may therefore distinguish between **cirrinodals** (having cirri) and **nudinodals** (lacking cirri) (Fig. 49,2). In some species, two or more columnals may share in bearing a cirrus; such columnals may be defined as **compound nodals** (Fig. 49,4). In a few fossil crinoids, like the camerate genus *Campptocrinus*, the cirri are equally carried by closely united columnals with a more or less vanished intercolumnal suture; these closely paired nodals are called **binodals** (Fig. 50).

All internodals of an internode may be identical, but they may also differ in diameter and height, according to their order of appearance and stage of growth (Fig. 49,1,2). Those first formed after the limiting nodals are the largest: they are distinguished as first-order internodals or **priminternodals**; those formed next, and therefore next in size, are second-order internodals or **secundinternodals**; in the same way, third-order internodals (**tertinternodals**), fourth-order internodals, and so on, may be recognized. In a very few stems, differences in height and diameter among cirrinodals have been also reported; this suggests either existence of two orders of nodals or secondary development of cirri on some internodals. The distinction between nudinodals and internodals, as well as between internodals of different orders, is always more obvious in proximal than in distal parts of the stem, where it tends to disappear and commonly vanishes completely.

#### PROXIMALE AND CENTRODORSAL

In a number of Articulata, at the top of the column occurs a large, undivided ossicle called **proximale**, which is formed by one enlarged columnal or by two or several fused proximal columnals (Fig. 51). It is permanently attached to the theca by an immovable articulation.

The proximale in Thiolliericrinidae and

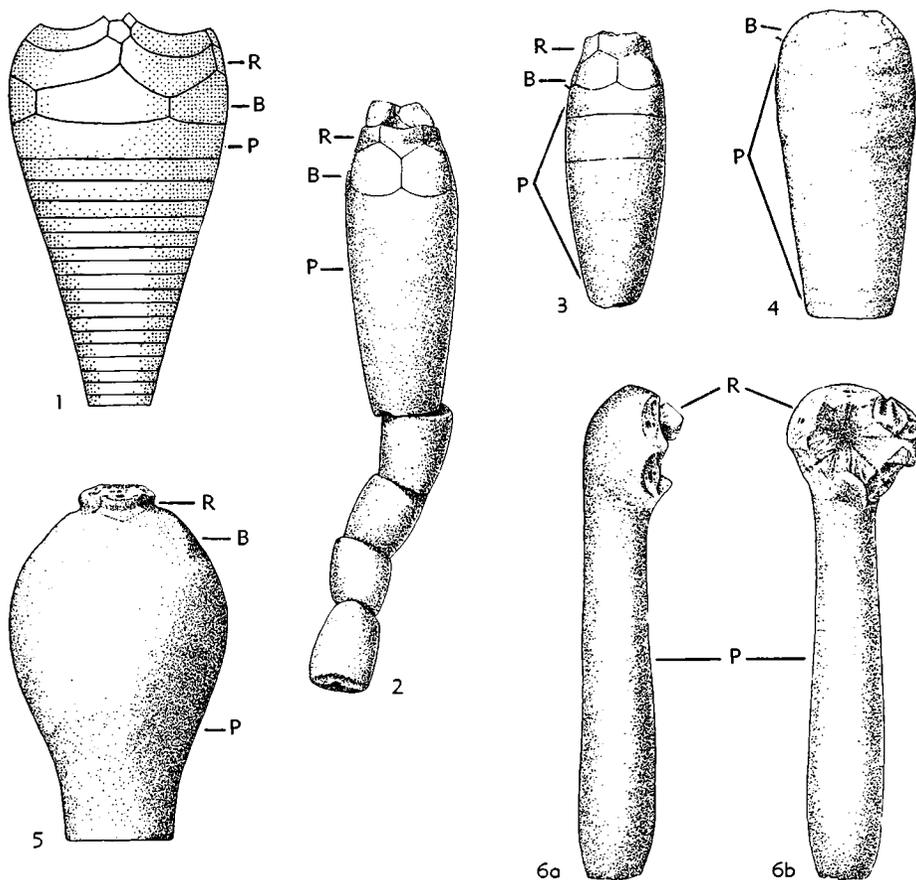


Fig. 51. Morphology of proximale. [Explanation: *B*, basal; *P*, proximale; *R*, radial.] (All Rasmussen, 1961, except 1, from de Loriol, 1882-84.)

- 1. *Apiocrinites meriani* DESOR,  $\times 0.5$ .
- 2. *Bourgueticrinus danicus* NIELSEN, U.Cret., Denmark,  $\times 5$ .
- 3. Same, with distinct sutures in the proximale,  $\times 5$ .
- 4. *Bourgueticrinus cylindricus* M'COY, U.Cret., Eng.,  $\times 2.5$ .
- 5. *Bourgueticrinus papilliformis* GRIFFITH & BRYDENE, U.Cret., Eng.,  $\times 5$ .
- 6a,b. *Hemicrinus canon* (SEELEY), L.Cret., Eng., lateral and adoral views of cup (fused with proximale),  $\times 1.25$ .

Comatulida is known as the **centrodorsal**, an unusually large, discoidal, hemispheric, columnal, or a more or less conical ossicle, which forms the aboral portion of the theca and generally bears numerous cirri, except on its aboral central area (Fig. 52). In some Comasteridae, the centrodorsal is reduced to a thin noncirriferous stellate plate, and in certain specimens of the Thiollieriacrinidae cirri are rudimentary or altogether lacking. The ontogeny of recent comatulids shows that only the top columnal is

involved in formation of the centrodorsal, to which, however, are also incorporated the infrabasals in species having infrabasals introduced during development. The centrodorsal has a more or less well-developed central concavity (**centrodorsal cavity**) for reception of the chambered organ and associated structures (Fig. 52,5,6); its inner wall is studded with minute pores, inner openings, or passageways leading to axial canals of the cirri. Five depressions or perforations (**radial pits**) that harbor

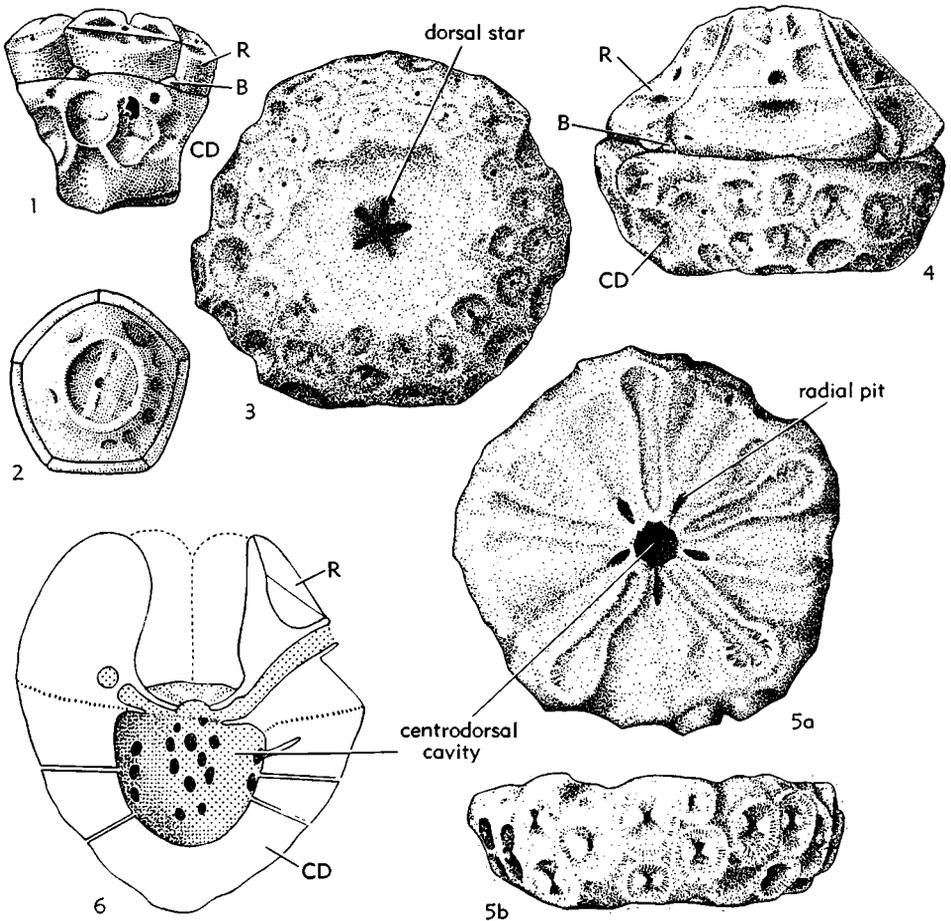


FIG. 52. Morphology of centrodorsal. [Explanation: *B*, basal; *CD*, centrodorsal; *R*, radial.]

1. *Thiolliericrinus ribeiroi* LORIOU, U.Jur., Portugal, side view,  $\times 2$  (Bather, 1900a).
2. *Thiolliericrinus favieri* (ÉTALLON), U.Jur., France, aboral view with articulum,  $\times 2$  (Bather, 1900a).
3. *Thiolliericrinus ribeiroi* (LORIOU), U.Jur., Portugal, dorsal view,  $\times 2$  (Bather, 1900a).
4. *Glenotremites discoidalis* GISEN, U.Cret., Czechoslovakia, adoral and side views of centrodorsal,  $\times 5$  (Rasmussen, 1961).
5. *Glenotremites discoidalis* GISEN, U.Cret., Czechoslovakia, dorsal view,  $\times 5$  (Rasmussen, 1961).
6. *Florometra asperima* (A. H. CLARK), recent, Alaska, vertical section through centrodorsal and radial circlet, enl. (Clark, 1915a).

- 5a. *Glenotremites discoidalis* GISEN, U.Cret., Czechoslovakia, dorsal view,  $\times 5$  (Rasmussen, 1961).
- 5b. *Glenotremites discoidalis* GISEN, U.Cret., Czechoslovakia, side view,  $\times 5$  (Rasmussen, 1961).

coelomic extensions may occur on the adoral surface outside the aperture of the central cavity unless that aperture is markedly lobate, in which case they emerge at the extremities of the lobes. They are lacking in the majority of recent comatulids, but are present in many fossil members of that group and in some extant species. In some forms they penetrate deeply into the skeleton of the centrodorsal and even may divide

and anastomose. In no recent comatulids do these canals appear to open on the dorsal surface, the body wall being continuous over their aboral end, but in some fossil species they perforate the centrodorsal completely and have aboral radial openings (possibly due to erosion, at least in some cases) commonly situated in the lobes of a stellate hollow around the dorsal pole. This is the so-called **dorsal star** of authors

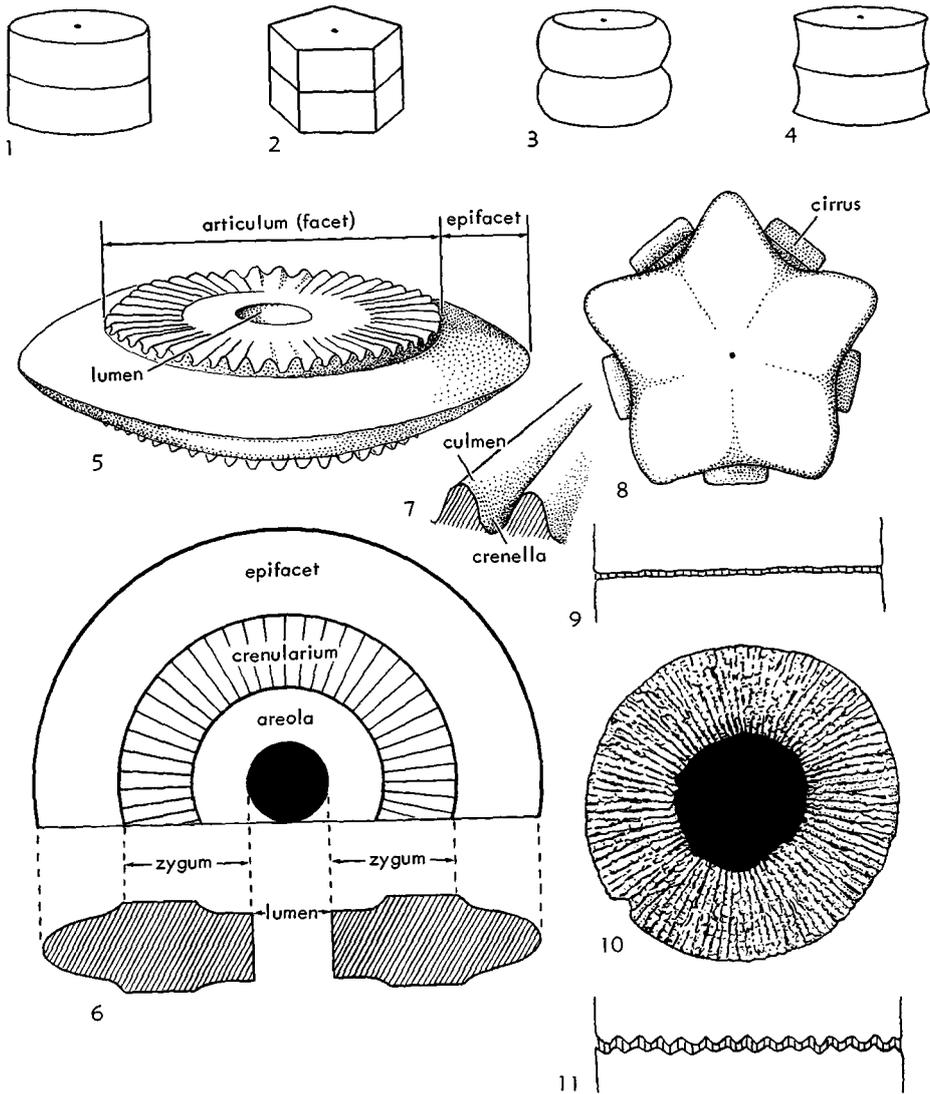


FIG. 53. Morphological features of crinoid columnals.

- 1-4. Various shapes of columnals (diagrammatic) (Bather, 1909a).
- 5,6. Downward and facetal views of a columnal with (below) median longitudinal section (Moore, Jeffords, & Miller, 1968).
- 7. Crenula formed of a culmen (ridge) and a crenella (groove) (Ubaghs, n).
- 8. *Isocrinus* nodal showing smooth surface of distal face as example of synstosomal type of articulation (Moore, Jeffords, & Miller, 1968).
- 9. Diagrammatic transverse profile of juxtaposed synstosomal facets (Moore, Jeffords, & Miller, 1968).
- 10. *Lomalegnum hornidium* MOORE & JEFFORDS, L. Miss., USA (Iowa), facetal view as example of symplectial type of articulation (after Moore & Jeffords, 1968).
- 11. Diagrammatic transverse profile of juxtaposed symplectial facets (crenulate suture) (Moore, Jeffords, & Miller, 1968).

(Fig. 52,3). The real functions of these coelomic extensions into the centrodorsal is

unknown (A. M. CLARK, 1972). In the Thiolliericrinidae the aboral side of the centrodorsal is occupied by a perforated articulation, which allows flexible union with the uppermost stem ossicle (Fig. 52,2). In the Comatulida, the articulation between the centrodorsal columnal next below it breaks at some time during ontogeny, and the animal becomes stemless and free. Exceptionally, remains of this articulation seem to have persisted during life in the shape of an indistinct petaloid impression on the aboral side of the centrodorsal. Not to be confounded with this figure is the so-called dorsal star, which has been just mentioned (Fig. 52,3).

### LATERA

A median longitudinal section of a columnal shows that the outward facing sides or *latera* (sing., *latus*) may be straight, convex, or (rarely) concave (Fig. 53). If the latera are straight and the transverse section circular, the stem is cylindrical (Fig. 53,1). It is basaltiform, if the latera are straight and the transverse section pentagonal (Fig. 53,2), and moniliform (Fig. 53,3), if the latera are markedly convex and the transverse section circular.

The term *epifacet* is given to the projecting *latus* that surrounds the *facet* or *articulum* (pl., *articula*) of a columnal, that is to say, the surface of a columnal serving for articulation with a contiguous columnal (Fig. 53,5). The epifacet may be considerably extended outward.

The latera of crinoid columns are variously ornamented by spines, nodes, ridges, grooves, and scars serving for attachment of cirri or other outgrowths.

Pores may also be present on the latera of columnals. If they are connected with the axial canal of the stem by passageways through the columnals, they may correspond to abortive cirri, for it happens that some of them are still associated with small cirrus scars. [Such pores are not to be confounded with the so-called *interarticular radial pores* (or interarticular pores of P. H. CARPENTER, 1884a) visible between the columnals in re-entrant angles of the quinquestellate stems of isocrinid crinoids; such pores are produced by the apposition of joint grooves radiating outward on the

joint-faces but without communicating with the axial canal.]

### ARTICULA

Any face of a columnal, or more generally of a pelma element that serves for articulation with a contiguous skeletal element is a joint-face or articular facet, technically called *facet* or *articulum* (pl., *articula*). It corresponds to proximal and distal facets of columnals or cirrals (component ossicles of cirri) as well as to cirrus scars on nodals. It is divisible into *lumen* or intercept of the axial canal in the plane of an articulum and *zygum*, which is the entire area of an articulum outside of the lumen (Fig. 53,6).

The lumen may be extremely minute, or, on the contrary, so large that the surrounding zygum is reduced to a narrow band. Generally, it consists of a single opening but it may be accompanied by generally five, more rarely three or four, accessory perforations partially or wholly separated from it and serving, like the central opening itself, as passageways for extensions of the coelom and nervous system. The shape of the lumen commonly is circular, but it may be elliptical, pentagonal, quadri- or quinquelobate, quadri- or quinqustellate (Fig. 54,1-5). The margin of the lumen is flush with the general surface of the joint-face, or raised to form a moderately broad elevated rim around it (*perilumen*); this may be smooth, granulose, tuberculate, or vermiculate (Fig. 55,3,4).

Surrounding the lumen (and perilumen if present) is generally a smooth or granular, circular or quinquestellate area (*areola*), which is even with the general floor of the joint-face, depressed below it, or slightly raised above it (Fig. 53,6; 55,1-4).

Between the areola and periphery of columnal articula a remaining space is generally differentiated as a tract called *crenularium*, characterized by radially disposed grooves (*crenellae*) and ridges (*culmina*). Combined crenellae and culmina are collectively designated as *crenulae* (Fig. 53,7). Some columnals have a narrow peripheral ridge termed *articular rim*. In some Mesozoic and Cenozoic articulate crinoids, the crenularium is replaced by a rosette (*petalodium*) composed of five lobed divisions (*petals*) each of which consists of a median

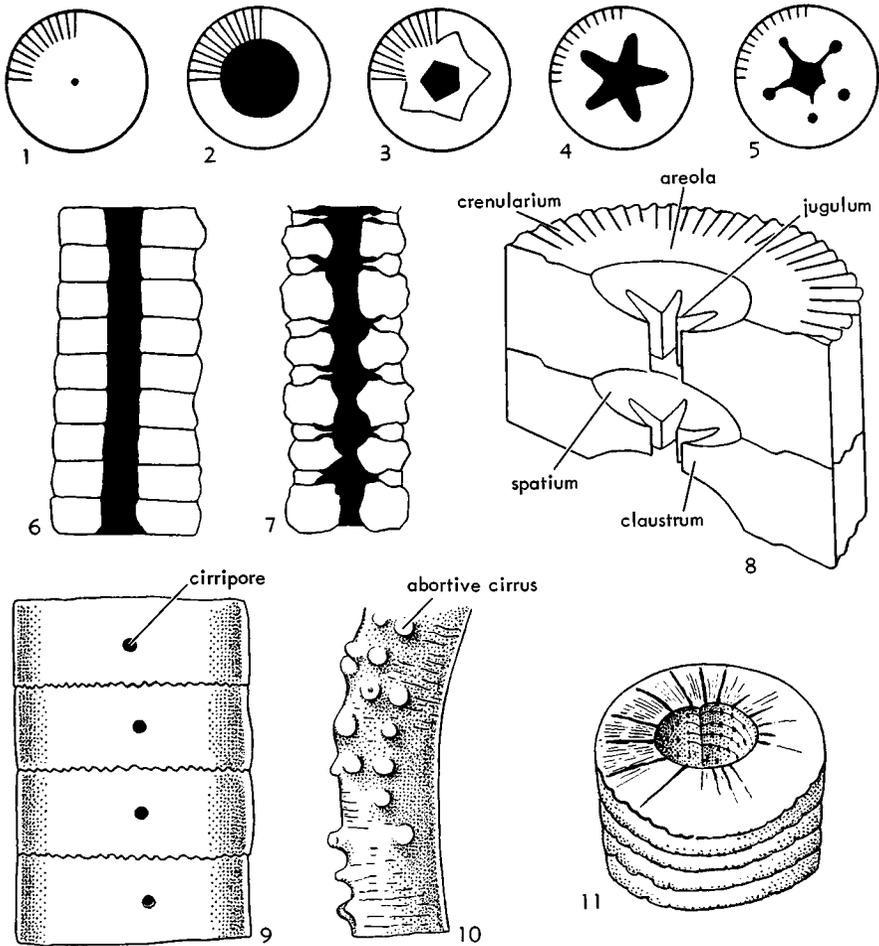


FIG. 54. Morphology of the axial canal in stems of crinoids (all from Moore, Jeffords, & Miller, 1968 (1-5, mod.), except 9, 10, Moore & Jeffords, 1968, and 11, Ubaghs, n).

- 1-5. Diagrammatic facetal views illustrating diversity in shape and relative size of lumen.
6. *Floricyclus granulatus* MOORE & JEFFORDS, U. Penn., USA (Texas), median longitudinal section of pluricolumnal with simple axial canal,  $\times 2$ .
7. *Heterosteichus texanus* MOORE & JEFFORDS, L. Perm., USA (Texas), median longitudinal section of pluricolumnal with complex axial canal,  $\times 2$ .
8. Diagrammatic oblique view of medially sectioned columnals illustrating features and terminology of axial canal.
9. *Mooreanteris waylandensis* MOORE & JEFFORDS, U. Penn., Texas, side view of pluricolumnal with cirripores,  $\times 8$ .
10. *Euvax eugenes* MOORE & JEFFORDS, L. Dev., USA (Tenn.), side view of pluricolumnal with abortive cirri,  $\times 2.35$ .
11. *Trybliocrinus flatheanus* GEINITZ, L. Dev., Spain, diagrammatic oblique view of pluricolumnal showing radiating grooves on articular facet and their openings into axial canal,  $\times 1.3$ .

ovoid floor surrounded by crenulae; the floor is mostly flush with the articular surface of the columnal, but it may be depressed or (rarely) slightly elevated. The

petals may be contiguous, and in that case the perradial crenulae (radial ridge groups) of adjacent petals alternate, or are gable-shaped or rectilinear; they may also be

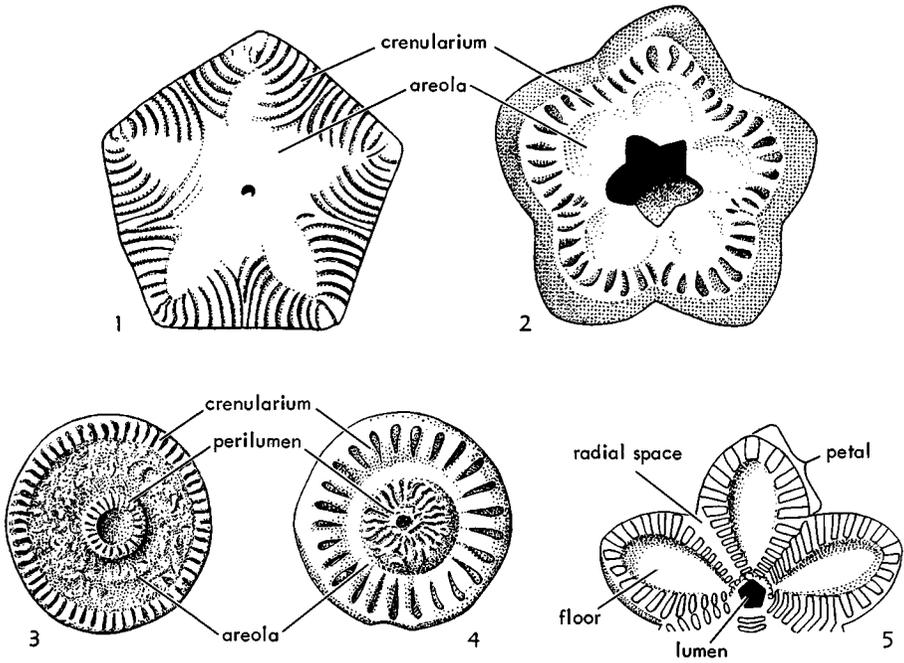


FIG. 55. Articular surfaces of crinoid columnals (all Moore & Jeffords, 1968, except 5, from Bather, 1909a).

1. *Pentagonostipes petaloides* MOORE & JEFFORDS, M.Dev., USA(N.Y.), symplectial articulation with petaloid crenularium, areola, and small rounded lumen,  $\times 8.5$ .
2. *Floripila florealis* MOORE & JEFFORDS, M.Dev., USA(N.Y.), symplectial articulation with narrow crenularium, petaloid areola, and large star-shaped lumen,  $\times 8.5$ .
3. *Dierocalipter doter* MOORE & JEFFORDS, L.Miss., USA(Ky.), symplectial articulation with narrow crenularium, wide areola, and crenulate perilumen,  $\times 3.5$ .
4. *Flucticharax undatus* MOORE & JEFFORDS, L.Miss., USA(Ky.), symplectial articulation with wide crenularium, narrow areola, and prominent perilumen,  $\times 3.5$ .
5. Isocrinid internodal, diagram of three sectors of articularium.

separated from one another by smooth areas known as radial spaces (Fig. 55,5).

### MAIN TYPES OF COLUMNAL ARTICULATIONS

Only ligamentary articulations are known in the pelma of crinoids, although distinct movements of the cirri and also of the stalk have been recorded in recent crinoids by many authors.

The simplest type of articulation, which is not very common, is characterized by essentially plane articular surfaces devoid of any sculptured features. Such juncture is termed **synostosis** and this type of articulation is called **synostosial** (Fig. 50,3; 53,8). The corresponding **sutures**, which are the externally visible edges of articularia, are

straight (Fig. 53,9). Short dermal fibers unite the apposed joint-faces, allowing small movement in all directions. Synostosis occurs between the nodal and infranodal joints of pentacrines and between paired nodals (**binodals**) in the camerate genus *Camptocrinus* (Fig. 50,1-3). When addition of small amounts of calcareous deposits to articularia reduce mobility practically to nothing, the synostosis becomes a **zygosynostosis** and the contact between apposed ossicles is a **close suture**. The zygosynostosis is rarely present in the stem itself, but exists commonly, along with complete fusion of ossicles (**ankylosis**), in the holdfast of crinoids. Opposite modification of synostosial articulation toward increased flexibility occurs in the stem of some primitive

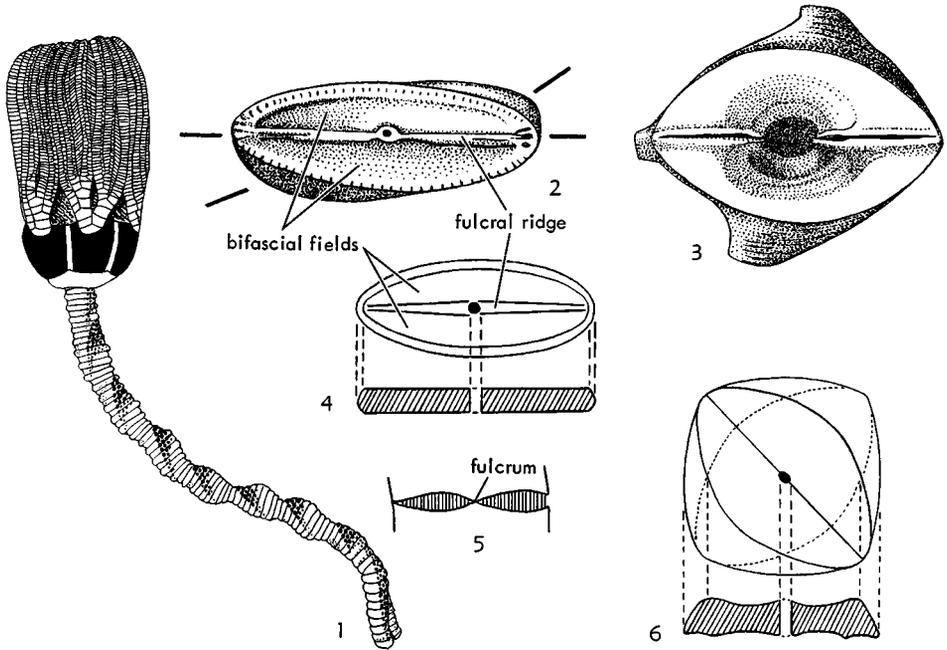


FIG. 56. Morphology of synarthrial type of articulation.

1. *Platycrinites symmetricus* (WACHSMUTH & SPRINGER), Miss., USA (Iowa), crown with twisted ribbonlike column,  $\times 1$  (Wachsmuth & Springer, 1897).
2. *Platycrinites* sp., L. Carb., Belg., with elliptical articular facets oriented differently on opposite sides (Ubaghs, n).
3. *Bourgueticrinus danicus* NIELSEN, U.Cret., Denmark, nodal, articular facet, with bifascial fields depressed into pits,  $\times 8.3$  (Nielsen, 1913).
4. Diagrammatic facetal view and median longitudinal section of elliptical columnal (Moore, Jeffords, & Miller, 1968).
5. Diagrammatic transverse profile of juxtaposed synarthrial articular facets (Moore, Jeffords, & Miller, 1968).
6. Quadrangular columnal with elliptical articular facets oriented differently on opposite sides (Moore, Jeffords, & Miller, 1968).

inadunates, in which the articula of columnal pentameres are distinctly concave (Fig. 48,6).

The most common type of articulation in cylindrical and basaltiform fossil crinoid stems is characterized by apposed faces that bear interlocking grooves (**crenellae**) and ridges (**culmina**), and their external sutures are **crenulate**. This type of union is called **symplexy** (adj., **symplectial**) (Fig. 53,10,11; 55,1-4). It allows very slight movement between columnals. [In the past, symplexy has been confused frequently with syzygy—an articulation common in the arms of some crinoids, but unknown in the pelma. In syzygy the culmina of apposed articula meet and the intervening crenellae are occupied by ligaments, so that the external

suture has a finely beaded (not crenulate) appearance.] Weakly marked symplectial articulations are called **cryptosymplexies** (adj., **cryptosymplectial**).

Columnals with elliptical or diamond-shaped outlines in views normal to their articula and some with circular cross section are distinguished by **synarthrial** (also called **bifascial**) articulations. In a **synarthry**, each joint-face bears a median **fulcral ridge** along the major axis of elliptical and rhomboidal columnals, with equal ligamentary shallow depressions (**bifascial fields**) flanking sides of the ridge (Fig. 56,4,6). The latter are smooth and generally broad and shallow, but in some Articulata (e.g., *Bourgueticrinus*, *Rhizocrinus*) they are depressed into moderately

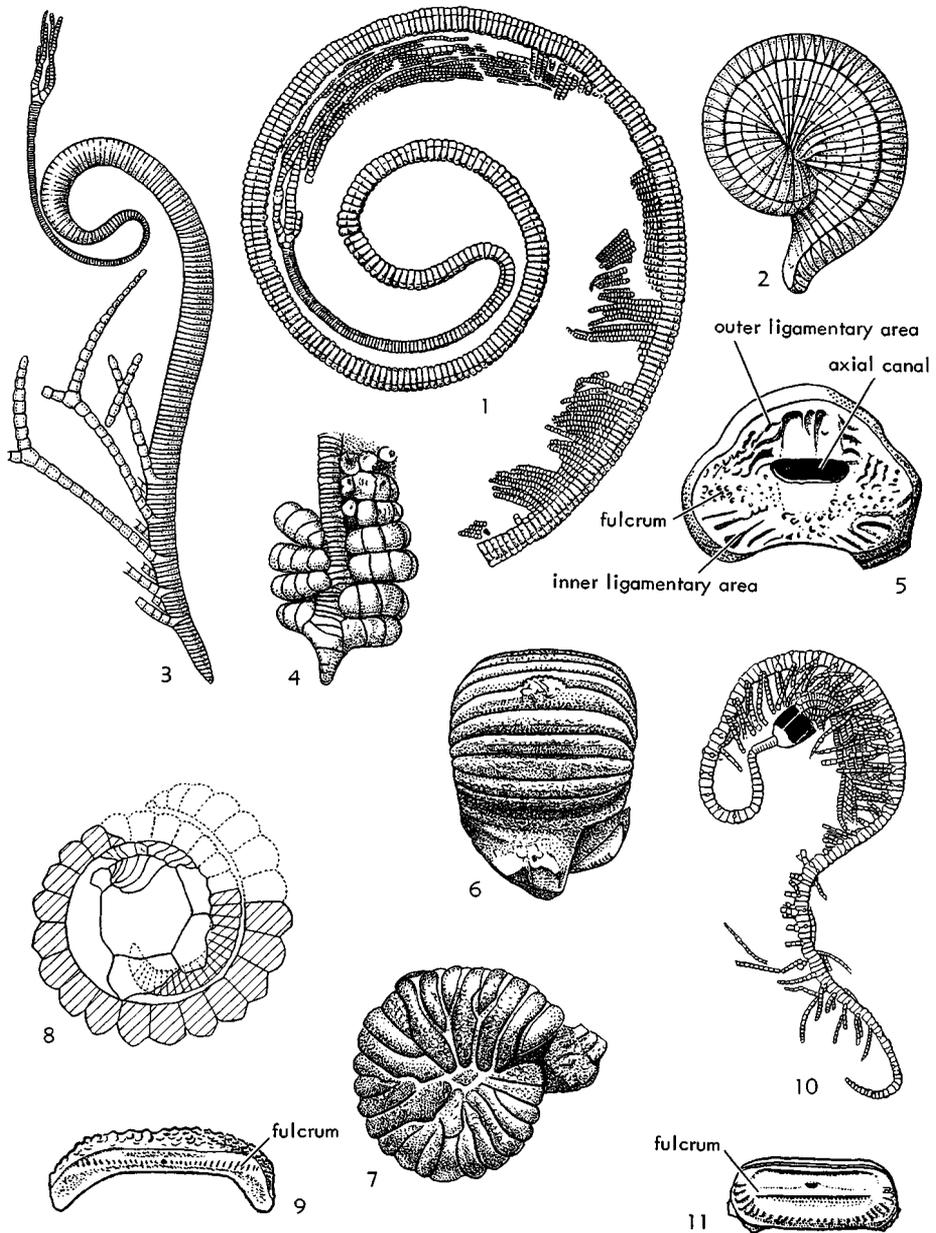


FIG. 57. Morphological features of coiled stems of crinoids.

1. *Herpetocrinus fletcheri* SALTER (Inadunata), U. Sil.(Gotl.), Sweden, slender crown and re-curved coiled stem with inward directed cirri,  $\times 0.75$  (Bather, 1900a).
2. *Myelodactylus ammonis* (BATHER) (Inadunata), U.Sil., USA(Tenn.), closely enrolled specimen with cirri entirely concealing crown,  $\times 1$  (Springer, 1926b).
3. *Crinobrachiatus brachiatus* (HALL) (Inadunata), M.Sil., USA(N.Y.), specimen with very small crown, tenuous proxistele, thick mesi- and dististele, and strong branching cirri,  $\times 1.5$  (Springer, 1926b).
4. *Brachiocrinus nodosarius* HALL (Inadunata), L. Dev., USA(N.Y.), distal part of stem terminating in a point, with ponderous cirri,  $\times 1$  (Springer, 1926b).

deep pits (Fig. 56,3). There is no crenularium, or if any, it is rudimentary. A narrow marginal rim may be present. The fulcral ridges of apposed faces are aligned with one another and provide for movements in direction normal to the fulcral ridges. Each columnal has a more or less marked skew, so that the ridge of the proximal face lies at an angle to that of the distal face. The extreme is reached in some square columnals (as viewed from their articular sides) with the ridges at right angles to each other. This progressive or abrupt shifting in orientation of the fulcral ridges enables the stem to bend in different directions. When the columnals are elliptical and the skew of each columnal is slight, the stalk may look like a twisted ribbon (Fig. 56,1).

Modified synarthral articulations occur in the coiled stem (Fig. 57) of the extraordinary homeomorphs, the inadunate *Myelodactylus*, the flexible *Ammonicrinus*, and the camerate *Camptocrinus*. In such crinoids, the stem is flattened or concave on the inner side of the coil throughout the greater part of its length and takes on a bilateral symmetry; in cross section, the columnals are elliptical or crescentic, and their articular faces bear fulcra separating two unequally developed areas, which, during life, were presumably occupied by ligamentary (and possibly contractile) tissues (Fig. 57,5,9,11).

### AXIAL CANALS

All columnals and cirrals are pierced by an axial canal. Generally (but not invariably) it occupies the center of the columnal. Its transverse shape and relative size as shown by outline and size of the lumen on joint-faces have been described above (p. T65) (Fig. 54,1-5).

In median longitudinal section, the axial canal of columnals may be **simple** (straight sided) (Fig. 54,6) or **complex** (provided with expansions or constrictions) (Fig. 54,7). If present, the expansions (**spatia**) are located between the columnals, while the constrictions (**claustra**) are placed at mid-height of the columnals (Fig. 54,8). As seen in longitudinal section, the spatia may be low, or tall and laterally rounded, truncate, or pointed; the claustra, clavate, truncate, or lanceolate. Adaxial surfaces of claustra may be convex, flat, or concave, and smooth or denticulate. The part of an axial canal limited by the adaxial faces of a claustrum is called **jugulum**; it corresponds to a distinct local narrowing of the axial canal, narrowing that may be longitudinally very short to moderately long and transversely circular or pentagonal to strongly quinquestellate (Fig. 54,8). The adaxial part of a claustrum bordering a jugulum may be thickened and form what is designated as a **jugular rampart**. The jugulum and the central part of spatia were probably occupied during life by coelomic and nervous extensions from the chambered organ, whereas the remaining part of the spatia was filled with dermal fibers.

Radially disposed simple or branched canals may be given off from the axial canal. If these side canals penetrate stereom and lead to cirrus scars on latera, they are termed **canaliculae**. If they are located between apposed joint-faces they are called **fossulae** (Fig. 50,3). In some stems these passageways emerge on the outer surface of columnals as small pores (**cirriopores**) of uncertain function (Fig. 54,9) or they terminate in diminutive nodicirral sockets or pimplelike protuberances (**abortive cirri**) (Fig. 54,10). In the camerate *Trybliocrinus* the joint-faces of columnals show radiating

(Continued from facing page.)

5. *Myelodactylus canaliculatus* (GOLDFUSS) (Inadunata), M.Dev., Ger., columnal articulum,  $\times 3.2$  (Sieverts-Doreck, 1954).
- 6,7. *Ammonicrinus wanneri* SPRINGER (Flexibilia), M.Dev., Ger., outer side and lateral views of tightly coiled specimen,  $\times 1$  (Krause, 1927).
8. Same, diagrammatic representation of a specimen with stem (longitudinally sectioned) completely enveloping crown,  $\times 2$  (Ubaghs, 1952).
9. *Ammonicrinus sulcatus* KONGIEL, M.Dev., Poland, columnal articulum,  $\times 2$  (Kongiel, 1958).
10. *Camptocrinus multicirrus* SPRINGER (Camerata), Miss., USA (Ill.), complete specimen,  $\times 1$  (Wachsmuth & Springer, 1897).
11. *Camptocrinus compressus* WRIGHT, L.Carb., Scot., columnal articulum,  $\times 5$  (Ubaghs, 1953).

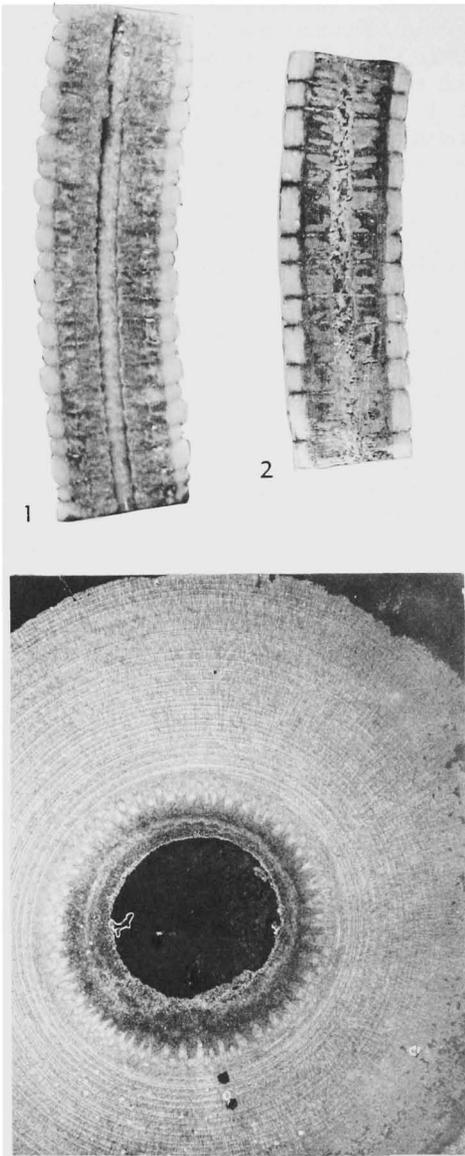


FIG. 58. Growth of crinoid stems indicated by microstructure.

1. Longitudinal median section of *Elytroclon elimatus* MOORE & JEFFORDS, L.Miss.(Osagian), New Providence F., USA (Ky.), showing dense light-colored cortical (outer) zone and spongy dark medulla surrounding axial canal,  $\times 1.7$  (Moore & Jeffords, 1968).
2. Longitudinal median section of *Ilmaterisma enamma* MOORE & JEFFORDS, L.Miss.(Osagian), New Providence F., USA (Ky.), similarly show-

ing well-marked cortical and medullary zones,  $\times 3.5$  (Moore & Jeffords, 1968).

grooves which open into the axial canal through small vertical slits and terminate near the periphery without communicating with the exterior (Fig. 54,11). A similar canal system occurs in the grapnel-like root of the inadunate *Ancyrocrinus*. Apparently these passages between or through the columnals served to transmit the nutrient fluid to cells secreting the stereom and to aerate the same fluid by bringing it near the surface.

### CORTEX AND MEDULLA

Sections of columnals may reveal the existence of more or less clear differentiation of the stereom into outer (**cortical**) and inner (**medullary**) portions, which may be very distinct or grade into each other (Fig. 58). The **cortex** shows generally a dense calcitic microstructure, whereas the **medulla** is more spongy or microlamellate to microreticulate. The medulla itself may be differentiated into a narrow adaxial zone of dense calcite (correlated with the perillumina of articular faces) and a relatively broad next abaxial zone of more spongy nature (corresponding with areolae of the joint-faces).

### INDICES OF COLUMNALS

Description of columnals and pluricol-columnals may require various measurements of morphological elements and means of expressing interrelationships between them. The latter can be expressed as **ratios**, which conveniently are multiplied by 100 in order to convert them to whole numbers. Such numbers are termed **indices** (MOORE & JEFFORDS, 1968).

Determination of columnal indices is simple in dealing with circular stem parts or features, but it needs computation of mean diameters consisting of the sum of measurements along two opposite radii when features of the columnals possess

3. Transverse section of columnal belonging to *Cyclocaudex plenus* MOORE & JEFFORDS, U. Penn.(Virgilian), Wayland Shale, USA (Texas), showing very wide cortex with concentric microstructure resembling fine tree rings and thin dark medulla next to large circular axial canal,  $\times 7$  (Moore, Jeffords, & Miller, 1968).

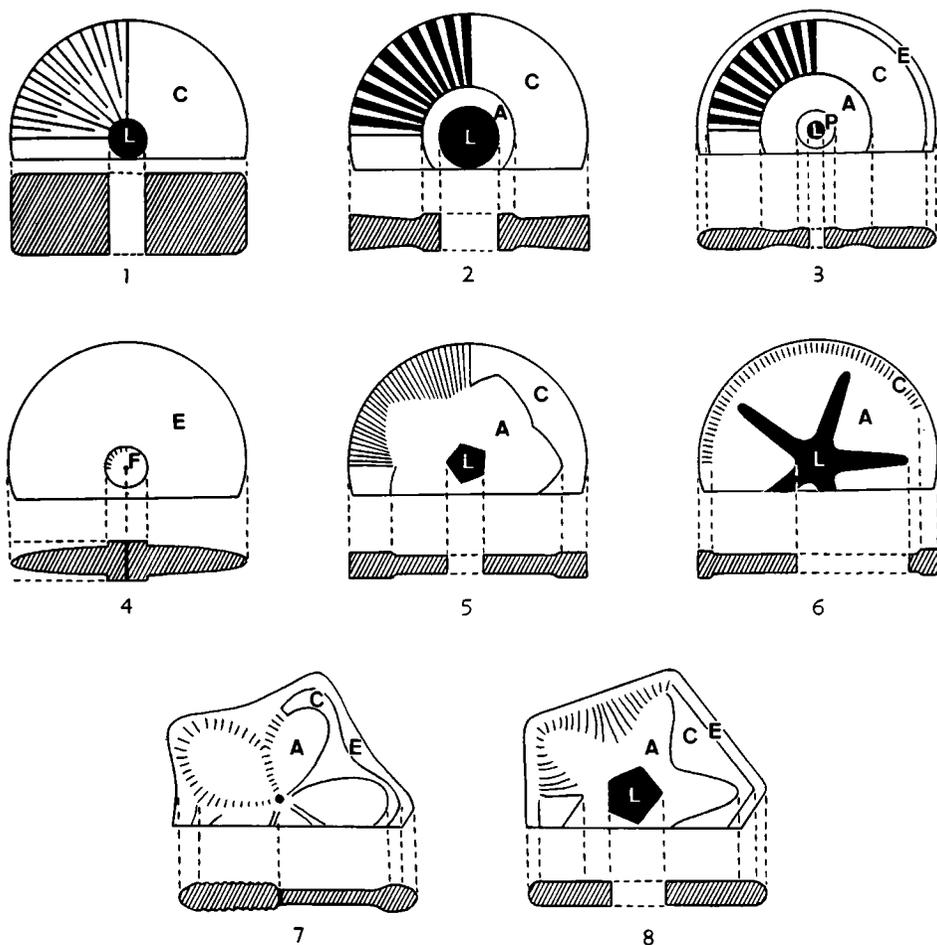


FIG. 59. Diagrammatic facet views and median longitudinal sections of columnals designed to illustrate determination of various columnal indices (Moore, Jeffords, & Miller, 1968). [Explanation: lumen, black; columnals in sections, oblique ruled; A, areola; C, crenularium; E, epifacet; F, facet; L, lumen; P, perilumen.]

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|--|---|
| <p>1. Circular columnal with wide crenularium lacking areola and perilumen.</p> <p>2. Circular columnal with narrow areola, no perilumen.</p> <p>3. Circular columnal with well-developed areola, perilumen and narrow epifacet.</p> | <p>4. Circular columnal with very wide epifacet and small articulum.</p> <p>5,6. Circular columnals with differently shaped areolae and lumina.</p> <p>7,8. Pentagonal columnals with petaloid and quinquestellate areolae.</p> |
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pentagonal, quinquelobate or quinquestellate outlines (Fig. 59). In elliptical columnals, maximum and minimum radii (disposed at right angles to one another) are chosen for determining the mean diameter (Fig. 56,4,6).

The main indices distinguished by MOORE & JEFFORDS (1968) are ratios all multiplied by 100, as follows:

**areolar index:** ratio of total width of areola to that of articular facet.

**articular facetal index:** ratio of total width of articular facet to that of entire columnal.

**crenularial index:** ratio of total width of crenularium to that of columnal articular facet.

**epifacet index:** ratio of total width of

- epifacet to that of entire columnal.
- height index:** ratio of height to total width of columnal.
- internodal index:** ratio of total height of internode to height of noditaxis containing it.
- jugular index:** ratio of total width of jugulum to that of columnal articular facet.
- luminal index:** ratio of total width of lumen to that of columnal articular facet.
- nodal index:** ratio of height of nodal to that of noditaxis containing it.
- periluminal index:** ratio of total width of perilumen to that of columnal articular facet.
- zygal index:** ratio of total width of zygon to that of columnal articular facet.

### STEM GROWTH

The growth of the stem in crinoids is a product of two factors: formation of new columnals and increase in size of individual columnals.

In homeomorphic stems new columnals are introduced at the proximal end of the stalk, so that proximal columnals are youngest and distal ones oldest. In heteromorphic stems it is the nodals that develop next to the cup, the internodals being intercalated between them subsequently at differing distances from the cup. Nodals are in contact with one another near the cup and just below are separated by one internodal. Next a new internodal is added on each side of the first one. Then two other internodals are inserted next below and above each of the just-formed internodals, and so on. Internodals present at successive growth stages would therefore number 0-1-3-7-15 . . . at least theoretically; in fact, the rate at which generations of internodals are introduced may be somewhat irregular (JEFFORDS & MILLER, 1968).

After a few generations, a characteristic number of columnals in each internode commonly is reached and formation of new internodals ceases, but the accretionary growth of individual columnals continues. This allows recognition of three stages (called ages by TERMIER & TERMIER, 1949) in development of the columnals, each one being located in a more or less distinct re-

gion of the stem. The first stage characterizes a usually short region located immediately below the cup, in which the nodals and first internodals are formed, and all columnals have a juvenile aspect (Fig. 60,1). The second stage corresponds to part of the stem in which various cycles of internodals are introduced, size of the columnals increases, and cirri (if any) develop. The third stage includes the rest of the stem in which no new internodals are inserted, and distinction between different generations of columnals, so obvious near the cup, tends to be lost (Fig. 60,2).

This mode of growth has a direct effect on flexibility of the stem. Since new columnals are introduced near the cup as very thin discs and then are enlarged by accretionary growth in axial direction, the flexibility, high near the cup, diminishes progressively toward the root.

All crinoid stems do not develop according to this pattern, however. In some forms, such as the cyrtocrinid articulates *Eugeniocrinites* and *Cyrtocrinus*, the stem is short and entirely composed of long, cylindrical segments, so that the whole stem must certainly have acted as a rather rigid support of the crown. In Jurassic Pentacrinitidae, such as *Seirocrinus*, the number of columnals in each internode is not limited and continues to increase geometrically in a distal direction, becoming enormous in species provided with a very long stem. Moreover, as alternation of smaller and larger columnals is more pronounced and diameter of the stem becomes narrower away from the cup, flexibility of the stem increases toward the root, rather than decreases. This trend does not persist indefinitely, however, for complete specimens show a rapid diminution of internodal intercalation near the distal end, along with a concentration of nodals, so that in the terminal stem region a dense tuft of cirri is produced and acts as a holdfast (SEILACHER *et al.*, 1968).

If nodals are introduced immediately below the base of the cup in most crinoids, the incorporation of the topmost columnal (or columnals) in the theca in some post-Paleozoic genera, producing a proximale or centrodorsal, stops formation of new columnals (at least above it). In some Paleozoic crinoids also, it seems possible that a

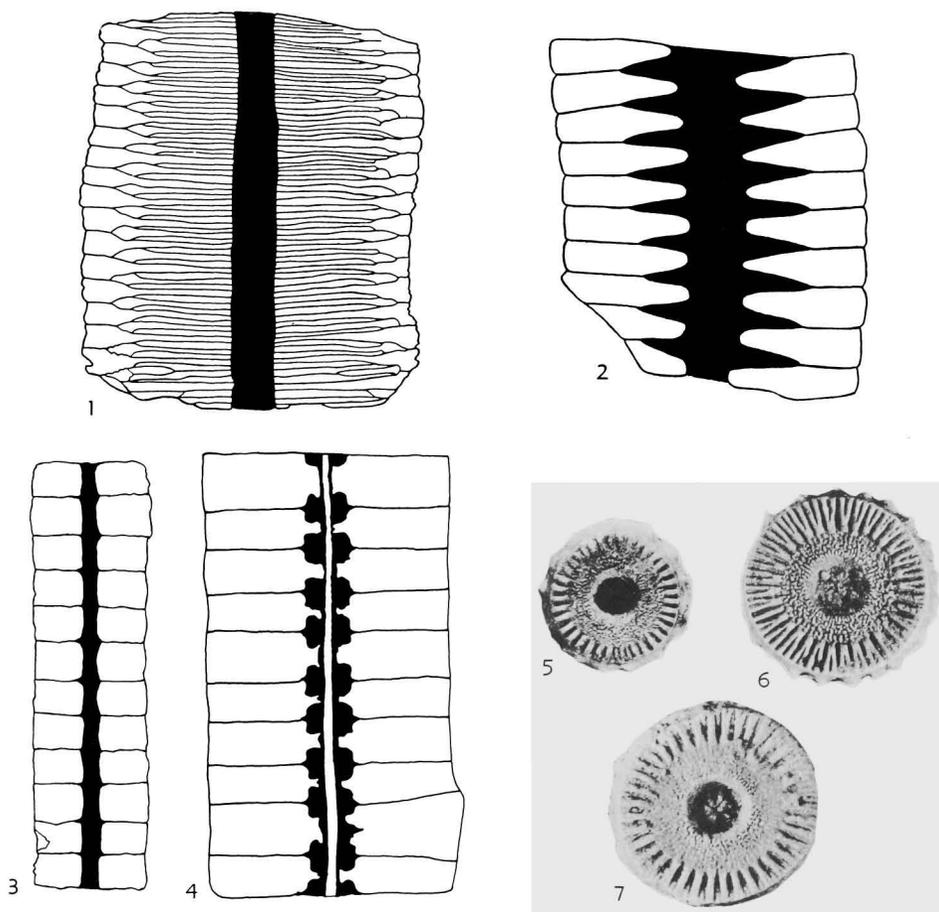


FIG. 60. Growth of crinoid column.

1,2. *Barrandeocrinus sceptrum* ANGELIN, U.Sil., Gotl., Sweden, median longitudinal sections showing shape of columnals and nature of axial canal in proximal (juvenile) and middle (mature) portions of stem,  $\times 6.5$  (Ubaghs, 1956).

3,4. *Preptopremnum rugosum* MOORE & JEFFORDS,

U.Penn., USA (Texas), median longitudinal sections showing nature of axial canals in juvenile and mature portions of columns,  $\times 2.65$  (Jeffords & Miller, 1968).

5-7. Same, articula showing increase in numbers of crenulae with increase in diameter of columnal,  $\times 2.65$  (Jeffords & Miller, 1968).

few of the most proximal columnals may be related to the theca in such a way as to prevent intercalation of new columnals between them and the cup. Examples are offered by species having a basally concave theca so shaped as to render captive columnals occurring within it. The name **basilarids** has been proposed by STRIMPLE (1963a) for these "captured" columnals.

Growth of individual columnals takes place in both axial and transverse directions.

This is clearly shown by growth lines (discernible in cross sections) (Fig. 58,3) and by observable changes in size, proportions, shape, nature of articular facets and other features of columnals along the stem from its youngest proximal part to its oldest distal region. Most of these changes can be described in terms of a few growth gradients, which seem to control a variety of adaptive modifications of the crinoid stem (SEILACHER *et al.*, 1968). This is well

illustrated by transverse growth, diameter of the nodals being controlled primarily by size of the generating area at base of the cup, size of the nodals in turn determining diameter of the initial internodals. If no other factor than cup growth intervened, diameter of the stem would increase from root to cup, but accretionary growth of the columnals transversely brings about secondary modifications, which work in the opposite sense and tend to produce tapering of the stem from root toward cup. The resultant of these two gradients is shown by stems which taper in proximal direction or in distal direction, or thicken at both ends.

Turning to shape, one may observe that in many crinoids the longitudinal growth of columnals is greater initially at the rim than in the center; this produces a saucer-shaped depression in the joint-face, which is filled by developing internodals (Fig. 60,1). Then follows a gradual flattening of the articular facet as a consequence of accretionary growth, and a tendency of columnals of different generations to become similar (Fig. 60,2).

Considering articular surfaces, growth may be reflected by progressive enlargement of the lumen, expansion of the areola, and multiplication of the culmina (Fig. 60,5-7). Generally also, the axial canal is simpler in juvenile parts of the stem than in mature regions where it may show a great complexity (Fig. 60,3,4).

### CIRRI

The cirri are jointed, generally undivided, appendages that arise from specialized columnals (nodals) along the stem of many crinoids, or are carried by the centrodorsal in most *Thiolliericrinidae* and *Comatulida*. They are formed by a row of skeletal ossicles called *cirrals*, which, like the columnals, are pierced by a central tubular canal that branches from the axial canal of the stem and contains coelomic and nervous extensions. Two or several cirrals in anatomical connection comprise a *pluricirral*. The most proximal segment of a cirrus that articulates with a columnal is distinguished as a *zygocirral*. In the distal region of the column, the cirri are replaced by the so-called *radicular cirri*, which form the root-

like anchorage of many crinoids and will be described later.

Along the stem, the cirri may be arranged 1) without any definite order, 2) in vertical rows, but not in whorls, 3) in verticils of three, four, five, or six cirri, 4) in a helix (rarely), and 5) in two vertical rows along one side of the stem. They may be present throughout the length of the stem, or restricted to some part of it, generally the proximal or distal one. Their number may or may not vary from one region to another in a single stem. In *Flexibilia*, so far as known, cirri, except radicular cirri, are missing. This is equally true for most representatives of other Paleozoic crinoid subclasses. Among *Camerata*, though cirriferous species are known from Late Ordovician onward, they never become very common. In the *Inadunata* they first appeared in Silurian times, but were not common until the Carboniferous period. Among stalked post-Paleozoic forms, they are observed in some *Encrinuridae*, well established in the *Isocrinida*, *Thiolliericrinidae*, and *Comatulida*, but lacking in *Millericrinida* and *Cyrtocrinida*.

On the centrodorsal of *Thiolliericrinidae* the cirri are arranged in one or several circles, or absent (in mature specimens) according to species. The centrodorsals of *Comatulida* bear closely placed cirri arranged in more or less distinct vertical rows or irregularly scattered. In the *Comasterina*, the cirri are rudimentary or lacking.

Regarding the formation of cirrals, it appears that new joints are added at the distal end of the cirri (and not at the base of the cirri, as sometimes erroneously stated). As no intercalation of cirrals takes place, the most distal ossicle is the last to be formed. The ontogeny of recent comatulids shows that the cirrals did not develop like the columnals. They appear at first as simple, round, fenestrated plates without a central perforation; this is formed later by absorption of the central part of the plate (MORTENSEN, 1920, p. 77).

The *cirrus sockets* (also called cirrus scars or cirrus facets), serving for attachment of cirri to a crinoid stem or centrodorsal are generally rounded, less commonly polygonal or elliptical in outline. They may be confined to sides of one columnal (nodal)

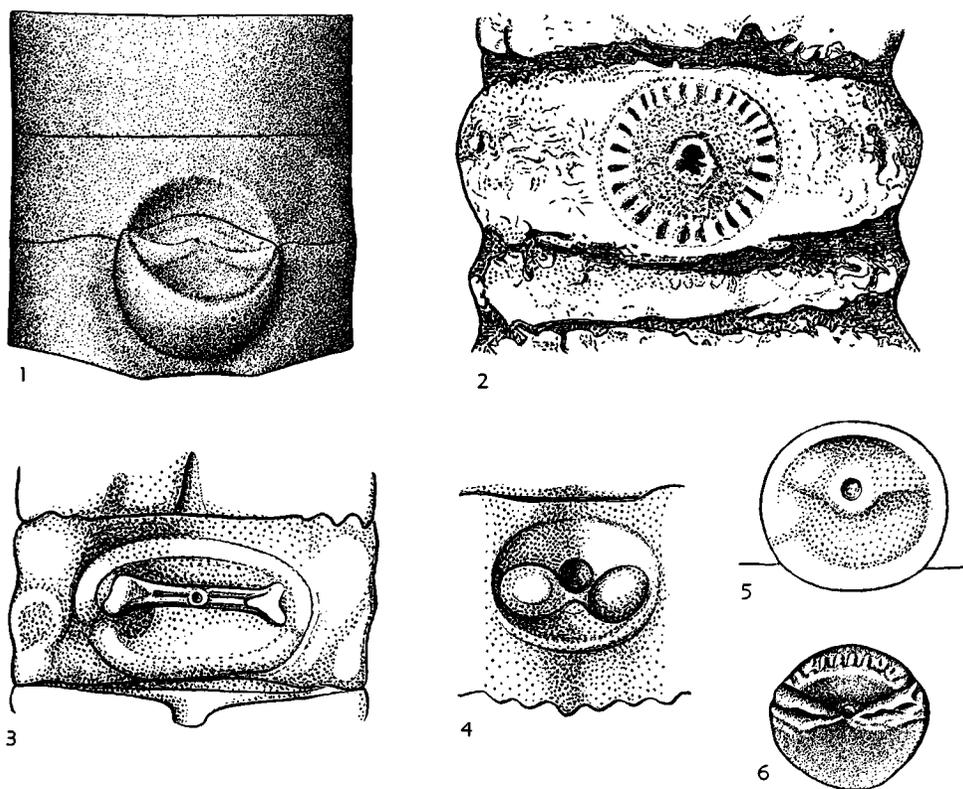


FIG. 61. Morphology of cirrus sockets and cirral articularia.

1. *Austinocrinus rothpletzi* STOLLEY, U.Cret., Ger., pluricolumnal with cirrus socket and first cirral directed upward,  $\times 5$  (Rasmussen, 1961).
2. *Preptopremnum rugosum* MOORE & JEFFORDS, U.Penn., USA (Texas), pluricolumnal with cirrus socket on nodal,  $\times 7$  (Moore & Jeffords, 1968).
3. *Isocrinus hercuniae* BATHER, Trias., Hungary, cirrus socket,  $\times 15$  (Bather, 1909a).
- 4,5. *Isocrinus tyrolensis major* BATHER, Trias., Hungary, cirrus socket, and distal articulum of cirral 2,  $\times 30$  (Bather, 1909a).
6. *Austinocrinus rothpletzi* STOLLEY, U.Cret., Ger., articulum of a cirral,  $\times 10$  (Rasmussen, 1961).

(Fig. 49,1), or be equally shared by two successive nodals (compound nodals and binodals) (Fig. 49,4; 50,1) or be impressed on several contiguous columnals (3 to 10 or more). When confined to single columnals, they are mostly placed at mid-height of the columnals, but in some stems they are much nearer to one joint-face of the columnal than the other, or may even project beyond the surface of the joint-face and occupy a notch in the next columnal (Fig. 61,1). They may be directed straight outward, upward, or downward, the corresponding cirri being more or less perpendicular to the column or growing along the column. In the camerate species *Campto-*

*crinus compressus*, from the Lower Carboniferous of Scotland, the cirrus sockets on binodal columnals are compound, that is, divided into several facets, each of which carries a cirrus (Fig. 50,5).

The cirrus sockets are concave. Each one (or each facet of a compound socket) is provided with a more or less central axial pore (lumen) which communicates with the axial canal of the stem through intracolumnal passageways (canaliculae) or intercolumnal passageways (fossulae). The cirrus sockets are smooth or provided with radiate crenulae, short and confined to the margin (Fig. 61,2) or extending to or near the lumen. They may also have a more or

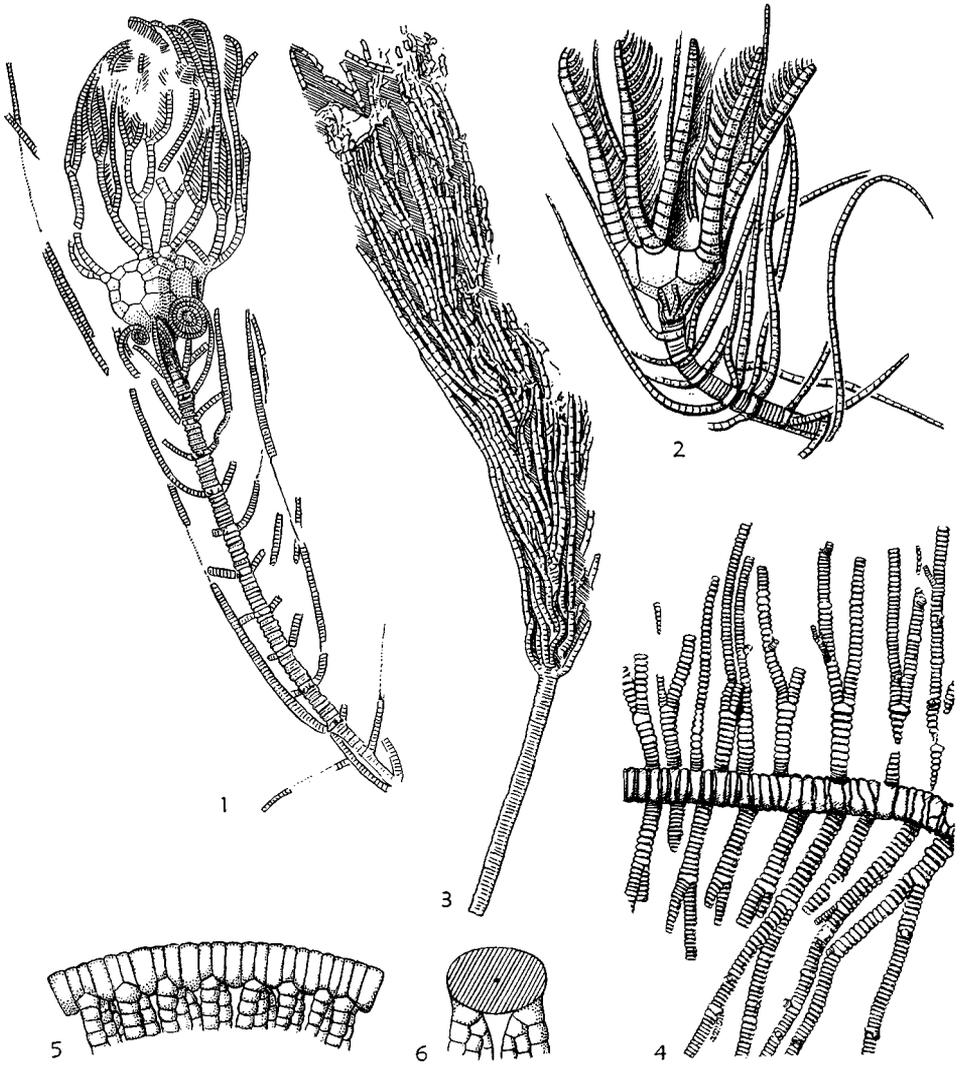


FIG. 62. Morphology of cirri in some Paleozoic crinoids.

1. *Clarkeocrinus troosti* GOLDRING, M.Dev., USA (N.Y.), crown and part of column, with circinate proximal cirri,  $\times 0.7$  (Goldring, 1923).
2. *Cordylocrinus plumosus* (HALL), L.Dev., USA (N.Y.), crown and part of column, with cirri longer than crown,  $\times 2.6$  (Goldring, 1923).
3. *Dichocrinus angustus* WHITE, L.Miss., USA (Iowa), extremely long cirri growing upward and enveloping small theca,  $\times 1$  (Springer, 1926b).
4. *Dicrocrinus ramulosus* W. E. SCHMIDT, L.Dev., Ger., pluricolumnal with branching cirri,  $\times 2$  (Schmidt, 1942).
- 5,6. *Camptocrinus myelodactylus* WACHSMUTH & SPRINGER, L.Miss., Indiana, lateral view ( $\times 3$ ) and transverse section ( $\times 6$ ) of pluricolumnal, showing mode of branching of cirri (Springer, 1926b).

less distinct articular transverse ridge, commonly with a tubercle at each end (Fig. 61,1,3); or the ridge is reduced to these two lateral tubercles (Fig. 61,4).

A detailed knowledge of the cirri of Paleozoic crinoids is lacking. They seem generally to be composed of short, cylindrical, rarely barrel-shaped ossicles. In at least

some species the lumen for passage of the axial canal was bean or dumbbell shaped, or even split into pairs. The way they are preserved and the aspect of their external sutures suggest that their articula did not allow a great amount of movement. In a few species, however, such as the Devonian camerate *Clarkeocrinus troosti* (Fig. 62,1), the cirri were able to coil in a plane as if they had properties similar to those of articulate crinoids. In the latter, articula of the cirrals (Fig. 61,5,6) are provided with transverse ridges which allow considerable motion in planes passing through the longitudinal axis of the body.

The length of cirri among fossil crinoids is quite variable. They may be extremely long, to the point of enveloping the theca wholly and part of the arms (Fig. 62,2,3). In the Silurian-Devonian Myelodactylidae (Fig. 57,1-5) and the Mississippian *Campocrinus* (Fig. 57,10,11) with coiled stems, part of the column was provided with long cirri disposed in such manner as to conceal and protect the crown. Generally, however, the cirri are moderately developed, rarely exceeding a few centimeters in length. In recent comatulids, they show great diversity in form and size, usually correlated with the mode of life and habitat of the animals.

Typically, the cirri are simple undivided jointed appendages, but fossil species are known in which the cirri are branched. Examples are furnished by cladid inadunates such as the Silurian *Brachioocrinus*, the Devonian *Dicirroocrinus* (Fig. 62,4) and by some species of the Mississippian camerate *Campocrinus* in which the first or first two cirrals are axillary (Fig. 62,5,6).

Abortive cirri, dwarfed in size and composed of a few small cirrals or even a single rounded ossicle without axial canal, occur in some Paleozoic crinoids. Stems of other crinoids have no actual sideward outgrowths but merely pores (cirripores) connected by passageways leading to the axial canal of the stalk (Fig. 54,9). Still other columnals possess irregular projections (**pseudocirri**), which resemble cirri in having an axial canal but differ from ordinary cirri in showing no division into component cirrals (Fig. 54,10; 63,1). Minute pimplelike ossicles of uncertain nature occur on some stems; when they fall, they leave on the

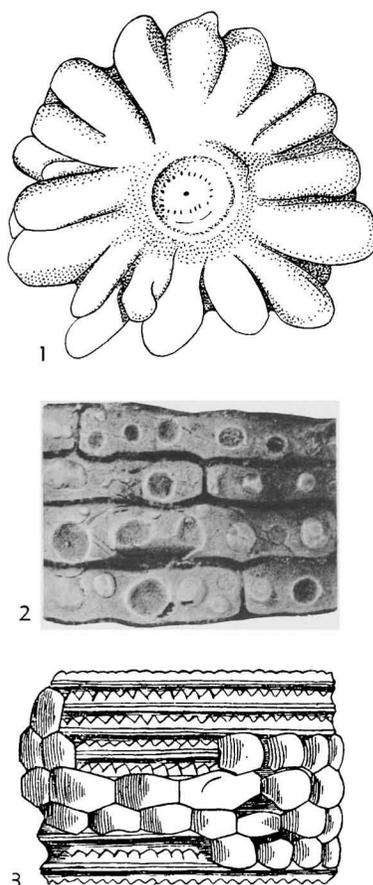


FIG. 63. Pseudocirri and structures of uncertain nature carried on latera of columnals.—1. *Hyperexochus immodiscus* MOORE & JEFFORDS, L.Dev., USA (Tenn.), facetal view of columnal provided with pseudocirri,  $\times 2.8$  (Moore & Jeffords, 1968).—2. *Polypeltes granulatus* ANGELIN, U.Sil., Gotl., lateral view of pluricolumnal showing pimplelike ossicles and concave nonperforated scars,  $\times 6.6$  (Ubaghs, 1956).—3. *Musivocrinus* sp. TERMIER & TERMIER, Perm., Tunisia, lateral view of pluricolumnal with partially preserved covering of small platelike ossicles (Termier & Termier, 1949).

columnal latera concave scars similar to cirrus scars except that they are not perforated (Fig. 63,2). In a genus based solely on stem parts, *Musivocrinus*, from the Permian of Tunisia, the stem apparently was covered with platelike contiguous unperforated ossicles, attached to double trans-

verse ridges on latera of the columnals; the origin of such structures is presently unknown (Fig. 63,3).

### HOLDFASTS

Any anchorage structure at and near the distal end of a crinoid column is called a **holdfast**. This term is applied chiefly in a functional sense, for the structures serving for attachment of crinoid stems are various and not necessarily homologous.

The attached end of the larval stalk of most recent comatulids expands into a soft disc inside which a fenestrated plate is located. This **terminal stem plate**, sometimes designated as the dorsocentral (a term not to be confused with centrodorsal) is always circular in very young larvae. During development it may acquire lobate, stellate, or digitiform outlines prior to detachment of the stem from the topmost columnal, which is incorporated in the theca. Whether such a terminal plate occurs in the ontogeny of stalked crinoids and what relation it could have with holdfasts of adults is not known.

From a purely morphological point of view, all crinoid holdfasts, in spite of their diversity, may be assigned to four fundamental types: 1) the so-called "*Hohlwurzel*" type, 2) the cirrus-bearing type, 3) the discoid type, and 4) the encrusting type.

1) As far as known, the "*Hohlwurzel*" type has been observed only in the archaic inadunate *Aethocrinus*. It consists of a hollow mass of small, irregular polygonal plates clustered around the distal extremity of the stem (Fig. 48,17). It may well represent the most primitive sort of stem termination among all crinoids (EHRENBERG, 1929), for a similar ending of the body occurs in primitive crinozoans such as the Lower Cambrian *Lepidocystis* and the Middle Cambrian *Gogia*. It is probable that it serves as anchor in soft muddy bottom sediment or at least helped the crinoid to maintain its balance by increasing weight of the distal region of the stem.

2) In the cirrus-bearing type, the distal end of the stem resembles what is usually called a "root" (**radix**). This root may consist of a single main trunk—the stem itself—which gives off branches (**radicular cirri**) at irregular intervals and attaches

the crinoid by penetrating into sea-bottom sediment or by creeping on the substratum (Fig. 64,1). Or the main trunk bifurcates and breaks into branches, which may divide further to form a cluster of rootlets given off from the dististele at short intervals or at approximately the same level (Fig. 64,2). The radicular cirri may be very long. They are immovable and formed of variously shaped segments having different sizes, united by synostosis, symplexy, or ankylosis, and invariably provided with an axial canal which, like the axial canal of the stem, contains coelomic and nervous extensions. The scars or facets left on the stem trunk or its branches may be restricted to the latus of a single ossicle or extended to latera of two or more consecutive joints. Their distal end may carry fingerlike processes which become fastened to firm objects encountered during growth.

3) The discoid type of holdfast consists of a relatively wide disc-shaped expansion or an inverted bowl-shaped body (Fig. 64,3-7). It provides fixation on rocky bottoms or solid foreign objects such as shells of brachiopods and mollusks, as well as stems of other crinoids. Such holdfasts may spread symmetrically in all directions and assume subcircular outlines, or grow chiefly on one side, and acquire more irregular contours. The margin may be entire or cut into lobes or short digitations. On their upper convex side, the region about the stem-scar may be depressed or flush with the surrounding surface. Many holdfasts of this type, like those of the recent *Calamocrinus* and *Phrynocrinus*, or of the fossils *Encrinus* and *Aspidocrinus* (Fig. 64,3-5) seem to be entirely massive. Some show a more complex structure. For instance, the Ordovician holdfast called *Lichenocrinus* comprises a plated upper surface, supported by numerous radiating lamellae, which rise vertically from a distinct floor plate; in the center of the upper surface, a deep plated crater contains the distal extremity of the stem (Fig. 64,6,7).

4) Roots primarily belonging either to the cirrus-bearing or discoid type may be covered by an unjointed crust of secondary stereom that extends onto the substratum and tends to transform the whole structure into a solid calcareous mass. All such en-

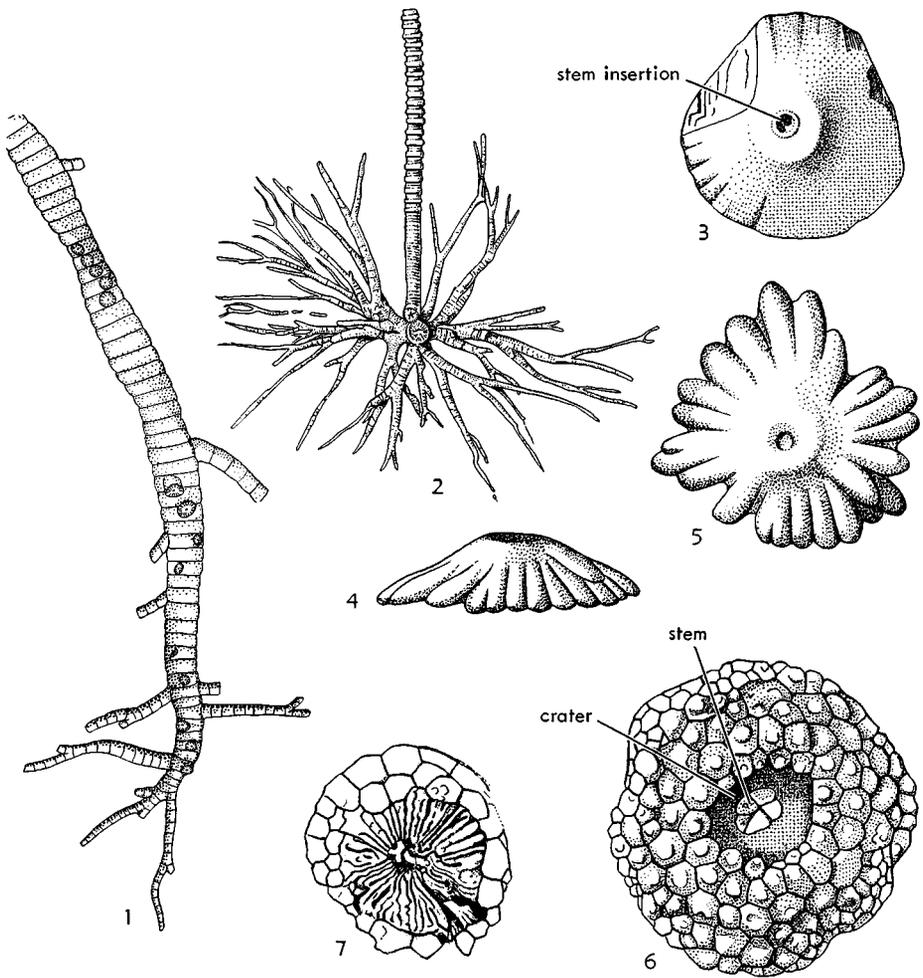


Fig. 64. Morphology of cirrus-bearing type (1,2) and discoidal type (3-7) of crinoid holdfasts.

1. *Platycrinites regalis* (HALL), Miss., USA (Iowa), distal portion of stem with radicular cirri given off at irregular intervals,  $\times 0.7$  (Wachsmuth & Springer, 1897).
2. *Eucalyptocrinites ovalis* (HALL), M.Sil. (Niag.), N.Am., clustered radicular cirri at distal end of column,  $\times 0.7$  (Wachsmuth & Springer, 1897).
3. *Aspidocrinus scutelliformis* HALL, L.Dev., USA (N.Y.), discoidal holdfast, upper side,  $\times 0.7$  (Goldring, 1923).
4. *Aspidocrinus digitatus* HALL, L.Dev., USA (N.Y.), discoidal holdfast, lateral and upper side views,  $\times 0.7$  (Goldring, 1923).
5. *Lichenocrinus milleri* FABER, U.Ord., USA (Ind.), discoidal holdfast, upper side showing deep crater at center for stem attachment,  $\times 2.5$  (Faber, 1929).
6. *Lichenocrinus nodosus* FABER, U.Ord., USA (Ind.), discoidal holdfast, upper side with part of outer plated covering removed to show inner radiating lamellae,  $\times 2.5$  (Faber, 1929).

crusting growths cause a more or less distinct deformation of primary root forms, which in extreme cases are entirely hidden. Encrusting roots occur chiefly in reef-dwelling crinoids and in forms living in

moving waters. Typical examples are found in the *Crotalocrinitidae*, *Cupressocrinitidae* (Fig. 65,1), *Apicrininitidae* (Fig. 65,2), *Millericrinidae* (Fig. 65,3,4), *Sclerocrinidae*, and *Eugeniocrinitidae*.

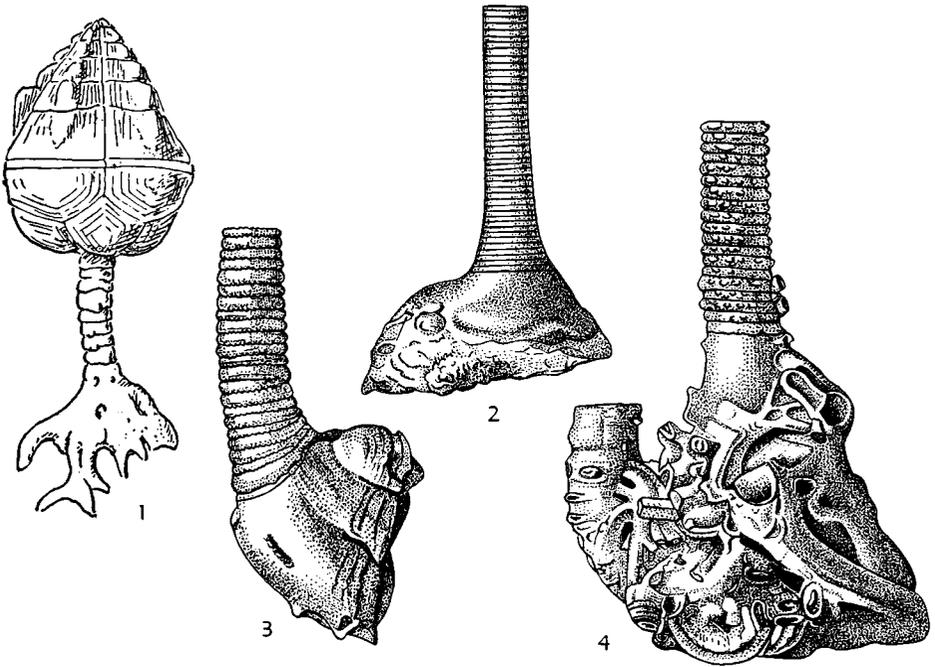


FIG. 65. Morphology of encrusting holdfasts.

1. *Cupressocrinites abbreviatus* GOLDFUSS, M.Dev., Ger., complete specimen,  $\times 0.7$  (Jaekel, 1918).
2. *Apiocrinites parkinsoni* (VON SCHLOTHEIM), Jur., W.Eu., dististele and root,  $\times 0.7$  (d'Orbigny, 1858).
3. *Millericrinus knorri* DE LORIOI, U.Jur., W.Eu., dististele and root,  $\times 0.7$  (de Loriol, 1882-84).
4. *Millericrinus horridus* D'ORBIGNY, U.Jur., France, two dististeles and roots encrusted with serpulid tubes,  $\times 0.7$  (de Loriol, 1882-84).

Holdfasts of some fossil crinoids are highly specialized. Already mentioned is *Lichenocrinus*, and still more curious are *Ancyrocrinus* and *Camarocrinus*.

The name *Ancyrocrinus* was given by HALL (1862) to grapnel-like bodies found in Devonian rocks of New York, and recently in the Givetian of Brittany (France) (MORZADÉC, 1967) (Fig. 66,1-5). The discovery of a stem and crown attached to the grapnel has demonstrated that the latter served as the holdfast of a botryocrinid genus (GOLDRING, 1942). The grapnel consists of the distal portion of the stem and true cirri covered over by a crust of secondary stereom. In some specimens the primary root, which is composed of numerous small polygonal plates and very short stumplike encrusting radicular cirri, is incorporated into the grapnel (Fig. 66,1,2); in other specimens no trace of the original root is present (Fig. 66,3-5), which sug-

gests that in such specimens the stem must have broken off between the original root and the undermost cirrinodal (or cirri nodals) included in the grapnel (McINTOSH & SCHREIBER, 1971). A secondary canal system, branching at irregular intervals along the axial canal of the stem and cirri, developed within the grapnel and its stereom crust up to the surface where they were sealed by a thin layer of calcite. The grapnel of *Ancyrocrinus* functioned probably less as a drag and ballast (KIRK, 1911) than as an anchor (EHRENBERG, 1929), giving the crinoid a secure and relatively stable base in a low- to moderate-energy environment (McINTOSH & SCHREIBER, 1971).

HALL (1879b) also introduced the name *Camarocrinus* for large, bulbous, chambered structures found at several localities in Lower Devonian rocks of North America, but also known since the middle of the 19th century from the Upper Silurian of

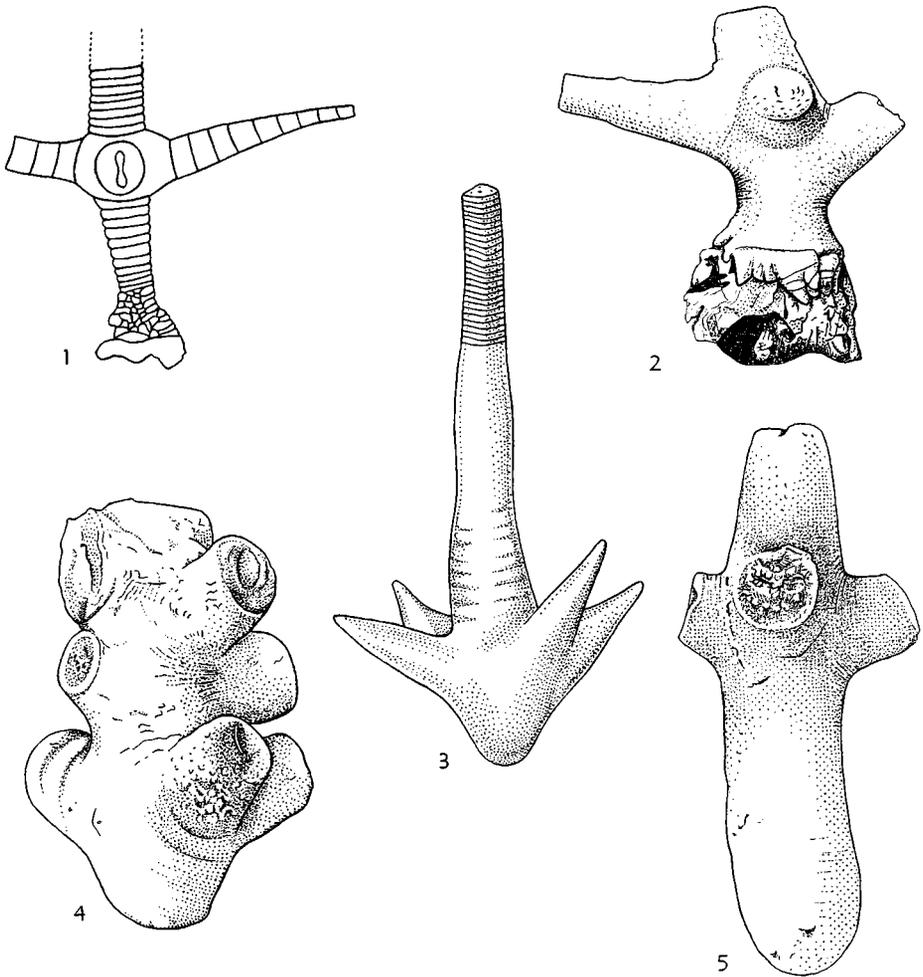


Fig. 66. Morphology of the grapnel-like holdfast of *Ancyrocrinus bulbosus* HALL, M.Dev., E.N.Am. (all McIntosh & Schreiber, 1971, except 3).

1. Primary root system of an immature specimen before build-up of secondary stereom; root attached probably to a brachiopod shell,  $\times 3$ .
2. Grapnel with radicular cirri of primary root attached to a coral,  $\times 2$ .
3. Typical grapnel without trace of primary root,  $\times 2$  (Hall, 1862).
4. Grapnel showing three distinct cirri levels,  $\times 2$ .
5. Grapnel with long segment of stem incorporated into it, but without any trace of primary root,  $\times 2$ .

Bohemia under the vernacular French name of *lobolithes* (Fig. 67, 68). HALL recognized their real nature as holdfasts of a crinoid, which now is determined almost certainly to belong to the camerate *Scyphocrinites*. Some bulbs reach or even exceed 20 cm. in diameter. In the center of their proximal face is fixed the distal end of the stem, which at this level divides into primary roots. By repeated divisions these

roots produce innumerable cirral elements that form the outer covering of the bulbs, as well as the partition-walls of inner chambers. *Camarocrinus*, therefore, belongs to the radicular cirri-bearing type of crinoid holdfasts. Two main, closely related sorts of bulbs have been distinguished (HAUDE, 1972). In the first one, known as the cirrus type (Fig. 67), the walls consist of a dense three-layered lattice work of numer-

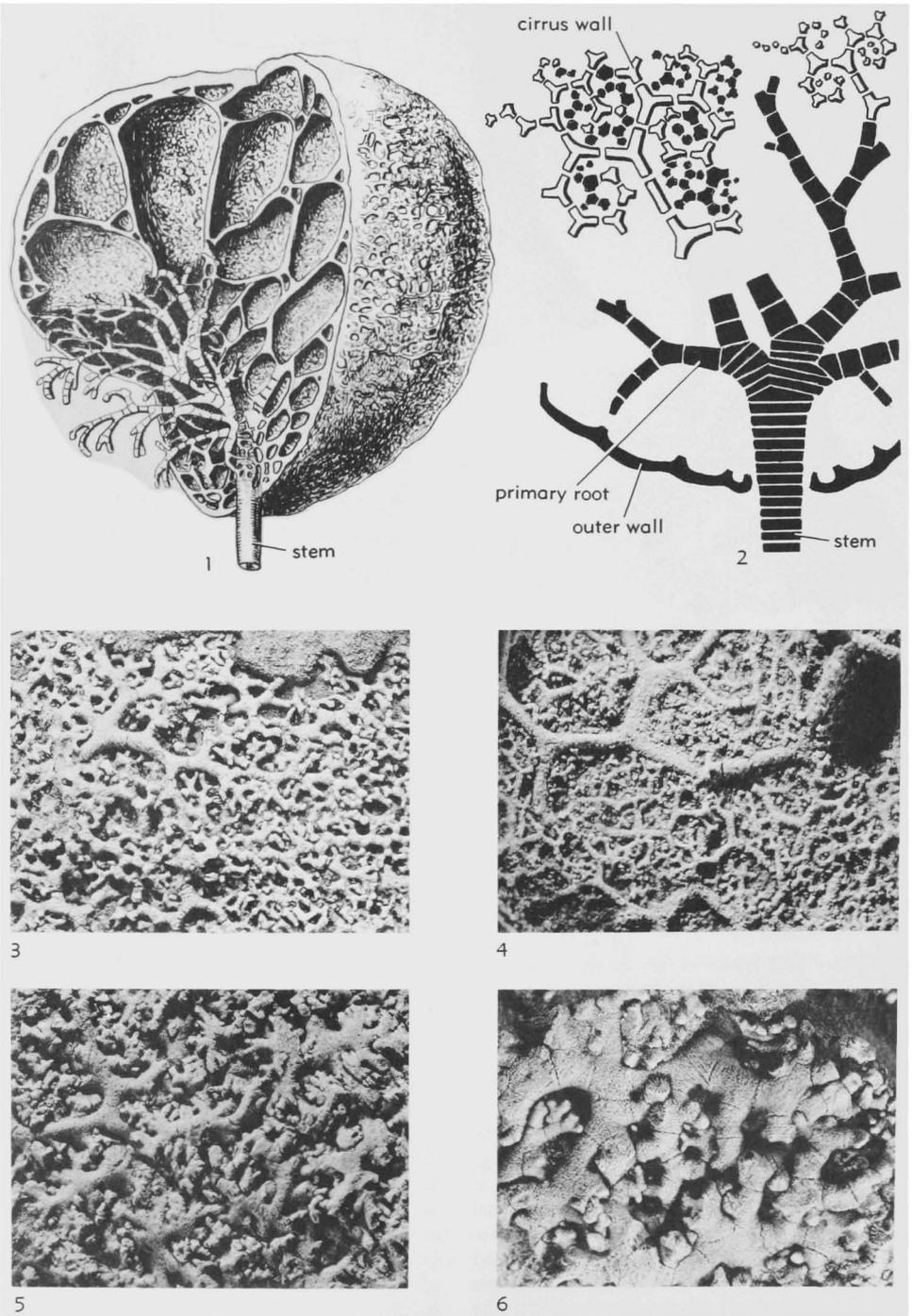


FIG. 67. Morphology of the cirrus type of the bulbous holdfast called *Camarocrinus* (all from Haude, 1972, modified in 1 and 2).

ous spiculelike skeletal elements (cirrals), the largest of which lie in the middle layer (Fig. 67,5,6), whereas the smallest fill remaining spaces to form the cover layers (Fig. 67,3,4); the outer cover of the bulb closes up against the distal end of the stem; the chambers have no openings, are arranged without distinct order, and range in number from a few to very many.

The second kind of bulb (Fig. 68,1) differs from the first in its plated appearance (Fig. 68,2), the occurrence of a short projecting collar around the stem base and presence of primary roots, associated with fewness of chambers (usually 4 to 7, apparently 11 at most), and existence of an opening to each chamber in the axil of the primary roots. The collar consists of a single layer of plates, but the remainder of the bulb is composed of a three-layered wall with a middle network of minute irregular cirrals over- and underlain by layers of plates, which are nothing else than thickened portions of cirrals belonging to the middle network (Fig. 68,3,5).

The bulbous holdfasts of *Scyphocrinites* have been interpreted as bodies of organisms belonging to an independent class of echinoderms (BARRANDE, 1887), as cystoids (SUN & SZETU, 1947), as genital sacs (JAEKEL, 1904), brood-pouches or receptacles (HAECKEL, 1896a), pathologic cysts induced by myxostomids (HAECKEL, 1896a; EHRENBERG, 1926), inflated roots serving for permanent or temporary settlement on muddy bottoms (SPRINGER, 1917), and floating organs (HALL, 1879b; SCHUCHERT, 1904; YAKOVLEV, 1953; STUKALINA, 1967; HAUDE, 1972). The last hypothesis seems to be the most plausible by far, for it is consistent with morphological characteristics of the bulbs, their worldwide distribution, approximation to a mechanical model (paradigm) for their function, and calculation of their buoyancy as attachments to living crinoids which floated on the surface or at shallow depths in widespread ancient seas (HAUDE, 1972).

Not all stalked crinoids have special terminal stem organs serving for fixation. Some appear to have effected attachment by nonradicular cirri, the stem lying down partly on the sea floor, or having lost its normal holdfast, or as in comatulids, having been discarded except for its topmost columnal transformed into a centrodorsal. Some others were fastened in place by the stem itself, primary fixation having been accidentally or normally abandoned. In the last cited possibility generally but not universally, the stem tapers distally (Fig. 69,3). At the same time, there is a marked tendency toward looping or coiling of the distal stem region, enrollment taking place upon itself or around foreign bodies. The coil may comprise one, two or several whorls, which touch or are separated from each other (Fig. 69,4). The coil may be in a simple plane, as in *Diamenocrinus* (Fig. 69,2), or form a conical structure as in *Acanthocrinus* (Fig. 69,1) and *Thallocrinus*, which probably functioned as ballast for the crinoid, maintaining it in an approximately vertical position. A similar function may be ascribed to terminal knobs produced by secretion of stereom, supposedly induced by and following disruption of the column.

### STEMLESS CRINOIDS

Sporadically in some crinoid groups and invariably in others the whole stem or most of it is lacking in adults. Five or six groups of such crinoids may be recognized, chiefly representing physiological developments, since they include widely divergent types. 1) One group contains forms which show a strong tendency to shorten the stem accompanied by more or less resorption of remaining columnals, as illustrated by the inadunate *Hoplocrinus estonus* ÖRİK (Fig. 70,1) and the articulate *Millericrinus prattii* (GRAY) (Fig. 70,2), in which the stem is reduced to a small conical knob or even to a single flat ossicle. 2) In a second

(Continued from facing page.)

1. Model of bulb partially open to show inner structures; stem downward according to presumed position during life.
2. Diagram showing clockwise and counterclockwise spiral arrangement of branching cirri that form the wall.
3. Aspect of outer wall,  $\times 4$ .
4. Aspect of chamber wall,  $\times 4$ .
- 5,6. Middle layer with major branches and spaces filled by smaller branchlets,  $\times 4$ .

group, the larval stem is discarded during ontogeny, except for the most proximal columnal, which fuses with infrabasals to produce the centrodorsal of the adult crinoid (see above, p. T71); this group corresponds to the articulate order Comatulida. 3) Somewhat similar in appearance, but very different in origin and structure is the Permian reef-dweller of Timor named *Timorocidaris* (Fig. 70,3); as interpreted by BATHER (1900a) and WANNER (1940, 1950), the skeleton of this strange crinoid is reduced to a single hemispherical calcite crystal which carries three (rarely two) arm facets on a small neck in the center of its flat surface. 4) Crinoids of a fourth group are characterized by the complete absence of a stem or of any anchoring structure, and by the presence of a central pentagonal apical plate in the cup; this plate is called *centrale* and, to the group belong the inadunate *Cryphiocrinus* (Fig. 70,4), members of the articulate order Uintacrinitida (Fig. 70,5,6), and the doubtful Saccocomidae (*Pseudosaccocoma*, Fig. 70,7). 5) Crinoids of the next group have no stem, no centrodorsal, and no *centrale*; examples of this condition are furnished by the rhodocrinitid camerate *Monstrocrinus*, by the inadunate *Agassizocrinus* (Fig. 70,9), the proximal cup plates of which fuse partly or completely, with accompanying secondary deposition of stereom, and by most representatives of the articulate order Roveacrinitida (*Poecilocrinus*, Fig. 70,8) (as interpreted by RASMUSSEN, 1961). 6) The members of a sixth group do not possess a jointed column, but as a rule are cemented to some solid object by a mass of stereom, the composition of which is conjectural; they comprise the inadunate *Pilidiocrinus* (Fig. 70,10,11), such flexibles as *Edriocrinus* (Fig. 70,12), *Permobrachypus*, *Calycocrinus* (Fig. 70,13), or *Palaeoholopus* (Fig. 70,14), and articulates like *Cotylederma*, *Eudesicrinus*, *Hemibrachiocrinus*, *Dibrachiocrinus*, *Cyathidium* (Fig. 70,15,16), and *Holopus*.

## CUP (OR CALYX)

### GENERAL FEATURES

The cup (equivalent to dorsal cup or aboral cup) or calyx<sup>1</sup> is part of the crinoid

theca located between the stem and origins of the free arms. Most fossil crinoids, unlike the majority of recent ones, have a well-developed calyx that includes the main and central part of the skeleton surrounding soft structure of the visceral mass.

As we have seen (p. T59), the cup in its simplest form comprises two or three circlets of five plates, with those of one circlet alternating with those in adjacent circlets (Fig. 71). The uppermost cup plates, except one or two on the side defined as posterior, are directly in line with the arms and therefore are designated as *radials* (*radialia*). The interradially located plates next below the radials are termed *basals* (*basalia*), since in many crinoids they form the base of the cup or calyx and rest on the column. In some crinoids a circlet of perradially disposed plates called *infrabasals* (*infrabasalia*) occurs beneath the basals. A base composed of one circlet of plates between radials and stem is termed *monocyclic*; it is said to be *dicyclic* if it comprises two plate circlets. In a wider sense, a crinoid with a monocyclic base of the cup or calyx is designated as monocyclic, and is called dicyclic in a crinoid provided with a dicyclic base.

The radials, basals, and infrabasals are the primary skeletal elements of the cup. Together they form what is sometimes called the *patina*, a term proposed by JAEKEL (1891). The addition of various elements to this basic structure produces an extension of the cup. Thus, in many crinoids the proximal ossicles of the arms are firmly incorporated as *fixed brachials* into the calyx. Generally, the fixed portions of the arms are joined laterally together by plates located between the rays and between branches of the rays (*interbrachials*). Usually also, extra plates, called *anals*, occur in the posterior interray, contributing to the width. In this way, a complex structure is

<sup>1</sup> The term "calyx," herein taken as a synonym of "cup," has been used, and is still used, by some authors for designating the whole theca (cup plus tegmen). The proposal recently made by MOORE & STRIMPLE (1973), to call "cup" that part of the theca that comprises only the lowermost two or three circlets of plates (including anal plate if present) next above the stem of stalked crinoids or at base of the skeleton in stemless crinoids and to designate as "calyx" a crinoid cup joined firmly with fixed plates above the radial circlet, is judged by UBACHS to be artificial and unnecessarily conflicting with common usage of these terms in both zoology and paleontology.

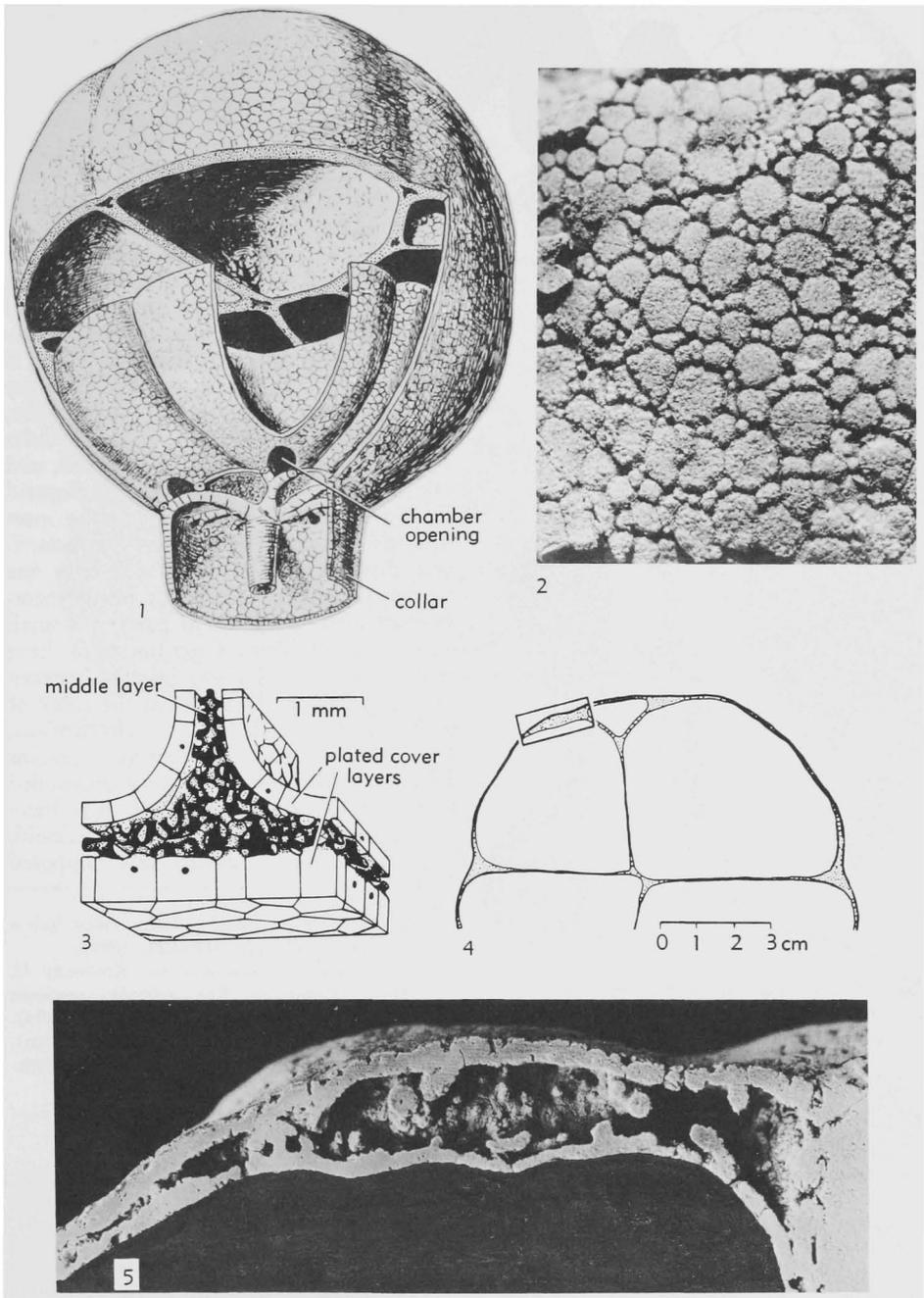


FIG. 68. Morphology of the plated type of the bulbous holdfast called *Camarocrinus* (all from Haude, 1972).

1. Model of bulb partially open to show inner structures, stem downward according to presumed position during life (modified).
2. Aspect of plated outer wall,  $\times 4$ .
3. Diagrammatic model of wall structure.
4. Equatorial section of bulb.
5. Detail of region limited by a rectangle in Fig. 4.

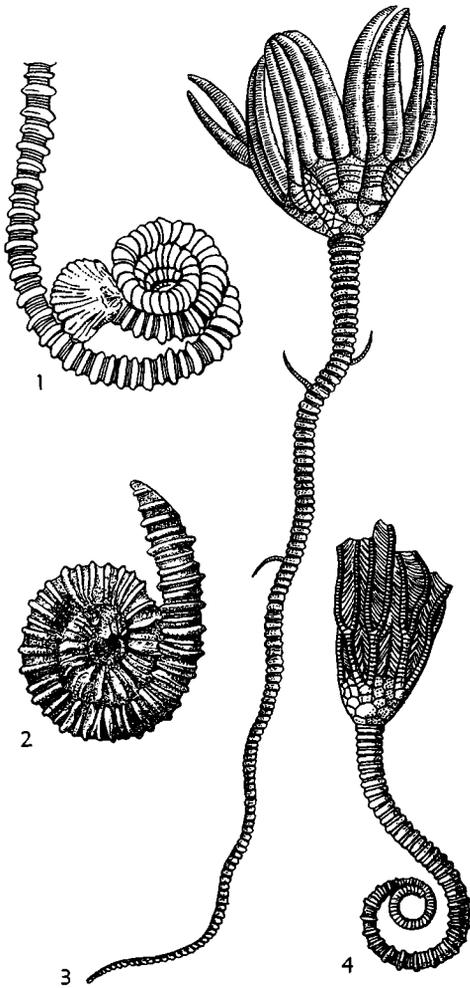


FIG. 69. Root-functions of the stem.

1. *Acanthocrinus rex* JAEKEL, L.Dev., Ger., distal portion of stem closely rolled into a conical coil,  $\times 1$  (Jaekel, 1895).
2. *Diamenocrinus jouani* OEHLERT, Dev., France,

formed, involving the participation of a varyingly large number of skeletal pieces of different origins.

It has been thought generally that all types of crinoids pass through an early phylogenetic stage in which the calyx is reduced to the patina. This, however, does not seem to accord with progressive decrease in size of the visceral mass that crinoids as a whole are judged to have undergone during their history, nor does it agree with the fact that ordinarily the cup of oldest crinoids has a more complex structure than that of later members. This is best illustrated by the inadunates. Contrary to typical representatives of this subclass, characterized by a cup that usually includes only infrabasals (if any), basals, radials, and one or more anal plates, several disparid inadunates among those judged to be most primitive (e.g., *Eustenocrinus*, *Dystactocrinus*, *Peniculocrinus*, *Ohioocrinus*) have one or two circlets or arm plates firmly incorporated with cup plates as parts of a small calyx; the Ordovician perittocrinids have numerous accessory plates inserted between basals, radials, and anals, and the calyx of such primitive cladids as *Aethocrinus*, *Cupulocrinus*, and *Ottawacrinus* contains fixed brachials which may be accompanied by well-developed interbrachials. It is therefore suggested that the calyx of the crinoid, like the column, originally was composed

distal portion of column closely rolled into a planispiral coil,  $\times 1$  (Oehlert, 1891).

3. *Woodocrinus macrodactylus* DE KONINCK, U. Carb. (L.Namurian), Eng., complete specimen with tapering stem,  $\times 0.3$  (de Koninck, 1854).
4. *Pycnocrinus dyeri* (MEEK), U.Ord., USA (Ohio), stem terminating in a loose coil,  $\times 1$  (Wachsmuth & Springer, 1897).

FIG. 70. Reduction and complete disappearance of crinoid stem.

1. *Hoplocrinus estonus* ÖPIK, Ord., Estonia, oblique side view of theca with stem reduced to small conical knob,  $\times 1.2$  (Öpik, 1935).
2. *Millerocrinus prattii* (GRAY), M.Jur., Eng., side view of theca with stem reduced to short stump of five columnals,  $\times 3$  (Carpenter, 1882a).
3. *Timorocidaris sphaeracantha* WANNER, Perm., Timor, oblique side view,  $\times 1.65$  (Lakeman, 1950).
4. *Cryphiocrinus girtyi* KIRK, U.Miss., USA (W. Va.), basal view of cup with small centrale concealing minute infrabasals,  $\times 2$  (Kirk, 1929c).
5. *Untacrinus socialis* GRINNELL, U.Cret., N.Am., theca from side,  $\times 0.6$  (Rasmussen, 1961).
6. *Marsupites testudinarius* (VON SCHLOTHEIM), U.Cret., Eu., stemless cup from the side,  $\times 0.7$  (Bather, 1900a).
7. *Pseudosaccocoma strombergense* REMEŠ, U.Cret., Italy, theca from aboral side showing perforated centrale,  $\times 2$  (Rasmussen, 1961).
8. *Poecilocrinus signatus* (PECK), L.Cret.-U.Cret., USA (Texas), theca from lateral side,  $\times 15$  (Rasmussen, 1961).

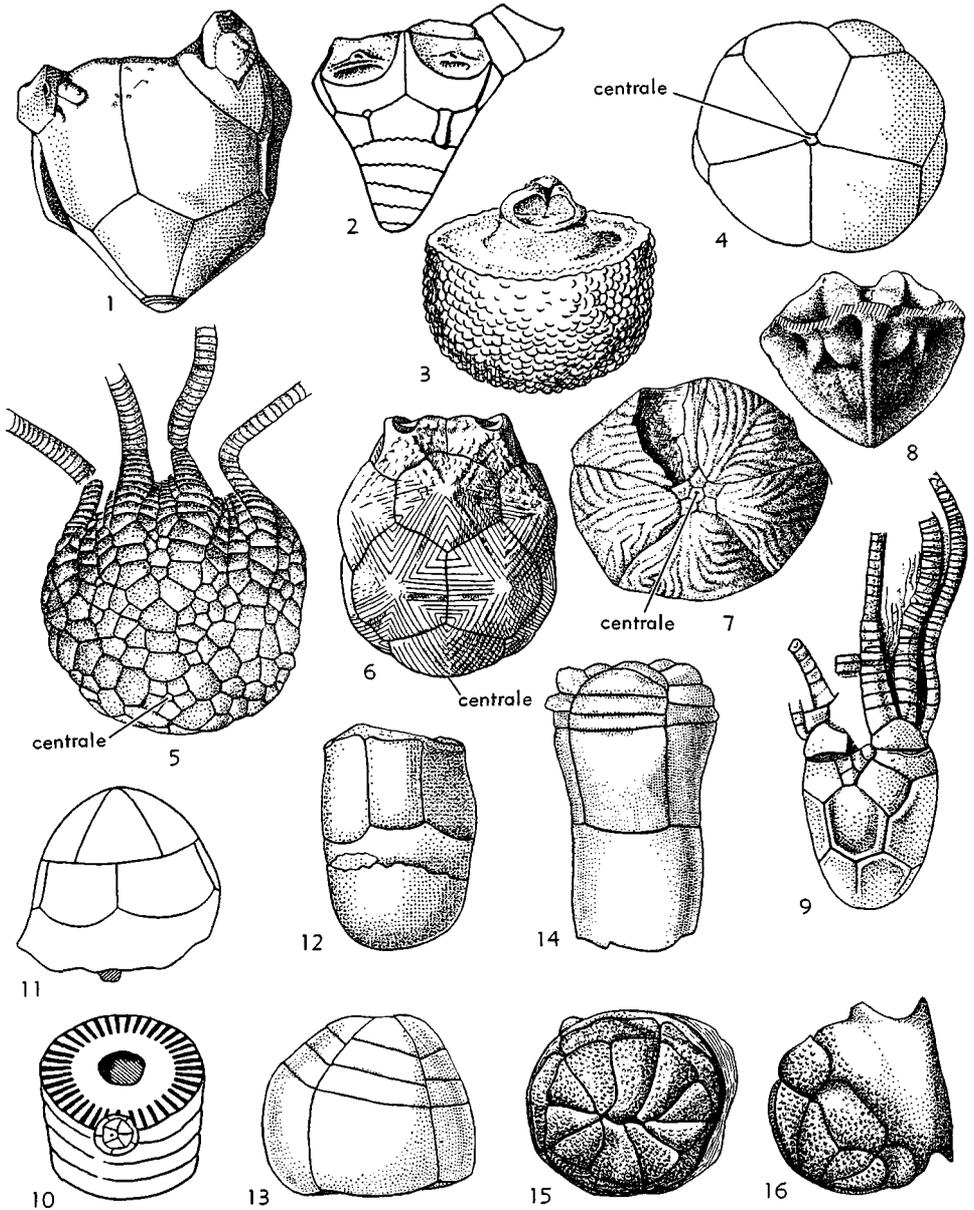


FIG. 70. (Explanation continued from facing page.)

9. *Agassizocrinus laevis* (ROEMER), U.Miss., N. Am., CD view of holotype, infrabasals not completely fused, stemless,  $\times 1$  (Springer, 1926b).
10. *Pilidiocrinus hackeri* ARENDT, L.Perm., USSR (Urals), specimen attached to crinoid pluricol-umnal,  $\times 3$  (Arendt, 1970a).
11. Same, complete specimen from the side,  $\times 8$  (Arendt, 1970a).
12. *Edriocrinus pocilliformis* HALL, L.Dev., N. Am., CD interray view of stemless theca,  $\times 2$  (Goldring, 1923).
13. *Calycoocrinus perplexus* WANNER, Perm., Timor, crown from side,  $\times 2.4$  (Wanner, 1930b).
14. *Palaeoholopus pretiosus* WANNER, Perm., Timor, crown from side,  $\times 1$  (Wanner, 1929a).
- 15,16. *Cyathidium holopus* STEENSTRUP, U.Cret., Eu., crown in adoral and lateral views,  $\times 2$  (Nielsen, 1913).

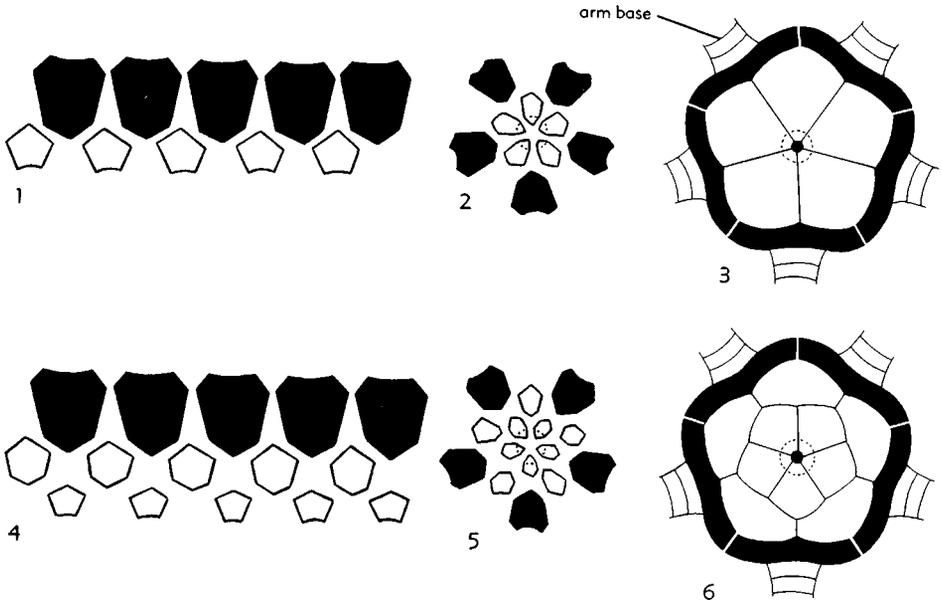


FIG. 71. Three different ways of representing basic calyx structures of crinoids with monocyclic (1-3) and dicyclic (4-6) bases (Ubaghs, n). [Explanation: radials black.]

of more or less numerous plates arranged without definite order; then, that it was progressively affected by a tendency toward pentamerous symmetry, as expressed by a gradual acquisition of definitive arrangement of plates, proximally in disposition of the successive plate circlets and distally in divergence of radial series extending beyond the theca as articulated outgrowths, which became the arm or brachia. Such a view seems to have recently received support from the discovery in the Middle Cambrian (Burgess Shale) of British Columbia of a crinoid-like form (*Echmatocrinus brachiatus*) with a conical calyx made up of numerous irregularly arranged plates and provided with an irregularly multiplicated, stemlike outgrowth serving for attachment (SPRINKLE, 1973a).

#### SHAPE OF CUP OR CALYX

The theca of crinoids beneath the tegmen and free arm attachments varies considerably in shape. For the description of different forms it is convenient to use well-defined terms, such as those proposed by MOORE & PLUMMER (1940) (Fig. 72). To

this end three different characters are considered: 1) main form of the cup or calyx, 2) ratio of its height to width, and 3) shape of its base.

1) *Main form*.—A cup or calyx may be cone, bowl, or globe shaped. It is said to be cone shaped when the sides flare upward with essentially uniform slope from the stem attachment, so that it reaches greatest width at the summit. It is defined as bowl shaped if the slope of its upward flaring sides becomes markedly steeper near the summit than adjacent to the stem attachment, greatest width remaining at the summit. It is described as globe shaped if the sides curve distinctly inward near the summit and if greatest width is below the summit.

2) *Ratio of height to width*.—The height of the cup or calyx is the distance measured along the aboral-adoral axis between the basal and summit planes. Width is the distance measured along a line perpendicular to the aboral-adoral axis and to the anteroposterior axis through the widest part of the cup or calyx. For each of the four main forms recognized one may distinguish

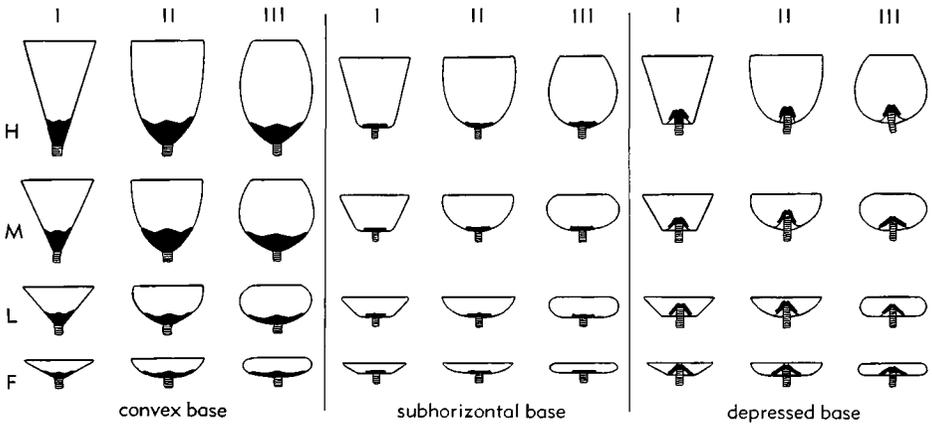


FIG. 72. Diagrams illustrating shapes of the calyx in crinoids (mod. from Moore & Plummer, 1940). [Explanation: I, cone shaped; II, bowl shaped; III, globe shaped; H, high; M, medium; L, low; F, flat; plates of base, black.]

1) a tall type with height greater than width, 2) a medium tall type with height approximately equal to width, 3) a low saucer-shaped type with height appreciably smaller than width, and 4) a flat or discoid type with height equal to or smaller than half of the width.

3) *Shape of base.*—The base may be convex and composed of plates flaring upward and visible in side view of the theca. It may be flat and composed of subhorizontal plates not visible in side view, with lowermost part of the cup or calyx appearing to be broadly truncated. The base may be depressed and the stem attachment concealed in a more or less deep concavity, the bottom of which is flat or concave.

#### ORNAMENTATION OF CUP OR CALYX

The outer surface of the cup or calyx plates may be smooth, finely granular, pustulose, covered with distinct lines or wrinkles, nodose, or spinose. Immobile spines may be present on some plates, and movable spines, attached to pitted tubercles, are known to occur on the calyx of some genera (e.g., *Arthroacantha*). According to WANNER (1942b), the paddle-shaped skeletal elements that envelop the proximal cirlet of plates in the genus *Paradoxocrinus* are modified movable spines attached to basals. Many, mainly Lower

Paleozoic crinoids have ridges radiating from the center of plates to the middle of the sutures (exceptionally to the angles), or following midlines of the rays and (in some camerates) the sagittal series of anal plates. All of these surface markings may distinguish large or small assemblages of crinoids. They have a varying important classificatory value.

#### INFRABASALS

The infrabasals are plates perradial in position that form the proximal cirlet of the base in dicyclic types. Typically they are five in number and equal. This condition (probably primitive) is preserved in most dicyclic camerates and many inadunates. However, genera of these subclasses are known to have four, three or two infrabasals, or all of these plates fused into a solid skeletal piece. On the other hand, all but a few flexible crinoids have three unequal infrabasals—a small (azygous) plate almost invariably located in the C ray and two large (zygous) ones. Most certainly, this restriction in number results from ankylosis of sutures between adjoining infrabasals.

The infrabasals may be prominent and upflared, forming a significant part of the cup enclosing the visceral mass (Fig. 73, I; 74, I). In the Silurian flexibles *Calpiocrinus* and *Homalocrinus* their enlargement is

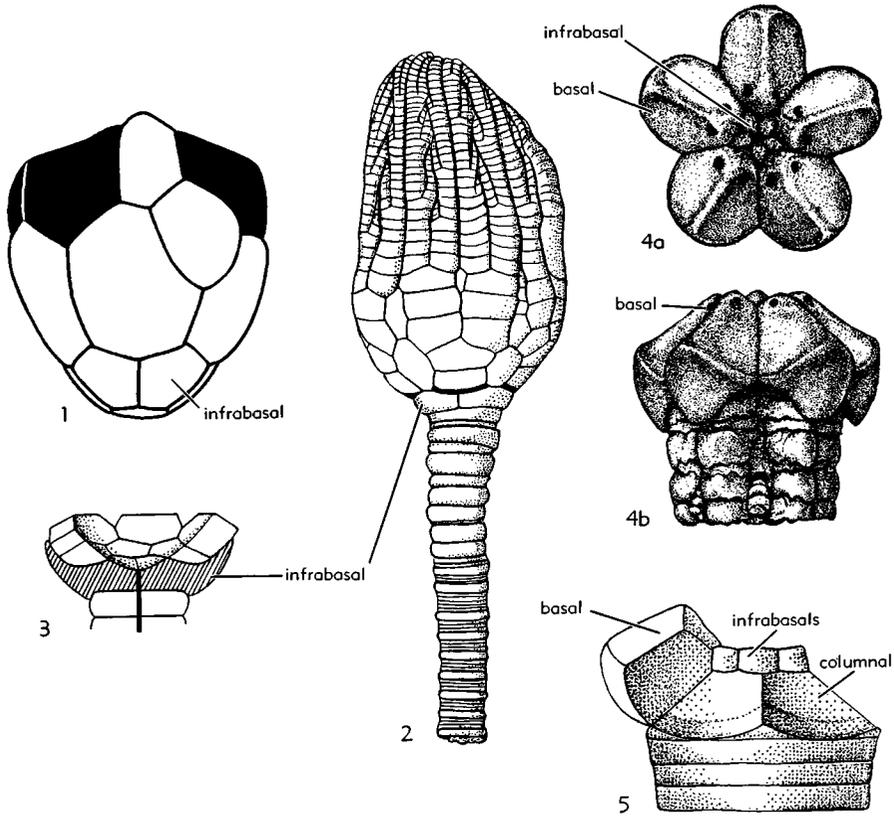


FIG. 73. Morphology of infrabasals. [Explanation: radials black.]

1. *Ulocrinus fistulosus* STRIMPLE & MOORE, Penn., Kans.; with upflaring infrabasals,  $\times 1$  (mod. from Strimple & Moore, 1971a).
- 2,3. *Calpiocrinus rotundatus* SPRINGER, U.Sil., Sweden (Gotland); 2, crown and part of stem; 3, diagrammatic vertical section of cup, basals and greater part of radials covered by hypertrophied infrabasals (redrawn from Springer, 1920).
- 4a,b. *Cainocrinus tintinnabulum* FORBES, Eoc., Eng.; reduced infrabasals, basals, and proximal columnals, in adoral and lateral views,  $\times 10$  (Rasmussen, 1972a).
5. *Millericrinus polydactylus* D'ORBIGNY, Jur., France; proximal columnals and reduced infrabasals after removal of all basals but one, lat. view, ca.  $\times 6$  (redrawn from de Loriol, 1882-84).

great enough to provide partial or entire concealment of basal and radial circllets by the infrabasals (Fig. 73,2,3). But this is an exceptional condition. Generally, they are small or medium-sized and take only a modest part in formation of the thecal wall. If they are recumbent or subhorizontal, the cup is truncated below and they are barely visible or invisible in side view, serving as support for overlying skeletal plates (Fig. 74,2,3). In cups or calyces with a basal concavity, they may be horizontal (Fig. 74,4) or downflaring (Fig. 74,5), according to their size and shape of

the basal concavity; of course they are not visible in side view.

In some crinoids the infrabasals show a marked tendency to become atrophied, to be resorbed, or to lose their identity by fusing with other elements. This is particularly true of articulate crinoids, but may be observed also in other subclasses. In the flexible *Icthyocrinus*, for instance, they are reduced to a diminutive plug entirely covered by the column (Fig. 74,3), or infrabasals are completely resorbed. A nearly similar condition characterizes the infrabasal circllet of isocrinid genera (Fig. 73,

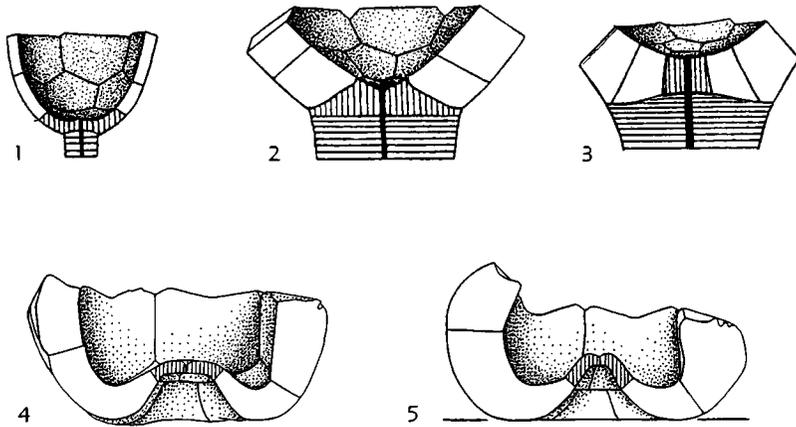


FIG. 74. Diagrammatic vertical sections of cups (1,4,5) and patinas of calyces (2,3) illustrating various conditions of infrabasals. [Explanation: infrabasals ruled vertically.]

1. *Lecanocrinus*, with upflaring infrabasals (Springer, 1920).
2. *Forbesiocrinus*, with subhorizontal infrabasals (Springer, 1920).
3. *Icthyocrinus*, with infrabasals reduced to a small plug, entirely covered by column (Springer, 1920).
4. *Delocrinus major* WELLER, L.Perm., USA (Texas); with horizontal infrabasals in basal concavity,  $\times 1$  (Moore & Plummer, 1940).
5. *D. subhemisphericus* MOORE & PLUMMER, Penn., Mo.; with downflaring infrabasals in basal concavity,  $\times 2$  (Moore & Plummer, 1940).

4,5). Among comatulids, these plates are present usually in the larvae as discrete elements but fuse later with the topmost columnal or columnals to form a proximale and take part in composing a centrodorsal. Such dicyclic crinoids, in which the infrabasals are not differentiated or absent in adults are said to be **cryptodicyclic** or **pseudomonocyclic**. It is very likely that among dicyclic fossil crinoids genera currently are classified as monocyclic because they offer no structural evidence to their dicyclic origin.

In various crinoids, however, the previous presence of infrabasals is suggested or definitely indicated by 1) orientation of the axial cords in the stem and of lobes in the chambered organ, invariably located perradially in pseudomonocyclic and dicyclic forms; 2) orientation of the columnal pentameres (liable to exceptions), outer angles of the stem, vertical sutures of the stem, angles of the lumen, and placement of cirri with reference to radial symmetry of the cup ("law" of WACHSMUTH & SPRINGER, see p. T61); 3) occurrence of infrabasals in immature growth stages; 4) paleontological demonstration of the former existence of these plates in ancestors; and

5) close relationship to genera that possess infrabasals.

### CENTRALE

In a few dicyclic crinoids and pseudomonocyclic ones lacking stem and cirri, space enclosed by the proximal cirlet of cup plates—either infrabasals or basals (if infrabasals are vestigial)—is occupied by a plate called **centrale**. Examples are the Upper Mississippian inadunate *Cryphiocrinus* (Fig. 70,4), the Jurassic and Lower Cretaceous articulate *Pseudosaccocoma* (Fig. 70,7), and the Upper Cretaceous articulates *Uintacrinus* (Fig. 70,5) and *Marsupites* (Fig. 70,6). The centrale, which is large in *Marsupites* but very small in other genera mentioned, is a nonperforated element (except in *Pseudosaccocoma*) lacking any sign of a stem attachment or partition into two or several pieces. It may conceal the infrabasals (as in *Cryphiocrinus*) or coalesce with them (as in some individuals of *Uintacrinus*).

The centrale has been the subject of much speculation and controversy (BATHER, 1896b, 1900a; CARPENTER, 1884a; CLARK, 1909, 1911a, 1915a; KIRK, 1911; SPRINGER, 1901). It cannot represent fused infrabasals



FIG. 75. *Ancyrocrinus bulbosus* HALL, M.Dev., USA(N.Y.); CD interray (1) and proximal (2) views of a calyx with lumen completely covered by polygonal plates after loss of column during life,  $\times 4$  (McIntosh & Schreiber, 1971).

(except perhaps in *Pseudosaccocoma*), or fused basals because it coexists with these plates in most of the cited genera. It is probably not the proximal stem ossicle, for it lies *within* the proximal circling of cup plates, instead of abutting against them on their outer or aboral sides, as does the proximal columnal when it takes part (as among comatulids) in formation of the cup. Its homology with the supposed distal columnal of the stem (so-called "dorso-central"), plus all columnals of the larval stem of comatulids, as suggested by CLARK, is purely speculative. It is certainly not a primary, primitive, constitutive element of the cup, since it occurs only in highly specialized genera, and never in early crinoids. Probably, therefore, it represents an entirely new element, introduced in genera characterized by a complete separation of crown and column, and serving to plug the opening through which the axial canal of the column communicates with the visceral cavity of the theca in stalked cri-

noids. A possible confirmation of this last interpretation seemingly is offered by some specimens of *Carabocrinus* and *Arachnocrinus* described by KIRK (1911), in which the introduction of a similar central plate within the infrabasal circling seems to have been brought about by disruption of the crown and column.

One may compare the random apparition of such a plate with that of a pavement of small polygonal skeletal elements completely covering the lumen of the cups or calyx of crinoids that have lost their stem during life. An example of this condition has been reported by McINTOSH & SCHREIBER (1971) for *Ancyrocrinus bulbosus* (Fig. 75).

### BASALS

The basals are plates of a circling typically located next proximal to radials. In the monocyclic type of base, such plates rest directly on the stem. In the dicyclic type, a circling of infrabasals occurs on their aboral side. In both, the basals are interradial in position.

The basals of the camerate genera *Cleioocrinus* and *Spyridiocrinus*, instead of being below the radials, are inserted between them, so that the latter rest directly on infrabasals (Fig. 76,1,2). This arrangement is not judged to be fundamentally distinct from the normal dicyclic condition because species of dicyclic camerates (e.g., *Paulocrinus biturbinatus*, *Rhipidocrinus crenatus*) and inadunates (e.g., *Syndetocrinus bohemicus*) have some radials, either as a rule or as individual variations, which may enter into contact with infrabasals (Fig. 76,3-7).

Almost without exception in dicyclic crinoids the number of basals is five. In monocyclic crinoids, their primary number is also five, but a widespread tendency to fusion is observed, their number being reduced to four, three, two, or all coalesced into a single solid plate. The plates that fuse are not invariably the same. Consequently the position of interbasal sutures varies, allowing recognition of different kinds of bases (Fig. 77-81 illustrating most of these recognized as distinctive at generic and specific levels). For the sake of brevity and easiness, in these figures and in the following text, the individual basal plates

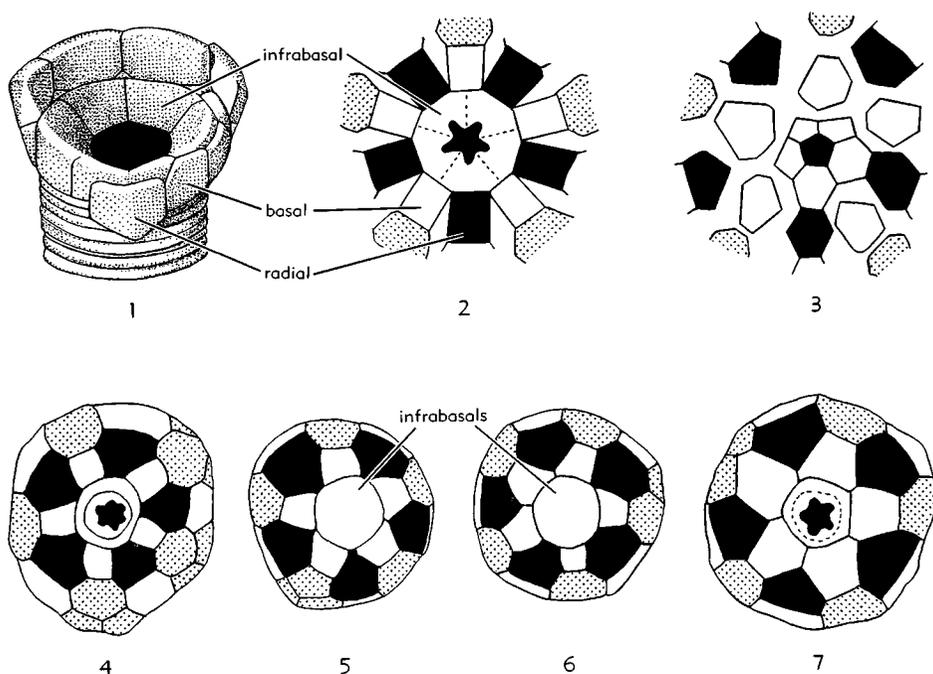


FIG. 76. Morphology of basals. [Explanation: radials and lumen of axial canal black; interbrachials stippled.]

1. *Cleioocrinus regius* BILLINGS, M.Ord., Can.; oblique lat. view of proximal parts of calyx and column, showing how basals and radials form a single circlet which surrounds the infrabasals,  $\times 4$  (Springer, 1905).
2. *Spyridocrinus cheuxi* OEHLERT, L.Dev., France; basals and radials all in contact with infrabasals (Ubaghs, 1950).
3. *Paucocrinus biturbinatus* SPRINGER, M.Sil., USA (Ind.); two radials in contact with infrabasals (Springer, 1926a).
- 4-7. *Rhipidocrinus crenatus* (GOLDFUSS), M.Dev., Ger.; various arrangements of proximal cup plates showing how in some specimens the radials, or some of them, may enter into contact with infrabasals (Breimer, 1960).

will be designated arbitrarily by the small letters: *p* (for posterior) being the posterior or *CD* basal, and counterclockwise in dorsal view, *q* the *DE* basal, *r* the *AE* basal, *s* the *AB* basal, and *t* the *BC* basal (see orientation, p. T61).

The change in number of basals among monocyclic inadunates, as well as in monocyclic camerates provided with a five-sided, more or less pentagonal base (see below), seems to have proceeded through mere ankylosis of plates, with consequent production of unequally quadripartite, tripartite, bipartite, or undivided bases (Fig. 77).

In such crinoids, having a quadripartite pentagonal base, the *r* basal usually fuses with *s* (Fig. 77,2), more rarely with *q* (Fig. 77,3), but in the hybocrinid inadu-

nate *Cornocrinus*, it is *p* and *t* basals that coalesce (Fig. 77,4).

A tripartite pentagonal base results from fusion of two pairs of original basal elements, giving two large (zygous) and one small (azygous) plate; the small plate is generally the *r* basal (Fig. 77,5), less commonly *s*, *p*, or *q* basals (Fig. 77,6,7,8), exceptionally (as in *Paradoxocrinus*) the *t* basal (Fig. 77,9). A bipartite pentagonal base has not been found among camerates, but it occurs in the disparid inadunate *Mycocrinus*, and is produced by the fusion of three ( $p + q + r$ ) and two ( $r + s$ ) basals (Fig. 77,10).

Much more complicated and difficult to explain is the position and relative size of basal plates in monocyclic camerates hav-

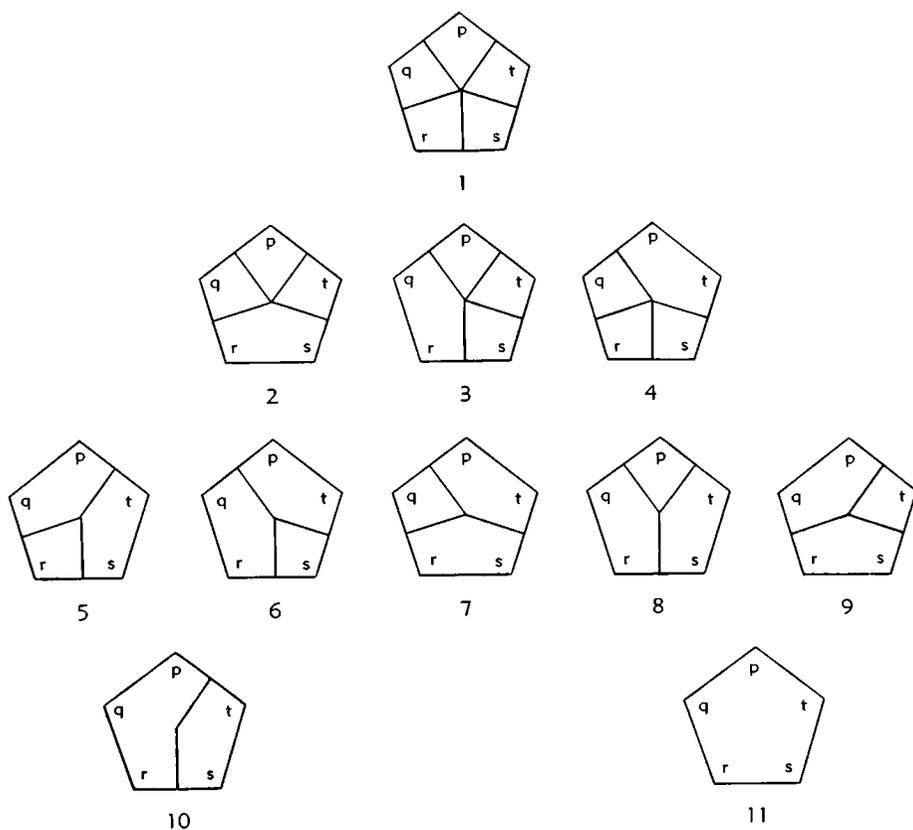


Fig. 77. Diagrams illustrating various arrangements of plates observed in monocyclic pentagonal bases (Ubahgs, n). [Explanation: *p-t*, individual basal elements as explained in text.]

ing an anal plate included in the radial circlet. In these the base is no longer five-sided or pentagonal, but becomes six-sided, that is to say more or less hexagonal in outline. The same condition is found in the curious disparid inadunate *Agostocrinus*, which has an equally tripartite hexagonal base supporting a circlet of six nearly equal plates composed of five radials and one anal plate.

According to WACHSMUTH & SPRINGER (1897) and WILSON (1916), the introduction of an anal plate into the radial circlet in camerates is secondary and therefore the pentagonal base of these crinoids is judged to be ancestral to the hexagonal base (Fig. 78,1-3). On the contrary, MOORE & LAUDON (1943a) and SPRENG & PARKS (1953) interpreted the pentagonal base of camerates as derivative from the hexagonal

base through upward elimination of the anal plate from the radial circlet (Fig. 78, 4-6). From these opposite views, the evolution of the hexagonal bases in camerates may be, and indeed has been, variously interpreted.

A quinquepartite hexagonal base (Fig. 78) is not known in these crinoids. Should it be discovered, it would probably show a large, posterior, truncated plate and four smaller subequal elements with pointed distal tips. The widening of the posterior plate (*p*) could have been achieved by enlargement of this plate either on one side (WACHSMUTH & SPRINGER) (Fig. 78,2) or on both sides (symmetrical enlargement) (WILSON) (Fig. 78,3); in either case, the interradial position of the basals would have been maintained. Quite different is the suggestion made by SPRENG & PARKS,

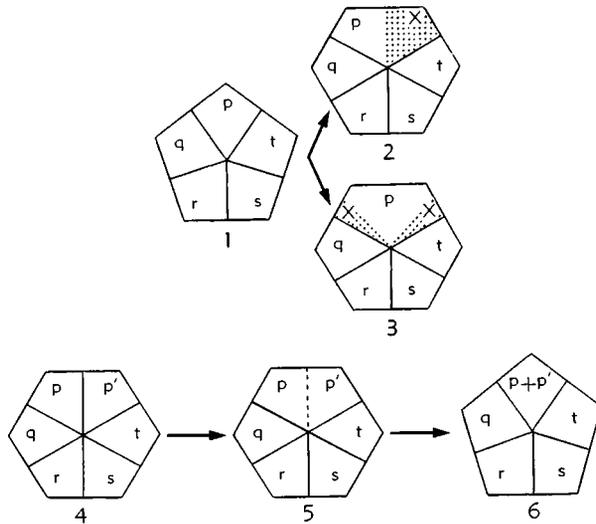


FIG. 78. Diagrams illustrating possible origin of the monocyclic hexagonal base in camerates, according to WACHSMUTH & SPRINGER (1,2), WILSON (1,3) and SPRENG & PARKS (4-6) (Ubaghs, n). [Explanation:  $p-p'$ , individual basal elements as explained in text; stippled areas (X) inferred plate increments.]

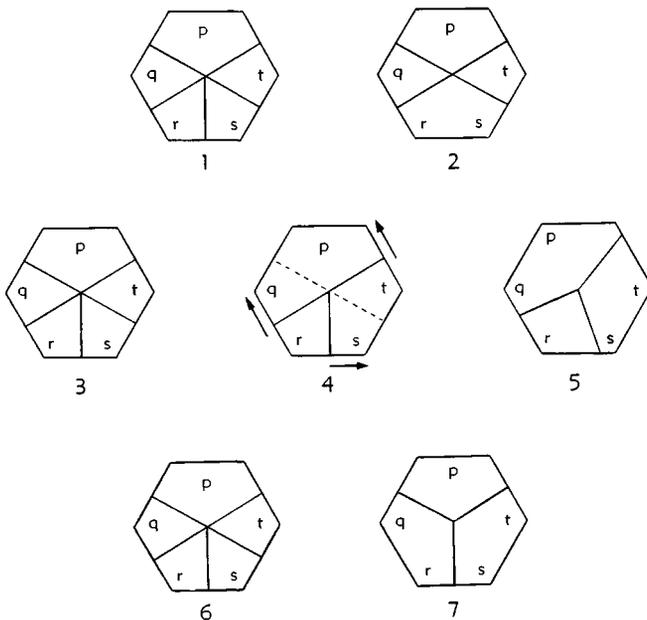


FIG. 79. Diagrams illustrating evolution of the quadripartite hexagonal base in camerates (1,2), of the unequally tripartite hexagonal base in some camerates (3-5), and of the equally tripartite hexagonal base of the inadunate *Agostocrinus* (6,7) (Ubaghs, n). [Explanation:  $p-t$ , individual basal elements as explained in text. Arrows running parallel to sides of bases indicate that the adjacent interbasal suture is being shifted in the direction of arrow.]

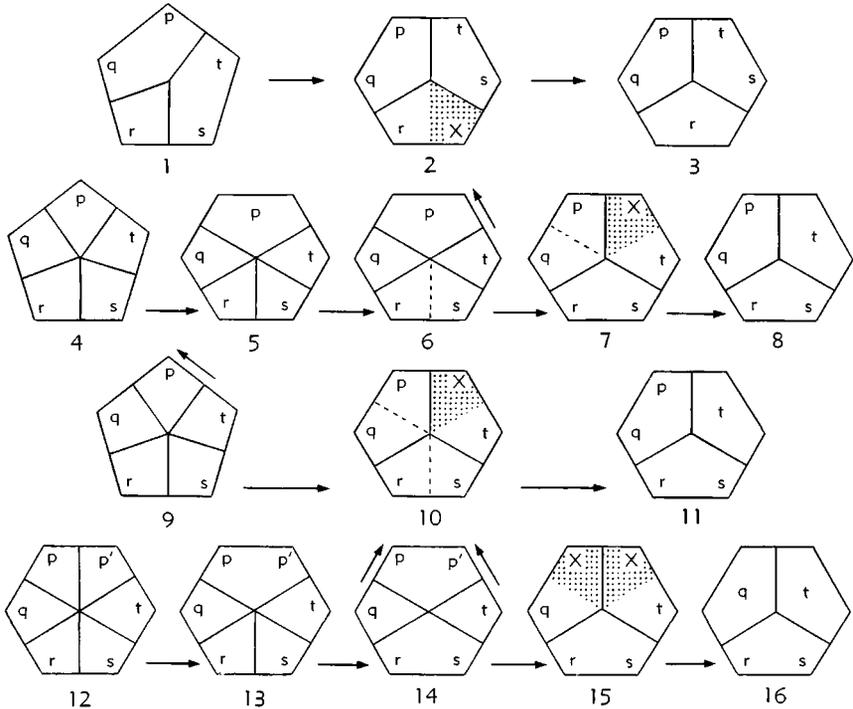


FIG. 80. Diagrams illustrating evolution of the unequally tripartite hexagonal base in camerates, according to WACHSMUTH & SPRINGER (1-3), WILSON (4-11), and SPRENG & PARKS (12-16) (Ubahgs, n). [Explanation:  $p$ - $p'$ , individual basal elements as explained in text, stippled areas (X) inferred to represent plate increments. For interpretation of arrows running parallel to sides of bases, see Fig. 79.]

who supposed that the posterior basal in the quinquepartite hexagonal base is a compound plate originating through fusion of two small posterior basals ( $p + p'$ ) belonging to a hypothetical ancestor with a heptapartite hexagonal base (Fig. 78,4-6).

The quadripartite hexagonal base is easily derived from a quinquepartite hexagonal base, for it only requires fusion of the  $r + s$  basals (Fig. 79,1,2). The unequally tripartite hexagonal base found in *Desmidocrinus* and *Methabocrinus* could have been produced by fusion of two pairs of basals ( $p + q$ ,  $s + t$ ) in a quinquepartite hexagonal base (Fig. 79,3-5). Similarly the equally tripartite hexagonal base of the disparid *Agostocrinus* might result from fusion of the  $q + r$  basals and  $s + t$  basals in a quinquepartite hexagonal base (Fig. 79,6,7).

Much more puzzling is the problem of the origin of equally tripartite or bipartite hexagonal bases, because such bases in

camerates have a posteriorly directed suture lacking in the other types of hexagonal bases. Let us consider first the equally tripartite hexagonal base. According to WACHSMUTH & SPRINGER (Fig. 80,1-3), this type of base derives from an unequally tripartite pentagonal base by 1) interpolation of an anal plate in the radial circlet and transformation of the pentagonal outline into a hexagonal outline; 2) enlargement of the right side of the  $r$  basal; and 3) shifting of the sutures separating the  $r$  and  $s$  basals and  $p$  and  $t$  basals. For WILSON (Fig. 80,4-11), who appeals to the process of truncation and widening of the posterior side as described above, the tripartite hexagonal base would derive from a quinquepartite pentagonal base either through intermediate quinquepartite and quadripartite hexagonal bases (Fig. 79,5-6), or directly from a pentagonal quinquepartite pentagonal base (Fig. 79,9-11); in both cases, the posteriorly directed suture would be homologous to the suture interposed be-

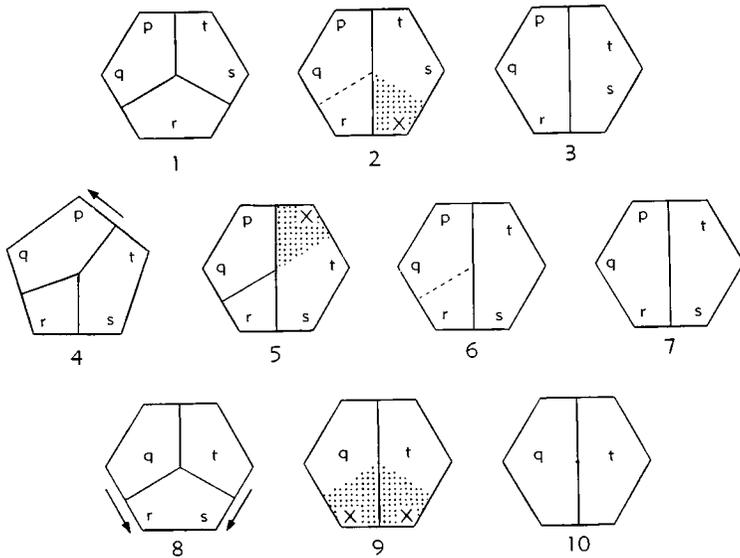


FIG. 81. Diagrams illustrating evolution of the bipartite hexagonal base in camerates, according to WACHSMUTH & SPRINGER (1-3), WILSON (4-7), and SPRENG & PARKS (8-10) (Ubahgs, n). [Explanation: *p-t*, individual basal elements as explained in text, stippled areas (X) inferred plate increments. For interpretation of arrows running parallel to sides of bases, see Fig. 79.]

tween *p* and *t* basals in the pentagonal base, which would have shifted its position through atrophy of the right half of the *p* basal and compensating hypertrophy of the left side of the *t* basal. The SPRENG & PARKS theory is different in supposing that the tripartite hexagonal base derives from a quadripartite hexagonal base through atrophy of the posterior *p + p'* basals and compensating overdevelopment of the adjacent *q* and *t* basals (Fig. 80,12-16).

The equally bipartite hexagonal base of camerates, according to WACHSMUTH & SPRINGER (Fig. 81,1-3) arises from a tripartite hexagonal base through ankylosis of the *p + q* and *r* basals and growth of the compound *s + t* basal on its left side, with consequent shifting of the suture between the *s + t* and *r* basals. For WILSON (Fig. 81,4-7), the equally bipartite hexagonal base originates from a tripartite pentagonal base; this supposes the interpolation of an anal plate into the radial circlet, acquisition of an hexagonal outline of the base, shifting of the suture between the *p* and *t* basals to a posterior position, and fusion of the compound *p + q* basal with the simple *r* basal on the same side. Finally, SPRENG & PARKS (Fig. 81,8-10), who believed that the bi-

partite hexagonal base derives from an equally tripartite hexagonal base, supposed nondevelopment of the compound *r + s* basal and symmetrical enlargement of the *q* and *t* basals until they join along a newly directed anterior suture.

At present, the validity of any of these various interpretations is practically impossible to ascertain, except perhaps in some particular cases. The reason for such a situation is that knowledge of the phylogeny of camerate crinoids is still in its infancy, and therefore no means are given for checking relationships postulated by the diverse theories. For detailed discussion of this problem, see BEYRICH (1871) and BATHER (1898-99, 1917b), besides authors already mentioned.

If the basals present a great diversity in number and arrangement, they show as large a variety of shapes, sizes, and modes of growth, as will appear in the systematic part of the present *Treatise*. In some crinoids (e.g., the dicyclic camerate *Orthocrinus*, inadunate *Calceolispongia* [Fig. 82,1; see also Fig. 501] or the bourgueticrinid articulate *Democrinus* [Fig. 82,2]), they enlarge to the point of becoming the largest elements of the cup; in *Democrinus*, the

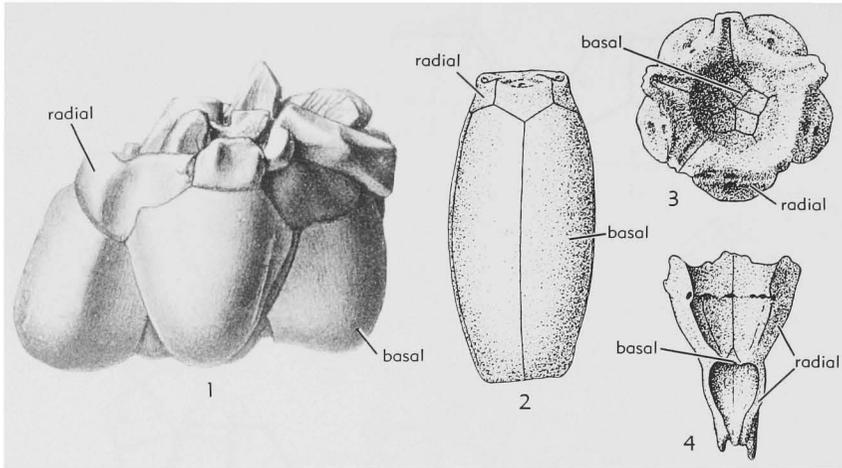


FIG. 82. Selected examples of crinoids with variously developed basals.

1. *Calceolispongia mammeata* (WANNER), Perm., Timor; CD-interray view,  $\times 1$  (Wanner, 1924).  
 2. *Democrinus maximus* (NIELSEN), U.Cret., Den-

- mark; lat. view,  $\times 5$  (Rasmussen, 1961).  
 3.A. *Roveacrinus communis* DOUGLAS, U.Cret., Eng.; 3, adoral view and 4, longitudinal section of calyx,  $\times 15$  (Rasmussen, 1961).

height of the basal ring may be eight times its proximal diameter. Another noteworthy and rather frequent modification is the enlargement of the posterior basal generally in support of the anal plates—a feature particularly remarkable in taxocrinid flexible crinoids.

An opposite tendency is reduction in size of the basals. In some fossil and most recent isocrinids, instead of forming a continuous ring, they make an interrupted basal cirlet, being externally visible as five small triangular plates between lower parts of the radials. In the camerate *Trybliocrinus*, as consequence of allometric growth of the proximal cup or calyx elements, they are transformed into an irregular structure entirely located inside the theca (BREIMER, 1962). According to RASMUSSEN (1961, 1971), the basals of the Roveacrinida, generally overgrown by the radials, form a thin wall separating a small proximal chamber from the main thecal cavity and may also take part in the formation of the lower part of the theca even in species where they are concealed by the radials (Fig. 82,3,4). In comatulids, the basals, which are still relatively well developed in earliest forms, are more and more reduced in the geologically younger ones, to the point of becoming in most recent repre-

sentatives of this order a sort of calcareous diaphragm, called the **rosette**, that covers the centrodorsal cavity and represents the central part of the coalesced basals remaining at a larval stage of calcification (for details on this structure, see chapter on recent crinoids, p. T27). Finally, the basals are unknown in sessile flexibles (Fig. 70,12-14) and articulates (Fig. 70,15,16), as well as in short-stemmed cyrtocrinids, which have radials directly articulated with the column or fused with the proximale (Fig. 51,6a,b).

### RADIALS

In most crinoids the **radials** (radialia) are easily recognized as the most proximal plates of the rays, and it is from their position with regard to the latter that they receive their name. They typically rest on the basals, with which they alternate. They are usually five in number and are followed directly by ray plates of free arms or by fixed brachials immediately above them. Very commonly, they are markedly larger than the succeeding arm plates, but in some crinoids they are approximately the same in size or distinctly smaller than the latter.

The radials are in lateral contact all around the cup or calyx so as to form an uninterrupted cirlet or they may be sepa-

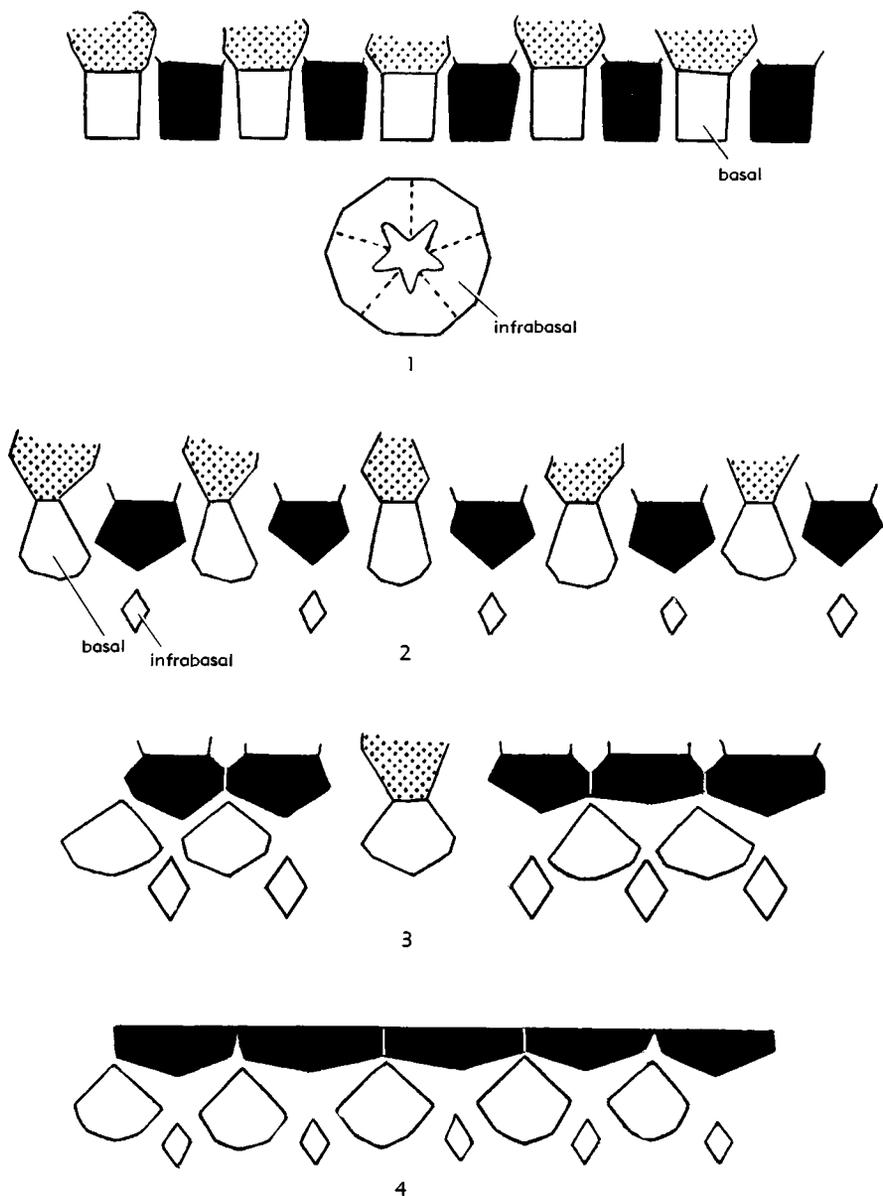


FIG. 83. Various arrangements of radials (Ubaghs, n).—1. *Spyridocrinus*, radials and basals forming a circling of ten plates.—2. *Rhodocrinites*, radials separated by interbranchials connecting basals.—3. *Dimerocrinites*, radials in lateral contact except on CD interray.—4. *Nyctocrinus*, all radials in lateral contact. [Explanation: interbranchials and anals stippled; radials black.]

rated from next neighbors at one or more places. Such separations may be accomplished in three different ways: 1) through intercalation of basals between radials, producing a circling of ten plates directly overlying the infrabasals (e.g., dicyclic camer-

ates *Cleiocrinus* and *Spyridocrinus*, Fig. 83,1); 2) through complete separation of rays, including the radials, by interbranchial plates connecting with the basals—an arrangement that characterizes, for instance, members of the camerate superfamilies

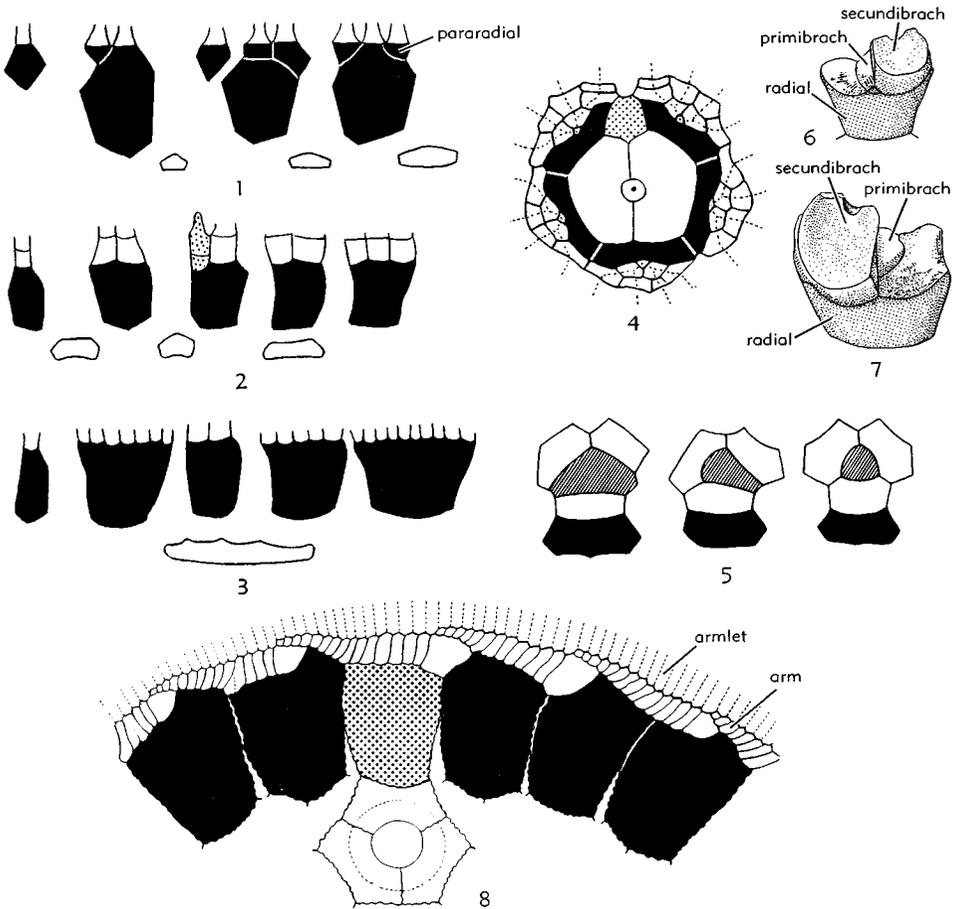


FIG. 84. Drawings suggesting how multiple-arms-bearing radials may have originated (1-3) by fusion of radials with pararadials, (4-7) by reduction of proximal brachitaxes so that several arms come to be borne by each radial, or (8) by fusion of radials with recumbent arms. [Explanation: radials black, primaxils oblique ruled, anal plate stippled.]

1. *Calycanthocrinus decadactylus* FOLLMANN, L. Dev., Ger. (Ubahgs, n).
2. *Allagecrinus austini* CARPENTER & ETHERIDGE, L.Carb., Scot. (Ubahgs, n).
3. *Neocatillocrinus incisus* WANNER, Perm., Timor (Ubahgs, n).
4. *Pterotocrinus pyramidalis* LYON & CASSEDAY, Miss., USA (Ky.); basal view of cup,  $\times 3$  (Springer, 1926b).
5. *Himerocrinus plenissimus* (LYON), M.Dev., USA (Ky.); reduction of primaxil in three rays of the same specimen (Springer, 1921a).
- 6,7. *Hexacrinites verrucosus* FRAIPONT, U.Dev., Belg.; reduction of primibrachs,  $\times 2$  (Ubahgs, n).
8. *Agostocrinus xenus* KESLING & PAUL, M.Ord., USA (Va.); plate diagram of calyx and recumbent arms (Kesling & Paul, 1971).

Reteocrinidae and Rhodocrinitacea (Fig. 83,2), as well as some later genera of flexible crinoids; and 3) through separation of the two posterior radials (C, D) by one or several anal plates (Fig. 83,3). Such interrupted radial circlets are common among Paleozoic crinoids, but unknown in

adults of post-Paleozoic forms (Articulata), which invariably possess uninterrupted radial circlets (Fig. 83,4).

In some crinoids, such as the disparid inadunate *Calycanthocrinus*, more than five arm-bearing plates occur in the radial circlet. These accessory "radials" have been

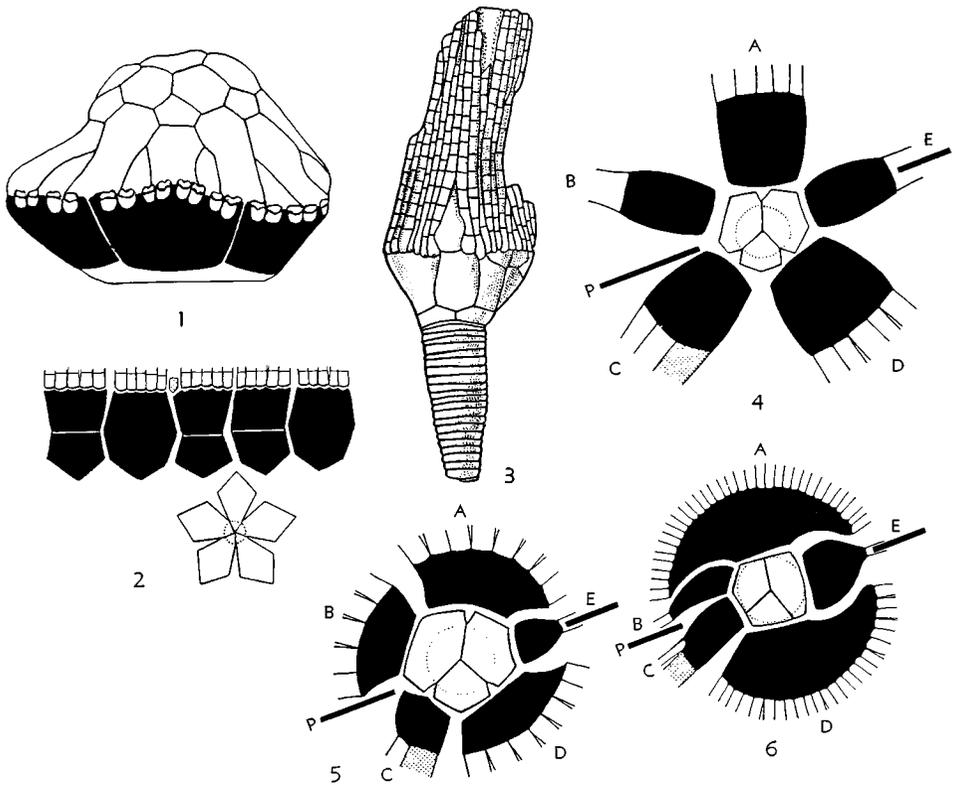


FIG. 85. Selected examples of crinoids provided with multiple-arm-bearing radials. [Explanation: *P*, plane of bilateral symmetry; rays identified by letter symbols of CARPENTER system; radials and biradials black, anal plate stippled.]

1. *Parahexacrinus jungiformis* SHEVCHENKO (Camerata, Parahexacrinidae), L.Dev., Siberia; lat. view of theca,  $\times 1.5$  (Shevchenko, 1967).
2. *Anamesocrinus lutheri* GOLDRING (Disparida, Anamesocrinidae), U.Dev., USA (N.Y.); plate diagram (mod. from Moore, 1962b).
3. *Catillocrinus turbinatus* SPRINGER (Disparida, Allagecrinidae), Miss., USA (Ky.-Tenn.); crown and proxistele, CD-interray view,  $\times 2$  (Springer, 1923).
4. *Wrightocrinus* MOORE (Disparida, Allagecrinidae), L.Carb., Scot., Perm., Timor; plate diagram (Moore, 1962b).
5. *Allocatillocrinus* WANNER (Disparida, Allagecrinidae), U.Miss.-L.Penn., USA, Scot.; plate diagram (Moore, 1962b).
6. *Metacatillocrinus* MOORE & STRIMPLE (Disparida, Allagecrinidae), L.Penn., USA (Okla.); plate diagram (Moore, 1962b).

named *pararadialia* by JAEKEL (1895) (Fig. 84,1). A somewhat similar condition, but possibly very different in origin, is shown by the recent comatulids *Promachocrinus* and *Thaumatoocrinus*, in which five "inter-radial radials" are interpolated between the five primary radials at a relatively late stage of development, producing a circllet of ten identical arm-bearing plates in adults.

Whereas each radial of typical crinoids supports a branched or unbranched arm, some fossil representatives are characterized

by the presence of two or more arms attached to individual radial plates. This peculiarity evolved independently in camerates (Parahexacrinidae) (Fig. 85,1) and some disparid inadunates (Calceocrinacea, Allagecrinacea) (Fig. 85,2-6). Very likely the multiple-arm-bearing radials are a product of fusion of radials either with pararadials (BATHER, 1900a; MOORE, 1962a,b) or with arm plates. Possible fusion with pararadials is illustrated in Figure 84,1-3. Fusion with arm plates may conceivably have

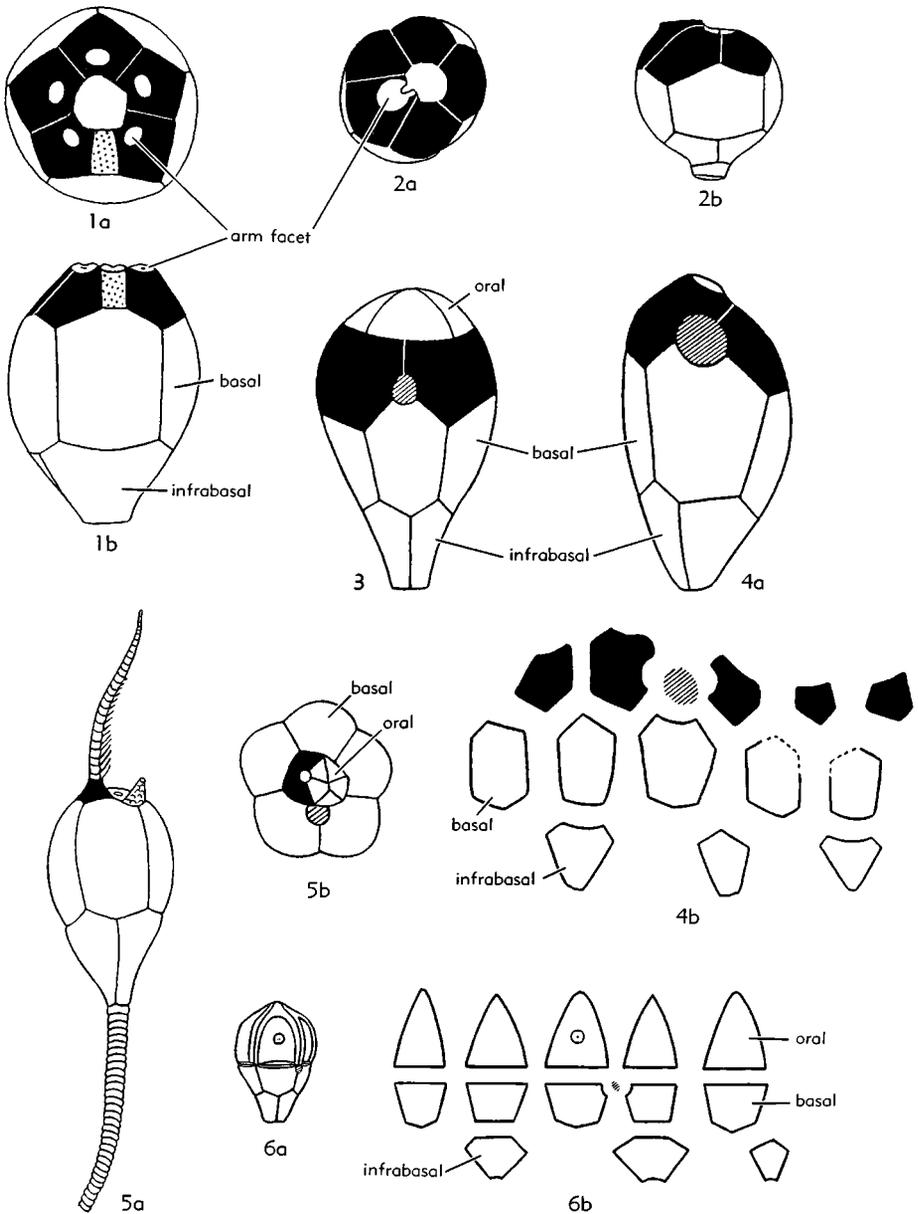


FIG. 86. Reduction of arms and radials in some Codiocrinacea. [Explanation: radials black, anal plate stippled; anus obliquely ruled. Circle with central dot in 6a,b represents the hydropore, the gonopore, or a common hydropore-gonopore.]

1a,b. *Hypocrinus schneideri* BEYRICH, Perm., Timor; five radials and five arms, adoral and post. views,  $\times 3.5$  (Wanner, 1929a).

2a,b. *Allosycocrinus pusillus* WANNER, Perm., Timor; five radials but only one arm, adoral and post. lat. views,  $\times 2$  (Wanner, 1924).

3. *Abrachiocrinus clausus* (AUSTIN & AUSTIN), L. Carb., Eng.; five radials but no arm,  $\times 7$  (Wanner, 1920).

4a,b. *Sycocrinites anapeptamenus* AUSTIN & AUSTIN, L. Carb., Eng.; five unequal radials and no arm; 4a, post. lat. side of cup, ca.  $\times 5$  (Wanner, 1920); 4b, plate diagram (Arendt, 1970a).

been accomplished in two different manners: 1) by repeated branching of arms at very short intervals combined with extreme shortening of brachials, tending to and eventually reaching complete reduction of the series of arm plates resulting from each division, so that several arm plates are brought into contact with radials (Fig. 84, 4-7); 2) by fusion of radials with uniramous series of arm plates totally recumbent on radials, each arm plate supporting a threadlike branchlet or armllet on its free side (Fig. 84,8).

An opposite trend to formation of multiple-arm-bearing radials consists of the simplification of ray structure and elimination of arms and even radials in some crinoids. This trend is well exemplified by the Codiocrinacea, a superfamily of dicyclic cyathocrinid inadunates that contains a large number of generally small crinoids (microcrinoids) (Fig. 86). In this very specialized group, besides several genera normally provided with five arms and five radials (Fig. 86,1), are genera having five radials but less than five arms (Fig. 86,2), or five equal radials but no arms (Fig. 86,3), or five unequal armless radials (Fig. 86,4), or fewer than five radials (Fig. 86,5), or even no radials and no arms (Fig. 86,6). The disappearance of radials in such dicyclic crinoids results in the production of cups composed of two circlets of plates like a monocyclic cup. But it is important to notice that here the remaining circlets are the basals and infrabasals, rather than the radials and basals, as in the true monocyclic condition.

The five components of a radial circlet are rarely perfectly equal, but, except for slight differences in shape and size, they are generally very similar. To this rule, however, noticeable exceptions are produced in different ways: 1) loss of arms by some radials, as shown by several representatives of the Codiocrinacea (Fig. 86,2,4), a loss that brings with it disappearance of the brachial facet on these radials and not un-

commonly their reduction in size or even complete atrophy (Fig. 86,4,6); 2) hypertrophy of certain radials, as illustrated by the Calceocrinacea and Allageocrinacea in relation with the number of arms borne by particular plates of the circlet (Fig. 85, 4-6) and inequality of the arms (Fig. 87); 3) transverse or oblique bisection of certain radials by a suture, in contrast to other radials which are undivided (see below, biradials); 4) differentiation of the C-radial in relation with support of the anal structures (see below, anal plates). To a large extent, these inequalities in size and structure of the radials contribute to make particularly obvious the existence of planes of bilateral symmetry in crowns of the concerned crinoids (Fig. 85,4-6; Fig. 87,3). In some genera they also have a clear adaptive significance, as in the Calceocrinacea where they are related to bending of the crown on the stem (Fig. 87,2,4).

### BIRADIALS

In many monocyclic disparid inadunates, some radials are transversely divided into two parts. Such bisected radials are diversely called **compound radials**, **multiple radials** (MOORE, 1962b), or **biradials** (a term herein proposed by MOORE, in a following glossary of morphological terms). The upper part of a biradial is named **superradial** and the lower part **inferredial**, two terms introduced by BATHER (1892a). In the organization of a crinoid, a biradial occupies the position, and serves the function of an undivided radial. Consequently, its two components together, rather than the inferredial alone (as suggested by MOORE, 1952a), are usually considered as equivalent to and thereby counted as a single radial plate. It is doubtful, however, that a real transverse bisection of certain radials ever occurred (WILSON, 1916). It seems more probable that the superradials and inferredials have always been distinct elements. If this is so, the simultaneous existence of biradials and undivided radials in some dis-

(Continued from facing page.)

5a,b. *Monobrachiocrinus fciiformis granulatus* WANNER, Perm., Timor; single radial with arm; 5a, reconstruction,  $\times 1$ ; 5b, adoral view of cup,  $\times 1$  (Wanner, 1924).

6a,b. *Lageniocrinus seminulum* DE KONINCK & LEHON, L.Carb., Belg.; no radials and no arms; 6a, post. lat. view of cup,  $\times 2$ ; 6b, plate diagram (Kirk, 1940e).

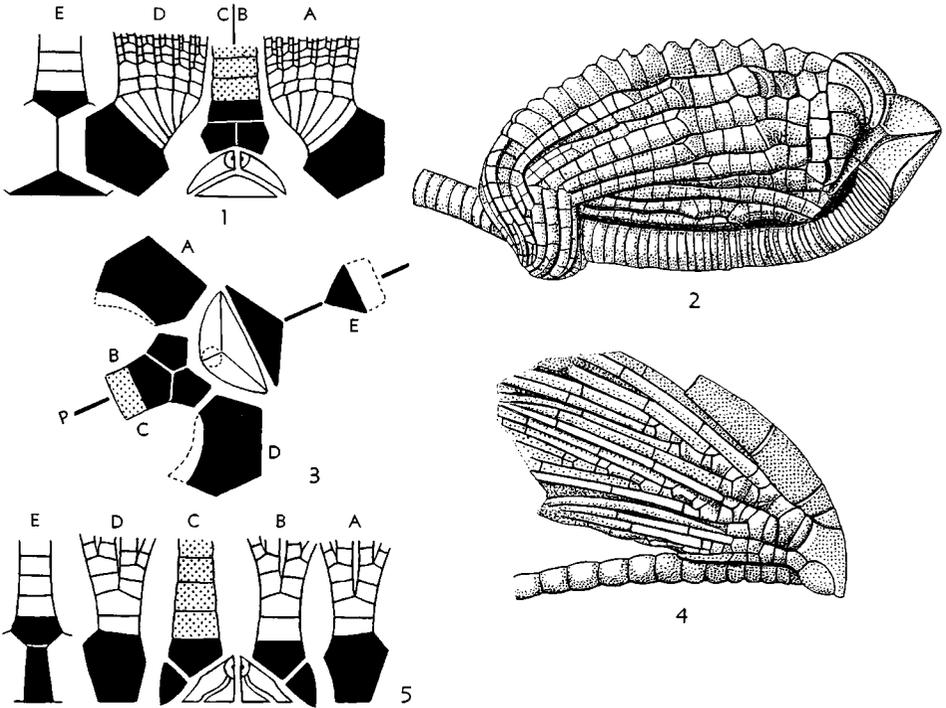


FIG. 87. Inequality of radials in relation to unequal arms in Calceocrinidae (Disparida). [Explanation: P, plane of bilateral symmetry; radials and biradials black; anal plates stippled; rays identified by letter symbols of CARPENTER system.]

- 1,3. *Halysiocrinus* sp. ULRICH, M.Dev.-L.Miss., USA; 1, analysis of cup and proximal part of arms (Springer, 1926a); 3, structure of cup (modified from Moore, 1962a).
2. *Halysiocrinus nodosus* (HALL), L.Miss., USA (Ind.); crown and proxistele, A-ray view,  $\times 1.5$  (Springer, 1926a).
4. *Cremacrinus decatur* SPRINGER, M.Sil., USA (Tenn.); crown and proxistele, A-ray view,  $\times 1.5$  (Springer, 1926a).
5. *Cremacrinus* sp. ULRICH, M.Ord.-U.Sil., N.Am.; analysis of cup and proximal part of arms (Springer, 1926a).

parid crinoids may conceivably be explained either by a marked inequality in size of the most proximal plate of each ray or by the fusion of a superradial and an inferradial resulting in the formation of a large undivided radial in some rays.

The biradials may occur in five rays, three rays (B, C, E), two rays (C and E or B and C), or possibly one ray (C). The first condition is difficult to prove, since it characterizes crinoids provided with five proximal ray plates that are perfectly similar. Nevertheless, the disparid genera *Eustenocrinus*, *Peniculocrinus* (Fig. 88,1a,b), *Ristnacrinus*, and the cladid genus *Ottawacrinus* have been interpreted in this way by MOORE (1962b)—an interpretation also pro-

posed by KESLING & PAUL (1971) for the highly specialized monocyclic inadunate *Acolocrinus* (Fig. 88,2). According to MOORE (1962b, p. 12), the ray plates that immediately follow proximal ones in such genera "seem rather surely to correspond to the superradial elements of the so-called compound radials of homocrinids, heterocrinids, and some other disparid inadunate families, especially where the cup includes only ray-plate pairs."

The occurrence of biradials in the B, C, and E rays is a distinctive feature of at least 43 genera of disparid inadunates belonging to the superfamilies Homocrinacea (Fig. 88,3), Calceocrinacea (Fig. 87,5), Pisocrinacea, and Allagecrinacea (Fig. 85,

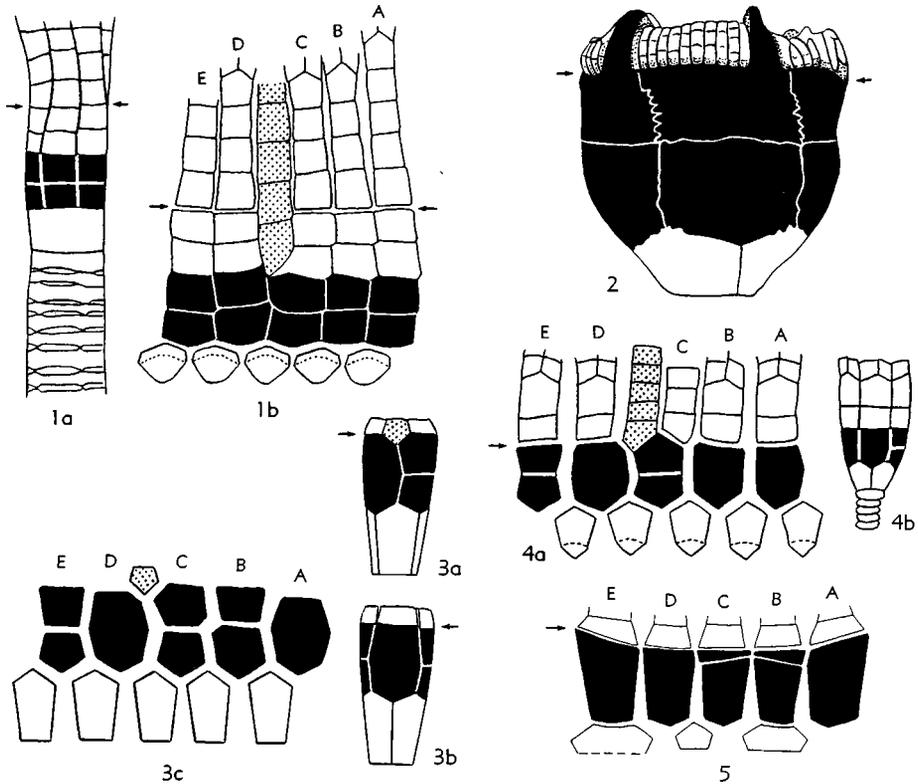


FIG. 88. Selected examples of disparid inadunates with biradials. [Explanation: radials and biradials black; anal plates stippled; top of calyx marked by small arrows; rays identified by letter symbols of CARPENTER system.]

- 1a,b. *Peniculocrinus milleri* (WETHERBY), M.Ord., USA (Ky.); 1a, part of crown and stem, A-ray view,  $\times 6$ ; 1b, analysis of cup and proximal part of arms and anal tube (Moore, 1962b).  
 2. *Acolocrinus hydraulicus* KESLING & PAUL, M.Ord., USA (Tenn.); crown, E-ray view,  $\times 4$  (Kesling & Paul, 1971).  
 3a-c. *Homocrinus parvus* HALL, Sil., USA (N.Y.);

- 3a,b, CD-interray and A-ray views,  $\times 8$ ; 3c, analysis of cup (Kirk, 1914).  
 4a,b. *Columbicrinus crassus* ULRICH, M.Ord., USA (Tenn.); plate diagram and A-ray view of proximal part of crown and stem (Moore, 1962b).  
 5. *Quiniocrinus* sp. SCHMIDT, M.Dev., Ger.; analysis of cup (Moore, 1962b).

2), whereas the presence of biradials in two rays distinguishes members of the disparid superfamilies Heterocrinacea (Fig. 88,4) and Anomalocrinacea, that have compound radials in the C and E rays, as well as the pisocrinid genus *Quiniocrinus* (Fig. 88,5), in which the compound radials are located in C and B rays.

The occurrence of a biradial in a single ray is not so evident, for it is a possibility that depends on interpretation given to proximal C ray plate in some crinoids. Problems that concern these plates in hybo-

crinid, perittocrinid, cladid inadunates, and flexible crinoids will be examined under anal plates (see below, p. T121). Here will be considered only the cases offered by the pisocrinid, iocrinid, and merocrinid crinoids.

In most pisocrinids, a family of disparid inadunates, two radials (A, D) are much larger than the others, and the B and C radials rest on a single plate, which with the two large radials forms the greater part of the cup (Fig. 89,3,5). This single plate has been interpreted by BATHER (1900a) as

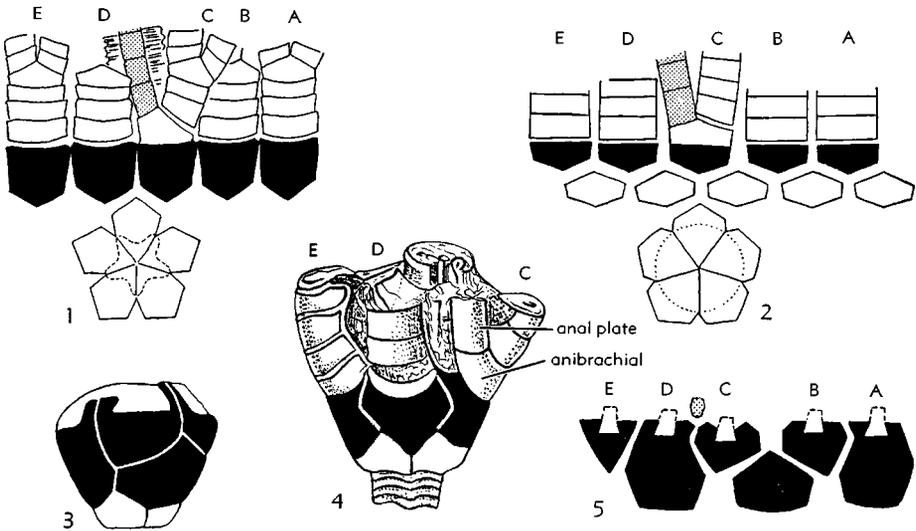


FIG. 89. Structure of pisocrinid, iocrinid, and merocrinid crinoids. [Explanation: radials and biradials black; anal plates stippled; rays identified by letter symbols of CARPENTER system.]

1. *Iocrinus* sp. HALL, ?L.Ord., Wales; M.Ord.-U.Ord., N.Am., Eu.; analysis of cup and proximal parts of arms and anal tube (Moore, 1962b).
2. *Merocrinus* sp. WALCOTT, M.Ord.-U.Ord., USA, Eng.; analysis of cup and proximal parts of arms and anal tube (Moore, 1962b).
3. *Pisocrinus pilula* DE KONINCK, U.Sil., Eu.; C-ray view of cup,  $\times 4.3$  (Bouška, 1956).
4. *Iocrinus crassus* (MEEK & WORTHEN), U.Ord., USA (Ohio); D-ray view of cup with attached parts of arms, anal tube, and stem,  $\times 2$  (Hall, 1872).
5. *Pisocrinus* sp. DE KONINCK, U.Sil., Eu., N.Am., Australia; analysis of cup (basals omitted) (Moore, 1962b).

the C inferradial displaced to the right into the BC-interray. If this is true, the pisocrinids are crinoids provided with a single biradial. If the plate below the B and C radials results from fusion of the B and C inferradials, however, as suggested by MOORE (1962b), they are classifiable with crinoids possessing biradials in two rays. The last interpretation is supported by structure of the pisocrinid genus *Quinocrinus* (Fig. 88,5).

The Iocrinidae (Fig. 89,1,4) and Merocrinidae (Fig. 89,2) are inadunate crinoids, the former monocyclic and the latter dicyclic. Both have radial circllets composed of five equal undivided plates, one of which, located in the C ray, supports an axillary plate bearing an anal plate series on its left

shoulder and an arm on its right shoulder. This axillary plate has been the subject of much controversy. In the view of some authors, because it has the same axillary function as the C superradial of such disparids as *Homocrinus* and *Heterocrinus*, it has to be considered to be a superradial or plate equivalent to a superradial, and accordingly the Iocrinidae and Merocrinidae are considered to be crinoids provided with a single biradial (BATHER, 1890a, 1900a; MOORE, 1950; RAMSBOTTOM, 1961; PHILIP, 1965). This axillary plate, however, 1) plainly has the appearance of an arm plate rather than radial; 2) is not included in the cup but located above the even summits of the five most-proximal ray plates (Fig. 89,1,2,4); 3) is supported by a

FIG. 90. Selected examples of crinoids with fixed ray plates. [Explanation: interbrachials and inter-pinnulars, stippled; radials, black.]

1. *Scyphocrinites elegans* ZENKER (Camerata), U.Sil., N.Am.; diagram of calyx structure (Springer, 1917, mod.).
2. *Icthyocrinus laevis* CONRAD (Flexibilia), Sil., USA (N.Y.); oblique basal view of crown; fixed brachials in lateral contact all around,  $\times 1$  (after Springer, 1920).
3. *Uintacrinus socialis* GRINNELL (Articulata), U.

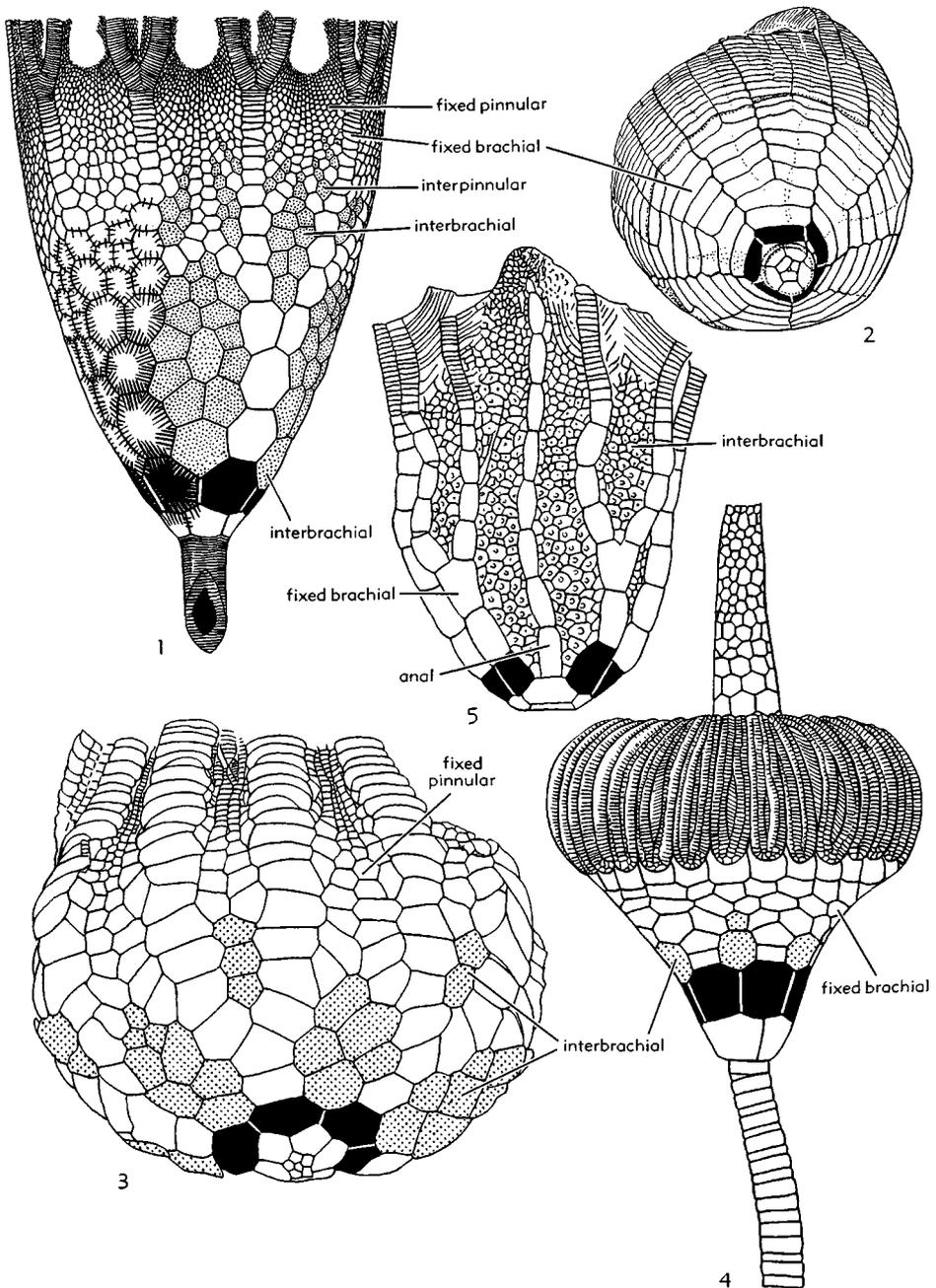


FIG. 90. (Explanation continued from facing page.)

Cret., N.Am.; oblique basal view of part of crown,  $\times 1$  (Springer, 1901).

4. *Eurochocrinus christyi* (SHUMARD) (Camerata), L.Miss., USA (Iowa-Ill.-Mo.); crown with at-

tached part of stem,  $\times 1$  (Wachsmuth & Springer, 1897).

5. *Xenocrinus penicillus* S. A. MILLER (Camerata), U.Ord., USA (Ohio); post. view of calyx,  $\times 3$  (Wachsmuth & Springer, 1897).

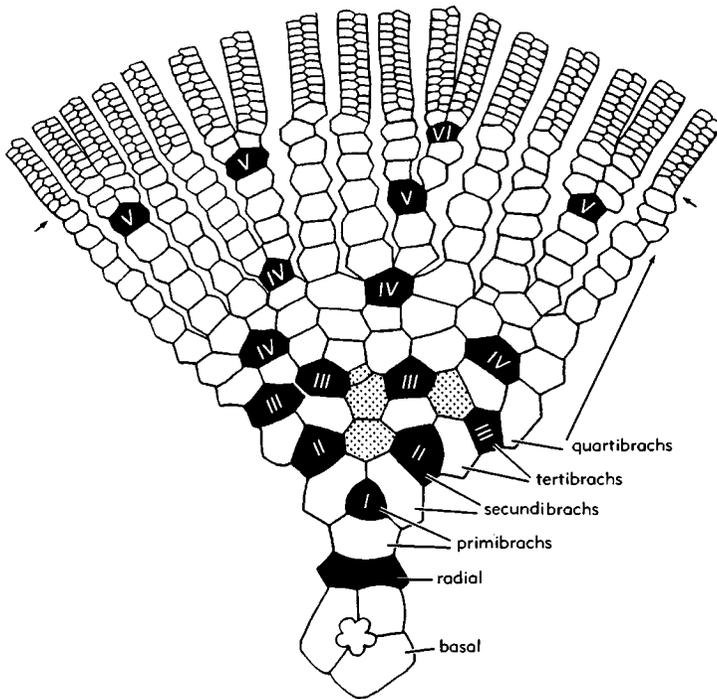


FIG. 91. Plate diagram of base and single ray of the camerate *Himerocrinus* SPRINGER, M.Dev., USA (Ind.) (after Springer, 1921a). [Explanation: radial black; axillary brachs black with Roman number indicating their respective order; interbrachials stippled; top of fixed part of ray marked by small arrows.]

cup plate with distal articular facet exactly like those of adjacent radials. For such reasons, it has been assumed by WACHSMUTH & SPRINGER (1879), UBAGHS (1953), and MOORE (1962b) that the Iocrinidae and Merocrinidae have no biradials but instead possess five undivided equal radials. Consequently, the plate supporting the anal plate series and an arm is a special brachial plate. The term brachial, applied to it by MOORE (1962b, p. 28), is judged inappropriate, since no known crinoids other than those here discussed has a branched or unbranched arm borne by an anal plate. Instead, this axillary plate of iocrinids and merocrinids is designated here as an **anibrachial**. It is morphologically comparable to the aniradials of many inadunates (e.g., Homocrinacea, Allagecrinacea, Belemnocrinacea).

Just as contiguous inferradials may fuse (Pisocrinidae), coalescence of superradials appears to have occurred in the Calceocri-

nacea. During paleontological history of these specialized disparid crinoids, the superradials belonging to the *B* and *C* rays have fused to form a single plate that supports anal structures (Fig. 87,1,2).

#### FIXED BRACHIALS AND FIXED PINNULARS

In a large number of Paleozoic crinoids, mostly camerates (Fig. 90,1,4,5) and flexibles (Fig. 90,2), but also in some early disparid and cladid inadunates (Fig. 88, 1a,b), as well as articulate-like *Apiocrinites* and *Uintacrinus* (Fig. 90,3), the cup or calyx includes ray plates above the summits of radials or biradials. Morphologically, as shown by both comparative anatomy and ontogeny, such ray plates are either arm ossicles (**brachials**, more simply brachs) or pinnule ossicles (**pinnulars**), (the pinnules being slender, unbifurcated branchlets typically borne on alternate sides of successive brachials in some crinoids). Because ray

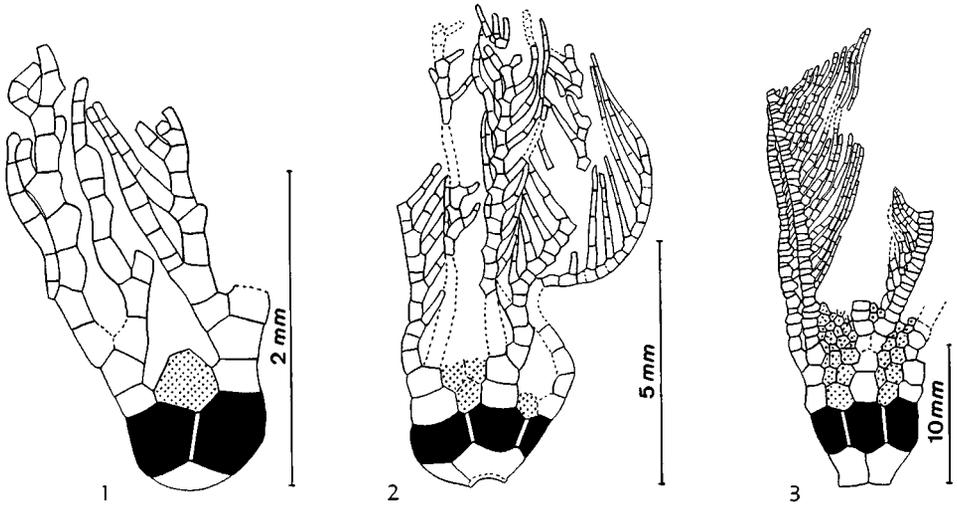


FIG. 92. *Eopatelliocrinus scythograxis* BROWER, U.Ord., USA (Ill., Mo.). Progressive incorporation of free arms in calyx and multiplication of interbranchials during growth; 1, 2 (Ill.), young stages; 3 (Mo.), adult stage (Brower, 1973). [Explanation: radials black; interbranchials stippled.]

plates that enter the composition of the cup or calyx are more or less firmly joined to neighboring thecal plates, they are identified as **fixed brachials** and **fixed pinnulars**,<sup>1</sup> whereas ray ossicles not incorporated in the theca are **free brachials** and **free pinnulars**. The transition between these two conditions may be very progressive (Fig. 90,1-3), or rather abrupt (Fig. 90,4). In early inadunates, in many camerates and flexibles, as well as in *Uintacrinus*, no clear distinction is found between fixed and free parts of the ray, and ray ossicles which are free in immature individuals may be fixed in full-grown individuals. In such early camerates as *Reteocrinus*, *Gaurocrinus*, *Canistrocrinus*, and *Xenocrinus*, the fixed ray plates stand in the most marked contrast with the minute, indefinitely arranged plates occupying the depressed areas between them, and their outer surfaces form strong, rounded ridges, whereas their inner side is deeply channelled (Fig. 90,5). Generally, however, the fixed ray plates share many characters with other plates of the calyx; they are united to each other and with adjacent interray plates by similar articulations and they are distinguished from other calyx

plates mostly by their serial arrangement and, in many genera, by the presence of more or less strong median ridges leading to the free part of the arms or of the pinnules.

The supposed morphological distinction between fixed brachials and the proximal ray plates classed as inferradials, superradials, and undivided radials appear very artificial, especially in early crinoids, for all ray plates included in the cup or calyx of these crinoids are very much alike, and distinctions between them depend mainly on their respective positions (Fig. 88,1b). On the other hand, the occurrence of fixed brachials in earliest representatives of inadunates (Fig. 88,1b), flexibles, and camerates (Fig. 90,5) suggests that these plates, or at least the most proximal of them, could have been parts, like the radials, of the original plating of the theca and were under the control of similar morphogenetical factors.

The number of fixed brachials may be as few as one or two to each ray (e.g., early disparids and cladids, and some camerates), or as many as 140 in an individual ray (as in the camerate *Himerocrinus*) (Fig. 91). It grows during ontogeny until it reaches a mean value, characteristic for each species (Fig. 92). Among camerates, if in some

<sup>1</sup> "Cup-brachials" and "cup-pinnulars" are junior synonyms (MOORE, 1952a) that are not used here.

members (e.g., Hexacrinitea, Platycrinitea) the arms resemble those of inadunates in showing a strong tendency to become free immediately above the radials, an opposite trend is evident in other forms; for instance, in the actinocrinitid *Strotocrinus* the regularly branched arms may be incorporated in the calyx up to the twelfth bifurcation. Such important enlargement of the calyx by incorporation of very numerous fixed brachials unquestionably represents a specialization. On similar ground, the occurrence of fixed ray plates in the thecal walls of some articulates (e.g., *Apiocrinites*, *Uintacrinus*) is judged to be an advanced feature of these crinoids.

The fixed part of a ray may consist of a single series of plates or includes one or several bifurcations, the branches thus produced leading to free arms (Fig. 91). Each bifurcation is effected on a special brachial called an **axillary**, which differs from other brachs in having two distal sloping edges or shoulders, which serve to support the two branches resulting from the arm division. Starting from the radials (or biradials) brachials up to and including the first axillary plate (**primaxil**) are identified as **primibrachials** or **primibrachs**; the following ones in each branch are classed as **secundibrachs**, the last one (if further division occurs) being the **secundaxil**; then come **tertibachs** (possibly including **tertaxils**), **quartibrachs** (possibly with **quartaxils**), and so on.

As stated previously, some pinnules, like the arms, may be incorporated in the calyx for a part or the totality of their length. This may be observed in some recent comatulids with proximal pinnules partly included in the thecal wall by a more or less plated integument. In such crinoids the fixed pinnulars are easily discriminated from neighboring ossicles. A similar condition occurs in many fossil crinoids (Fig. 90,3). In some genera, however, the fixed pinnulars, probably owing to loss of their normal function, growth of adjoining plates, and lack of space available for their accommodation, tend to lose their original shape, ornamentation, size, and linear arrangement. Eventually they become entirely similar to other thecal plates. The Silurian and Early Devonian genus *Scypho-*

*crinites* is a good example of such an extreme modification (Fig. 90,1).

### INTERBRACHIALS AND INTERPINNULARS

In disparid inadunates, some flexibles such as *Ichthyocrinus* (Fig. 90,2), the camerate *Cleioocrinus*, and in some species of the articulate *Apiocrinites*, fixed parts of the rays are contiguous without plates lying between them, except generally in the *CD* interray. More commonly, however, the fixed parts of rays above radials are united by a more or less plated integument, which contributes with primary elements of the calyx and fixed brachials to enclose the thecal cavity. Thus, in many living crinoids, the proximal brachial plates are united by a flexible integument containing minute supplementary plates and a similar plated membrane may extend between the secundibrachs and tertibrachs of each single ray. A pliant integument studded with small, irregular plates or granules occurs between the rays and their divisions in some early camerates (Fig. 90,5) and in most representatives of the flexible order Taxocrinida. The small plates may increase in size and thickness sufficiently to form a well-defined pavement that binds together adjacent ray plates more or less firmly. Such a condition occurs in most camerates (Fig. 90,1,4), many members of the flexible order Sagenocrinida, early cladid inadunates such as *Aethocrinus* (see Fig. 94, 1a,b) and *Cupulocrinus*, Mesozoic *Apiocrinitidae*, and the Cretaceous articulate *Uintacrinus* (Fig. 90,3). Calyx plates located between the rays (except anals, fixed pinnulars, and basals where such plates occur in the radial circlet) are classed as interbrachials, as well as those placed between brachs of a single ray (Fig. 90,1,3-5). More specifically, interbrachials located between fixed primibrachs of adjacent rays or above them are named **interprimibrachs**, interbrachials located between fixed secundibrachs or above them are called **intersecundibrachs**, higher interbrachials include **intertertibachs**, **interquartibrachs**, and so on. Similarly the plates located between fixed pinnulars or between fixed pinnulars and fixed brachials of the same ray are called interpinnulars (Fig. 90,1). In spite of di-

versity of designation, all these secondary calyx elements are judged to be morphologically equivalent.

Generally, proximal interprimibrachs rest on radials (Fig. 90,1,3,4). In some camerates, however (e.g., *Spyridiocrinidae*, *Rhodocrinitacea*), they are supported by basals, thus contributing to separate the rays throughout their full length (Fig. 83,1,2). No other crinoids show the same arrangement, except sporadically or in some rays, but in some later species of the flexible genus *Taxocrinus*, a tendency of interprimibrachs to penetrate between radials and to connect by short faces with basals is observed. In the early camerate *Xenocrinus*, they sink deeply between the radials, but do not reach the basal circlet. On the contrary, in the patellocrinid *Briarocrinus*, they rest on the contiguous first primibrachs or even primaxils.

In many crinoids provided with interbrachials, these plates merge with elements of the tegmen (Fig. 90,5). This probably represents the primitive condition. In more specialized genera, they are separated from the tegmen by fixed brachials and (or) fixed pinnulars (Fig. 90,1,3,4). This arching of interbrachials by ray plates may be produced in various ways, such as 1) increase in area occupied by the rays in distal parts of the calyx, 2) increase in number of arms, 3) reduction in size (with or without accompanying decrease in number) of interbrachials in distal direction, and so on.

The interbrachials may be very numerous and their arrangement ill defined. Examples of this condition are seen in such early camerates as *Reteocrinus* and *Xenocrinus* (Fig. 90,5). Generally, however, these plates are limited in number and regularity of placement (Fig. 90,4). Enlargement of individual elements and accompanying reduction in their number appear to be common evolutionary trends, and, in some genera, a single large interbrachial plate may occupy each interray of the calyx. An opposite tendency toward extension of the plated areas between rays and their branches may also have characterized the paleontological history of some lineages. Thus, the development of interbrachial plates shows a large range of variations, which constitutes an important

taxonomic feature of many groups of crinoids.

During ontogeny, the number and size of interbrachials may change considerably. Species are known in which young individuals have few or no interbrachials, in contrast to adults which have many (Fig. 92). On the other hand, in the juvenile growth stages of some comatulids interbrachial plates, which are soon resorbed, develop between the radials. These observations, together with those just recorded about phylogeny, indicate that tendencies toward increase or reduction of interbrachials may occur among crinoids.

### ANAL PLATES

The posterior or *CD* interray in most Paleozoic crinoids is easily distinguished from other interrays by the presence of special plates conveniently called **anal plates** (anals, analia) because they are directly or indirectly connected with the anus. In the cup or calyx these may be located between basals, radials, fixed brachials, or all three. They may be found also partly or entirely above the upper limit of the cup. The widening of the posterior interray resulting from their occurrence allows room for internal organs, particularly the rectum, and furnishes a support for overlying anal structures. In some crinoids their presence is accompanied by enlargement or an asymmetrical development of the *C* and *D* radials, or (and) by an enlargement of the posterior (*CD*) basal.

The anal plates may have different origin and it is far from proved that they are homologous throughout the class. We shall therefore consider them separately in 1) disparid inadunates; 2) hybocrinid and cladid inadunates and flexibles; 3) articulates; and 4) camerates.

In disparid inadunates, the anal plates have an intimate relationship with the adjacent *C* ray. They may rest 1) directly on the *C* radial or superradial, which, instead of supporting an arm, bears a long series of anal plates as sole appendage (e.g., *Eustenocrinus* (Fig. 93), *?Ramseyocrinus*, and the calceocrinid genera *Cremacrinus* and *Senariocrinus*) (Fig. 87,5); 2) directly on the *B* and *C* superradials, which have fused in a single plate and do not carry any arm (e.g., calceocrinid genera except those just

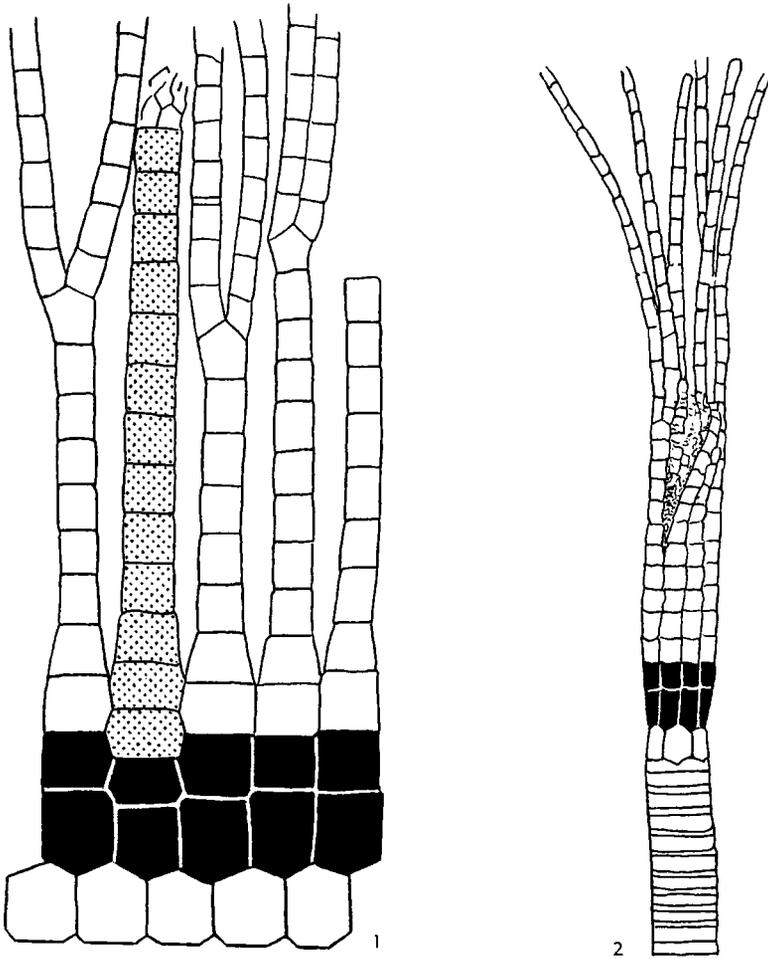


FIG. 93. *Eustenocrinus springeri* ULRICH (Disparida), M.Ord., Can.(Ont.); interpreted as having five compound radials (Ulrich, 1925).—1. Analysis of cup, arms, and anal tube.—2. A-ray view of crown with attached part of stem, ca.  $\times 2$ . [Explanation: biradials black; anal plates stippled.]

mentioned) (Fig. 87,1); 3) on the left shoulder of an undivided *C* radial, which supports an arm on its right shoulder; as restricted by MOORE (1962b), the term **aniradial** may serve in a supplementary manner for designating a *C* radial or biradial that assumes such axillary functions (e.g., *Synbathocrinus*, most allagecrinid genera) (Fig. 84,2); 4) on the left shoulder of the second *C*-ray plate, which is either included in the calyx and then considered to be an axillary superradial (aniradial) (e.g., *Ectenocrinus*, *Heterocrinus*, *Homocrinus*) (Fig. 88,3,4), or is just above the upper rim of the cup having the appear-

ance of an axillary primibrach (anibrachial) (see p. T116, T118) (e.g., *Iocrinus*, *Myelodactylus*, *Herpetocrinus*) (Fig. 89, 1,4); 5) on the left shoulder of the third *C*-ray plate, which is axillary (anibrachial) (e.g., *Peniculocrinus*) (Fig. 88,1b). Alone among dicyclic inadunates, *Merocrinus* shows the same anal plate structure as *Iocrinus* (Fig. 89,2).

These privileged relations of the anal plates with *C*-ray plates in disparid crinoids and *Merocrinus* and the fact that in many of them the anal structures are supported by an elongate, segmented, armlike appendage have led to the supposition that

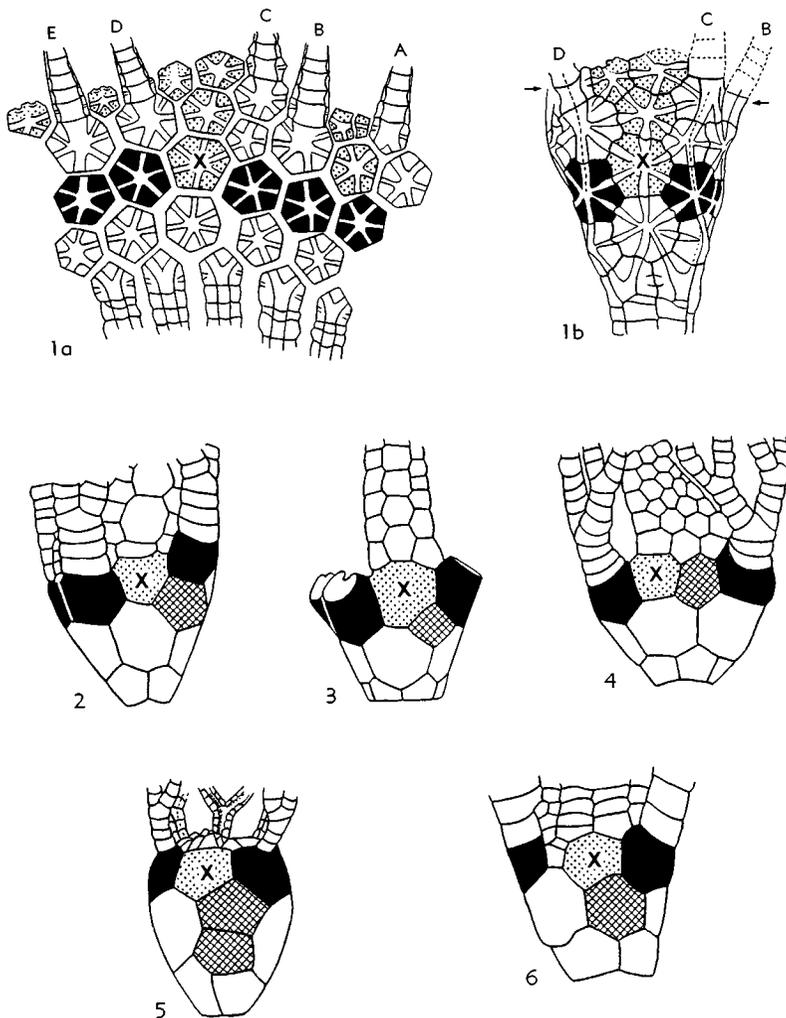


FIG. 94. Position and relationship of radianal in various cladid inadunate crinoids. [Explanation: radials black; radianal cross ruled; other anals and interbrachials stippled (X designates anal X); top of calyx marked by small arrows; rays identified by letter symbols of CARPENTER system.]

- 1a,b. *Aethocrinus moorei* UBAGHS, L.Ord., France; most proximal C-ray plate (= radianal of other inadunates) not distinguishable from ordinary radials,  $\times 2.7$  (Ubahgs, 1969).
2. *Cupulocrinus humilis* (BILLINGS), U.Ord., N. Am.; post. side,  $\times 2$ .
3. *Botryocrinus cucurbitaceus* (ANGELIN), M.Sil., Sweden(Gotl.); post. side,  $\times 3$ .
4. *Parisocrinus crawfordsvillensis* (MILLER), Miss., USA(Ind.); post. side,  $\times 1.5$ .
5. *Carabocrinus* BILLINGS, M.Ord.-U.Ord., Can., USA, Estonia; post. side, ca.  $\times 1$ .
6. *Thenarocrinus gracilis* BATHER, M.Sil., Eng.; post. side,  $\times 3.6$  (2-6, Ubahgs, 1953, mod., from *Traité de Paléontologie*, v. 3, copyright 1953, courtesy Masson & Cie, Paris).

this anal appendage was produced by an evolutionary modification of the arm or left proximal branch of the arm belonging to the C ray. If this is so, then the first

anal plate of these crinoids must have originated as a plate morphologically equivalent to an ordinary brachial.

In all monocyclic hybocrinid and peritto-

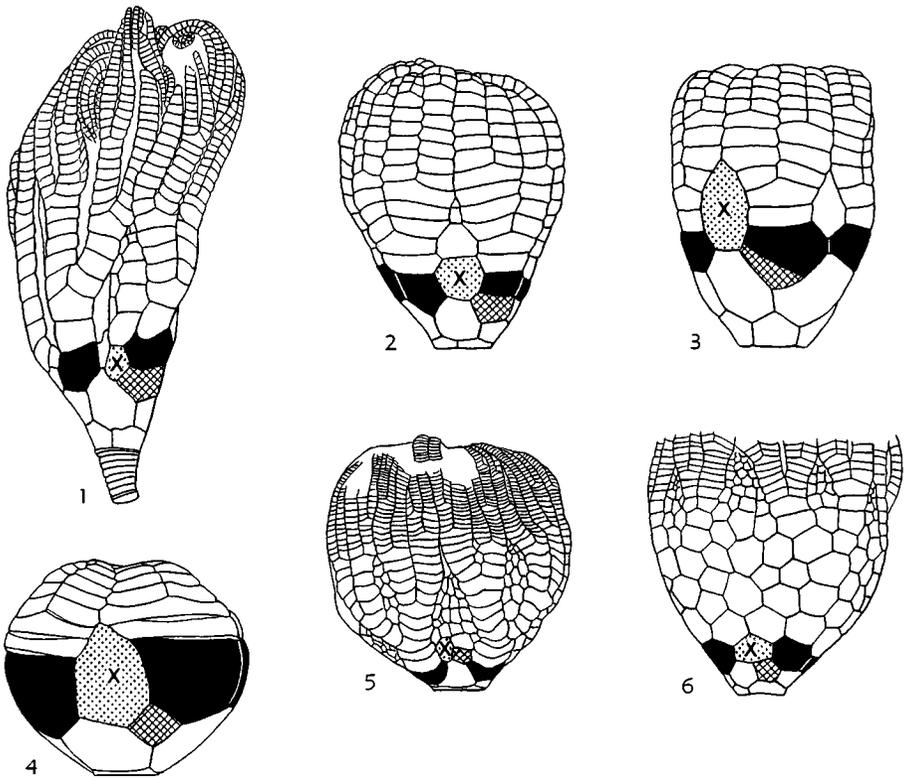


FIG. 95. Position and relationship of radianal in various flexible crinoids. [Explanation: radials black; radialianal cross ruled; anal X plate stippled.]

1. *Protaxocrinus laevis* (BILLINGS), M.Ord., Can.; post. side of crown,  $\times 2$  (Springer, 1911b).
2. *Clidochirus pyrum* ANGELIN, U.Sil., Sweden (Gotl.);  $\times 2$ .
3. *Anisocrinus greenei* (MILLER & GURLEY), M.Sil., USA (Ky.-Tenn.);  $\times 2.2$ .
4. *Lecanocrinus pisiformis* (ROEMER), M.Sil., USA (Ky.);  $\times 2$ .
5. *Forbesiocrinus wortheni* HALL, L.Miss., USA (Iowa);  $\times 0.5$ .
6. *Sagenocrinites expansus* (PHILLIPS), M.Sil.-U.Sil., Eng., Sweden (Gotl.);  $\times 1.1$  (2-6, all post. side of crown, Ubaghs, 1953, mod., from *Traité de Paléontologie*, v. 3, copyright 1953, courtesy Masson & Cie, Paris).

crinid inadunates, in most dicyclic cladid inadunates (except *Merocrinus*) and flexibles, two elements especially characterize the anal series; the radianal and the so-called anal X.

The radianal is the most proximal C-ray plate, which migrated upward and leftward during phylogenesis, contributing to expand the posterior interray, and thus became an anal plate (Fig. 94, 95). Its name, proposed by BATHER (1890a), suggests its origin as a radial element and indicates its special relationship to anal plate structures.

The radianal may occupy various positions. In some early cladids (e.g., *Aethocrinus*, *Ottawacrinus*), the C radial is entirely similar to the other radials, except that, like the D radial, it is laterally in contact with proximal anal plate (Fig. 94, 1); this condition is here judged to represent the state of the C ray before any differentiation of its most proximal plate as a radianal. In other early but perhaps less primitive cladids (e.g., *Dendrocrinus*) and in early flexibles (e.g., *Protaxocrinus*), the C radial has the appearance of a biradial; its upper

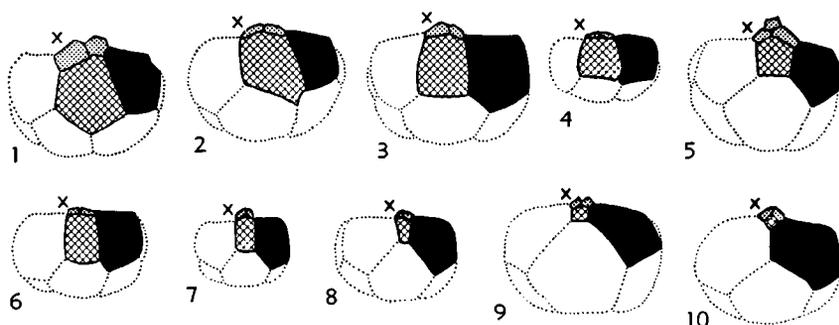


FIG. 96. Variations of the radianal in specimens of *Cadocrinus variabilis* (WANNER) (Cladida), Perm., Timor; 1-10, selected specimens, post. view,  $\times 0.87$  (Moore, 1962b). [Explanation: C radial black; radianal cross ruled; anal X and other anal plates stippled.]

part is conveniently known as the C radial, its lower part as the radianal (Fig. 94,2; 95,1,2). From this position, in both flexibles and inadunates, as well as in hybocrinids and perittocrinids, the radianal appears to have migrated in the direction of the CD interray in such a manner that it came to support the C radial on its right margin and so-called anal X plate on its left side (Fig. 94,3; 95,3,4). It may even reach the same level as the C and D radials (Fig. 94,4; 95,5), but (except in small part) never lies above them or rises out of the cup. In some genera, it tends to be reduced and eventually disappears (Fig. 96). In a few forms (e.g., the inadunates *Thenarocrinus*, *Carabocrinus*, and the flexibles *Sagenocrinus*, *Homalocrinus*) the radianal is located between two basals and it enters into contact with the infrabasal cirlet (Fig. 94,5,6; 95,6). Moreover, the radianal of *Carabocrinus* is transversely bisected and therefore said to be composed of an infer- and a superradianal (Fig. 94,5). A similar condition has been recorded in the flexible *Ammonicrinus* (UBAGHS, 1952) but, as only one cup of this genus is known, it is possible that it is an abnormal individual feature (WANNER, 1954).

Even in its most primitive condition (under C radial) the radianal is found invariably to adjoin the anal X plate. In its lateral migration, it plays a part in supporting other anal plates and functionally becomes the most proximal anal plate, but it never loses its connection with the C radial. With respect to neighboring plates, it may

be relatively large, moderate in size or small. In some genera and even within some species, its dimensions and relationships to surrounding elements show a large amount of variation (Fig. 96).

The radianal, whatever its ultimate function and location, is a ray plate in origin; it constitutes the most proximal plate of the C ray, as shown by comparative morphology of the flexibles and cladid inadunates. It has been considered generally to be a special modified inferradial, though it differs from such plates in disparid inadunates by 1) its constant relation with the anal X plate, and 2) its marked tendency to migrate, losing its primary position and function as a ray plate—two features observed in no disparid inferradials. Another possibility is to regard it as the C radial itself (as suggested by the plate structure in *Aethocrinus* and *Ottawacrinus*), and to suppose that, after its move toward the posterior interray, it has been replaced by its original function assumed by the next-to-proximal C-ray plate. Similar changes seem to occur in the ontogeny of recent comatulids: their larval anal plate (herein judged to be a radianal) develops in the midline of the C ray like a true radial; then a new plate appears to its right side, which, during growth, acquires a radial position by pushing the anal plate to the left and becomes the definitive C radial. If such similarities are not mere analogies, they at least suggest that 1) the paleontological history of the C radial has been much alike in cladid, flexible, and articulate (and pos-

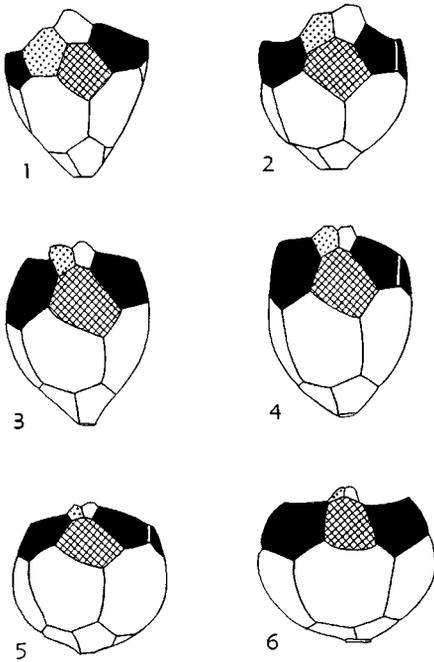


FIG. 97. Variations of anal plates in specimens of *Ureocrinus bockschii* (GЕINITZ) (Cladida), L.Carb., Scot.(Wight); 1-6, selected specimens, post. views,  $\times 1$  (Wright, 1955-60). [Explanation: radials black; radialanal cross ruled; anal X plate stippled.]

sibly hybocrinid and perittocrinid) crinoids; and 2) this history has been very different in disparid inadunates.

The anal X (or azygous plate of earlier authors) is located between C and D radials (Fig. 94, 95). It may rest on the radialan or on the posterior (CD) basal, or partly on both. Unlike the radialan, it may be above the upper limit of the radials and, if resorbed, it is not within the cup but above it (Fig. 97). Its origin is far less evident than that of the radialan, which is basically a ray plate, and indeed it has been variously considered by authors to be a secondary element suddenly introduced, a plate of the anal tube that gradually sank into the cup, a modified brachial plate homologous to the proximal anal plate of disparid crinoids, or an interbrachial. The fact that in the oldest known cladid inadunates (Fig. 94,1a,b), the anal X is already present as a large plate resting on the posterior basal, in lateral contact with the C radial, and unre-

lated in any way to arm plates supports none of these interpretations, except possibly its postulated status as a special interbrachial. This suggests at least that anal X originated as an interradially located element, which, along with other main components of the cup or calyx, may have become differentiated from original plating of the theca in correspondence with need for an enlargement of the posterior area.

Occurrence of anal plates in the cup or calyx of adult articulate crinoids has never been recorded, but in juvenile growth stages of various comatulids an anal plate develops and is resorbed before maturity. As explained in the chapter on recent crinoids (p. T29), the fact that this plate appears in the midline of the C-ray like a true radial, and then is pushed to the left by a new plate that becomes the definitive radial suggests strongly that it is homologous to the radialan (CLARK, 1915a; SPRINGER, 1921a) rather than to the anal X of fossil crinoids (BATHER, 1918a; MORTENSEN, 1920), of which plate no certain equivalent has been found in the ontogeny of comatulids.

The anal plates of Camerata are very different from those of other crinoids. In their more typical aspect, they are arranged in a median series (anitaxis) which splits the posterior interray along the sagittal (crinoidal) plane of bilateral symmetry, whereas plates similar and surely homologous to ordinary interbrachials fill up the spaces on other sides (Fig. 98,1,2). In some early genera (e.g., *Reteocrinus*, *Tanaocrinus*, *Glyptocrinus*), the anitaxis, composed of many conspicuous plates in a linear series, bears a prominent ridge (anal ridge) analogous to the axial ridges of ray plates (Fig. 98,3). The connection of the anal ridge with ridges uniting the posterior basal with the C and D radials seems to indicate that a nerve cord passed along it (BATHER, 1900a). Such structural features have led some authors (MOORE & LAUDON, 1943a; SPRENG & PARKS, 1953) to suggest that the anal series of camerates could have its origin in a sixth ray. Very early in some lineages (e.g., *Anthracocrinus*, *Deocrinus*), more belatedly in others (e.g., *Opsiocrinus*), the anal ridge disappeared. In some families, a marked tendency to-

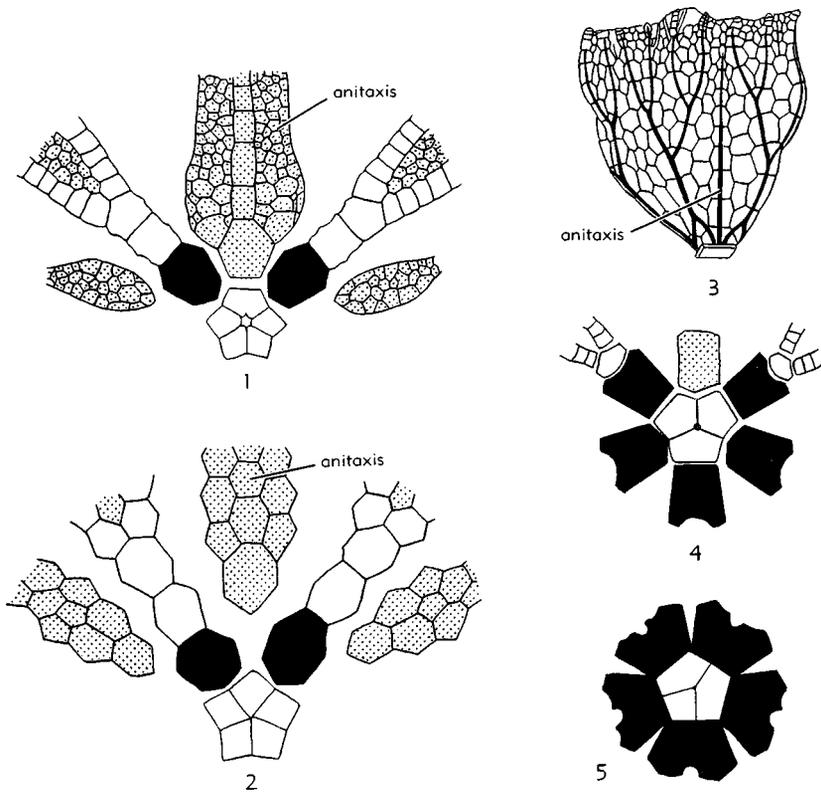


FIG. 98. Anal plate structure of camerates (Ubaghs, n). [Explanation: radials black; anals, interbrachials stippled.]

1. *Canistrocrinus* WACHSMUTH & SPRINGER, U.Ord., USA (Ohio); plate diagram.
2. *Glyptocrinus* HALL, M.Ord.-U.Sil., N.Am.; plate diagram.
3. *Compsocrinus harrisi* S. A. MILLER, U.Sil., N. Am.; calyx, with ray and anal ridges indicated by heavy lines,  $\times 2.5$ .
4. *Hexacrinites* AUSTIN & AUSTIN, U.Sil.-U.Dev., Asia, Australia, Eu., N.Am.; plate diagram.
5. *Platycrinites* MILLER, ?U.Sil., L.Dev.-U.Perm., Eu., N.Am., E.Indies; plate diagram.

ward reduction of extra plates in the posterior interray led to forms in which a single anal plate was left (e.g., *Hexacrinites*, *Dichocrinus*) (Fig. 98,4) or no anal plate remained in the calyx (e.g., *Eucalyptocrinites*, *Platycrinites*) (Fig. 98,5). Although no hard and fast rule can be stated, it is observed that anal plates generally are poorly developed in species provided with a central anus or a central conspicuous anal tube or other tegmental structure (e.g., *Calliocrinus*, *Eucalyptocrinites*).

The most proximal anal plate is called **primanal**, a term proposed by JAEKEL (1918) and of which the term "tergal" (MOORE, 1952a), not used here, is a junior

synonym. The primanal may be followed by a single secundanal or by more than one secundanal. Higher anal plates are designated as tertanals, quartanals, quintanals, etc. Among all these plates, the primanal is the most important, because its relations with other cup or calyx elements have a classificatory value. In dicyclic camerates, except *Cleioocrinus* and *Nyctocrinus*, the primanal is inserted between C and D radials resting on a basal or basals (Fig. 99,1,2). It may be similar to the first interbrachials, where these plates separate the radials, as in Rhodocrinitacea (Fig. 99,1), although ordinarily it supports three secundanals followed by other anals, instead

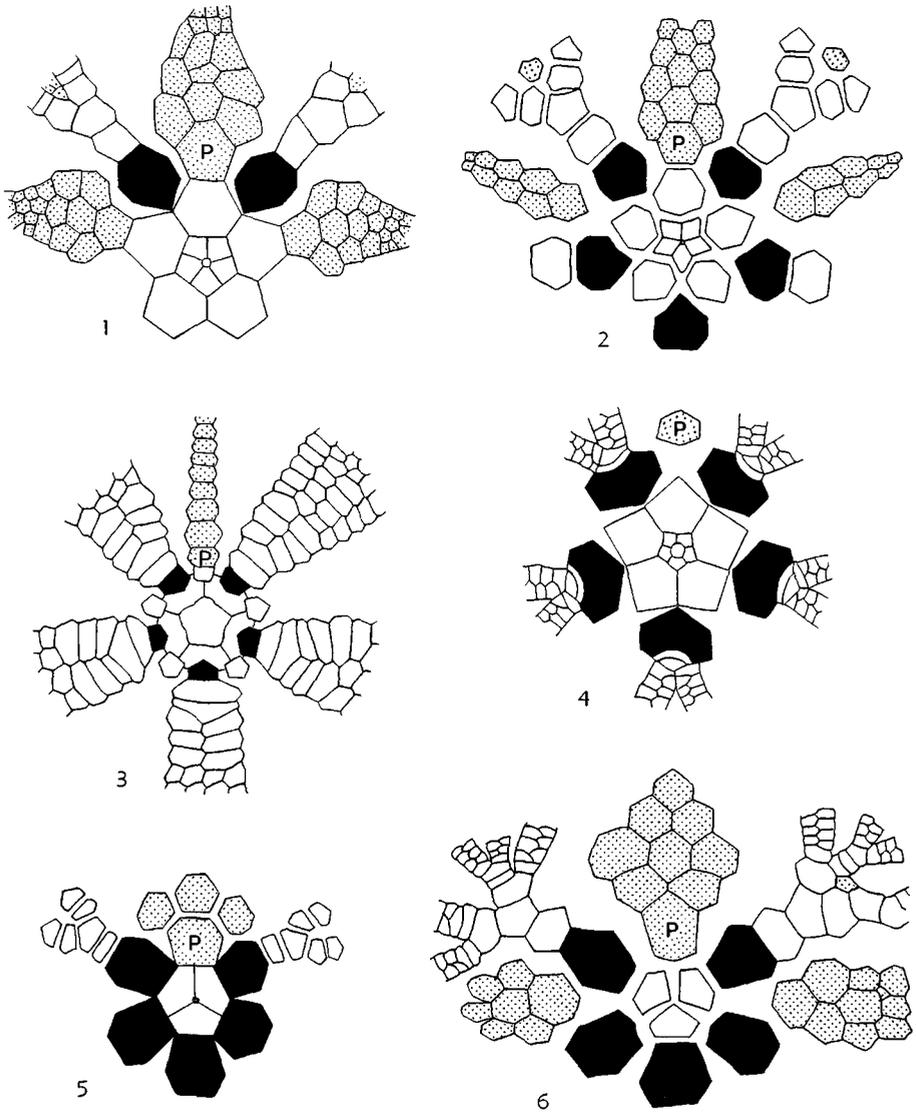


FIG. 99. Relations of primanal in camerates shown by plate diagrams (Ubaghs, n). [Explanation: radials black; anal plates, interbrachials stippled; P, primanal.]

1. *Rhodocrinites* MILLER, L.Carb., Eu., N.Am., Asia, ?Australia.
2. *Dimerocrinites* PHILLIPS, M.Sil.-M.Dev., Eu., N.Am.
3. *Cleiocrinus* BILLINGS, M.Ord., N.Am.
4. *Nyctocrinus* SPRINGER, M.Sil., N.Am., USA (Tenn.).
5. *Batocrinus* CASSEDAY, U.Miss., USA.
6. *Actinocrinites* MILLER, L.Miss., ?Perm., Eu., N.Am., N.Afr., Australia, ?E.Indies.

of commonly two interbrachials above a most proximal interbrachial in the *AB*, *BC*, *DE*, and *EA* interrays (Fig. 98,2).

In *Cleiocrinus*, the primanal is carried by the posterior basal, but because this plate occurs within the radial circling, it stands

on a level with the first primibrachs (Fig. 99,3). In *Nyctocrinus*, the primanal rests upon the *C* and *D* radials, and lacks contact with the basals (Fig. 99,4).

Turning now to the monocyclic camerates, it appears that in these crinoids two main types of anal-plate arrangements occur, providing basis for division into two suborders: Compsocrinina, with primanal interpolated in the radial circlet (Fig. 98,1); and Glyptocrinina, with primanal resting on two plates (*C*, *D*) of the radial circlet (Fig. 98,2). The primanal of compsocrinine camerates is succeeded by three secund-anals in the next higher range (Fig. 99,5), except in the Amphoracrinidae, Actinocrinitidae, and advanced members of Paragiacocrinidae, where only two plates rest on the primanal (Fig. 99,6). Many camerates, belonging to various unrelated families (e.g., Spyridiocrinidae, Anthracocrinidae, Clonocrinidae, Eucalyptocrinitidae, Platycrinidae), have the anal side scarcely recognizable in the calyx.

In many respects, the anal plates of camerates are unlike those of flexibles and inadunates, since they include no plate corresponding to the radianal, and lack any special relation with the *C*-ray or tendency to migrate upward-leftward in the direction of the *D*-ray. However, according to BROWER (1973, 1974b), comparison of the ontogeny of living comatulids and presumed phylogeny of camerates suggests a possible homology of the camerate primanal with the anal (radianal) plate of the young comatulids. But this homology is admittedly highly speculative.

Analogies which the primanal may show with the anal *X* plate of disparid and primitive cladid inadunates such as *Aethocrinus* and *Ottawacrinus* do not allow recognition of these elements as morphologically equivalent. Even within the camerates, homologies of the primanal still are uncertain, as likewise is its origin. This plate has been variously interpreted as 1) a plate originally belonging to a sixth ray (MOORE & LAUDON, 1943a; SPRENG & PARKS, 1953); 2) an ordinary interprimibrach; 3) as a plate homologous with the anal (radianal) plate of the larval comatulids (BROWER, 1973, 1975); 4) a posterior element remaining after loss of lateral plates, from a cycle of primary interbranchials interpolated between

the radials (CARPENTER, 1886); 5) a new plate introduced in the radial circlet as progenitor of succeeding anals in linear series in manner similar to the "interradial radials" (pararadials) of recent *Thaumato-crinus* interpolated between the five primary radials; 6) one of "supplementary pieces developed as occasion arose in the position where they are found" (BATHER, 1900a); and 7) a new plate introduced between the latero-distal margins of the *C* and *D* radials, that is to say in such a position that a proximal growth and a distal inhibition of the plate would have pushed it into the radial circlet, whereas a distal growth with a proximal inhibition would have placed it above the radial circlet (WILSON, 1916). At present no evidence allows a satisfactory choice between these possibilities.

#### ACCESSORY PLATES

The calyx of Ordovician monocyclic perittocrinid inadunates includes about 14 accessory plates located between the basals, radials, or radials and anals (Fig. 100). The origin and homology of these elements is quite obscure. They have been considered as equivalent to the interbranchials of camerates (JAEKEL, 1902, 1918) or as plates possibly remaining from a multiplicated primitive condition, in relation with the development of respiratory structures (UBAGHS, 1972).

Very different are the accessory plates inappropriately called "subradials" by WACHSMUTH & SPRINGER (1897) and "superbasals" by BATHER (1900a), but conveniently designated as **intercalaries** by MOORE & PLUMMER (1938) (Fig. 101). Known only in the camerate family Acrocrinidae, they form one or several (up to 25) circlets between the basals and radials. Their number ranges from six to about 700, according to the species. Those immediately above the basals are smallest, and apparently ones latest-formed during ontogeny; those located next below the radials are largest and seemingly first to be introduced during development. Typically, those in the posterior (*CD*) interray and, but not so generally, those in the anterior (*A*) ray form single series; the others are more or less irregularly arranged, some of them being radial in position and others interra-

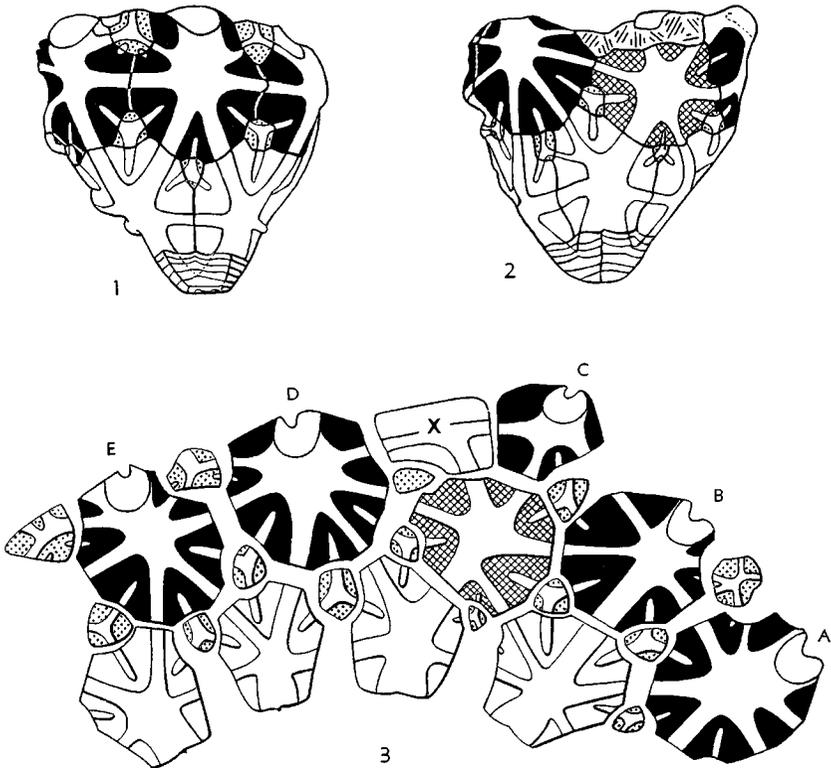


FIG. 100. Accessory plates of perittocrinid inadunates. [Explanation: radials black; radial cross ruled; X, anal X plate, accessory plates stippled; rays identified by letter symbols of CARPENTER system.]—1-3. *Tetracionocrinus transitor* (JAEKEL), L.Ord., Baltic regions; 1,2, calyx with attached portion of stem, in A-ray and CD-interray views,  $\times 5$ ; 3, analysis of cup (Ubaghs, 1971a).

dially located. The structure of the Acrocrinidae has been interpreted (JAEKEL, 1918; SPRINGER, 1926b; MOORE & STRIMPLE, 1969) as indicating an evolutionary reversion from the simple theca of *Dichocrinus* to a cystoid-like form, in which the thecal plates lack any definite arrangement. The intercalaries are certainly new plates and not elements inherited from a multiplated ancestor. Their development results from a highly specialized trend, which was active in a dichocrinid stock during a long time period extending from the Early Mississippian to the Late Pennsylvanian.

#### ARTICULATIONS BETWEEN CALYX PLATES

The nature of articulations between plates of the calyx is one of the main

features used in classification of crinoids. In articulates, inadunates, most camerates, and partly in flexibles, plates of the calyx typically have flat (rarely very slightly concave), smooth or weakly ornamented joint faces. Such articulations essentially belong to the *zygosynostosial* type. In some crinoids, radiating ridges (culmina) and furrows (crenellae) cover a part (ordinarily the outer part) of the joint faces and interlock with the ridges and furrows of the opposed joint faces, producing crenulate sutures. When the crenulae cover the whole surface of the facet, the articulation may be referred to as *symplexy*. Complete fusion of plates (*ankylosis*), with obliteration of sutures, occurs commonly in the proximal circllet of plates (basals or infra-basals), less generally in the radial circllet.

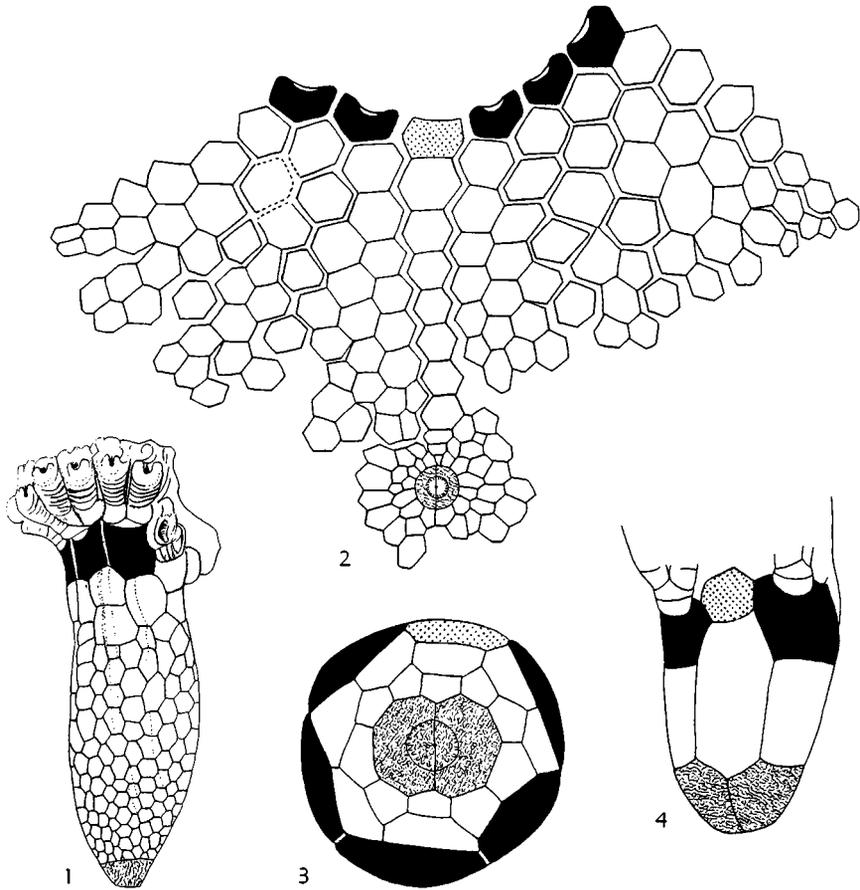


FIG. 101. Accessory plates (intercalaries) of acrocrinid camerates. [Explanation: basals shaded; primanal stippled; radials black.]

1. *Amphoracrocrinus amphora* (WACHSMUTH & SPRINGER), U.Miss., USA (Ala.); side view of calyx with arm bases,  $\times 2$  (Wachsmuth & Springer, 1897).
2. *Globacrocrinus pirum* (MOORE & PLUMMER), L.Perm., USA (Okla.); analysis of cup (Moore & Plummer, 1938).
3. *Planacrocrinus ambix* MOORE & STRIMPLE, L. Penn., USA (Okla.); aboral view of calyx,  $\times 12$  (Moore & Strimple, 1969).
4. *Protacrocrinus primitivus* (LAUDON & BEANE), L.Miss., USA (Iowa); CD-interray view of cup with arm bases,  $\times 5$  (Moore & Strimple, 1969).

All of these unions allow only slight movements, or none at all, and so are classified as immovable.

In most flexible crinoids, and some Pennsylvanian inadunates (STRIMPLE & MOORE, 1971), plates of the calyx are commonly connected by articularia in which relatively deep and large depressions for the lodgement of connective tissue are surrounded by a generally crenulated rim that provides

contact between the plates (Fig. 101). Within the fossae irregular elevated areas may rise nearly to the level of the marginal rim. To these basic elements may be added, in articulations between radials and first primibrachs and between successive fixed brachials, a weak transverse elevation separating an outer fossa from a single inner fossa or paired inner fossae (Fig. 102,2,5). Upon the proportion of size of fossae to

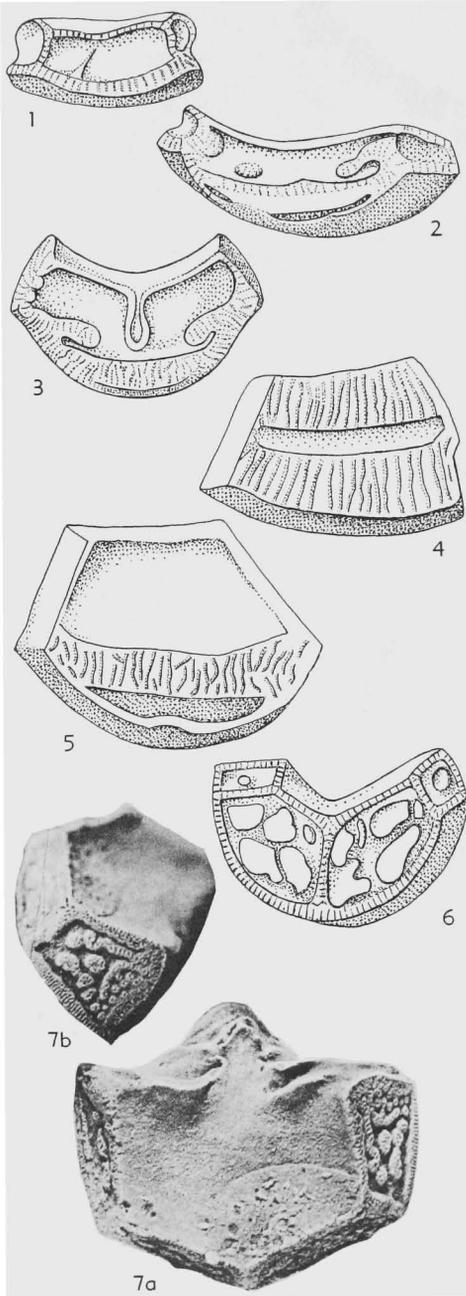


FIG. 102. Articula on selected calycinal plates of flexible (1-6) and inadunate (7) crinoids. [Explanation: aboral (outer) side of each ossicle directed downward.]—1-3. *Forbesiocrinus nobilis* DE KONINCK & LE HON, L.Carb., Belg.; 1, proximal face of basal; 2, distal face of radial; 3, distal face

contact areas depended the amount of flexibility of the calyx wall. This type of articulation, though probably derived from a synostosomal one, differs from typical synostosis in depth of fossae and rimmed peripheral edges. It has been inappropriately called "loose suture" (BATHER, 1900a; SPRINGER, 1920) or "pseudosyzygy" (GISELÉN, 1924). The term **manosynostosis**, which literally means loose synostosis, is herein proposed to designate it.

A similar mode of union between calyx plates developed independently in the probably pelagic camerate genus *Scyphocrinites*. Each facet of its calyx plates shows one or several more or less large and deep depressions limited outward and inward by crenulated rims (Fig. 103). These rims, varying in width and sinuous, may be so reduced as to become almost nonexistent. Crenulae originate in the deepest part of the depressions, radiate outward, and cross the rim suggesting that this kind of articulation is a modified symplexy. In the distal region of the calyx, the joint faces of fixed brachials and adjacent fixed pinnulars have deeply inward-sloping fossae, which give the thecal wall the fallacious appearance of being composed of an inner pavement supporting thick pillars with constricted bases (Fig. 103, 4a-c).

All of the articulations so far described are ligamentary. This means that plates of the calyx are or were held together by fibrils probably of primarily collagenous nature. Such tissue is reputed not to allow autonomous movements of the adjoining plates, but it may bestow a certain amount of flexibility to the thecal wall. Muscular articulations between plates of the calyx invariably are lacking except probably in the Calceocrinacea where a hingement, located between the basals and the radials,

of second primibrach,  $\times 2.6$  (Springer, 1920).—4, 5. *Taxocrinus colletti* WHITE, U.Miss., USA (Ind.); 4, proximal face of basal; 5, proximal face of first primibrach,  $\times 6.7$  (Van Sant in Van Sant & Lane, 1964).—6. *Onychocrinus exculptus* LYON & CASSEDAY, Miss., USA (Iowa-Ill.); distal face of primaxil,  $\times 6.7$  (Wachsmuth & Springer, 1897).—7. *Delocrinus subhemisphericus* MOORE & PLUMMER, U.Penn., USA (Kans.); 7a, b, dual plate consisting of both a radial and primibrach 1 viewed from interior and left lateral side,  $\times 4.4$  (Strimple & Moore, 1971d).

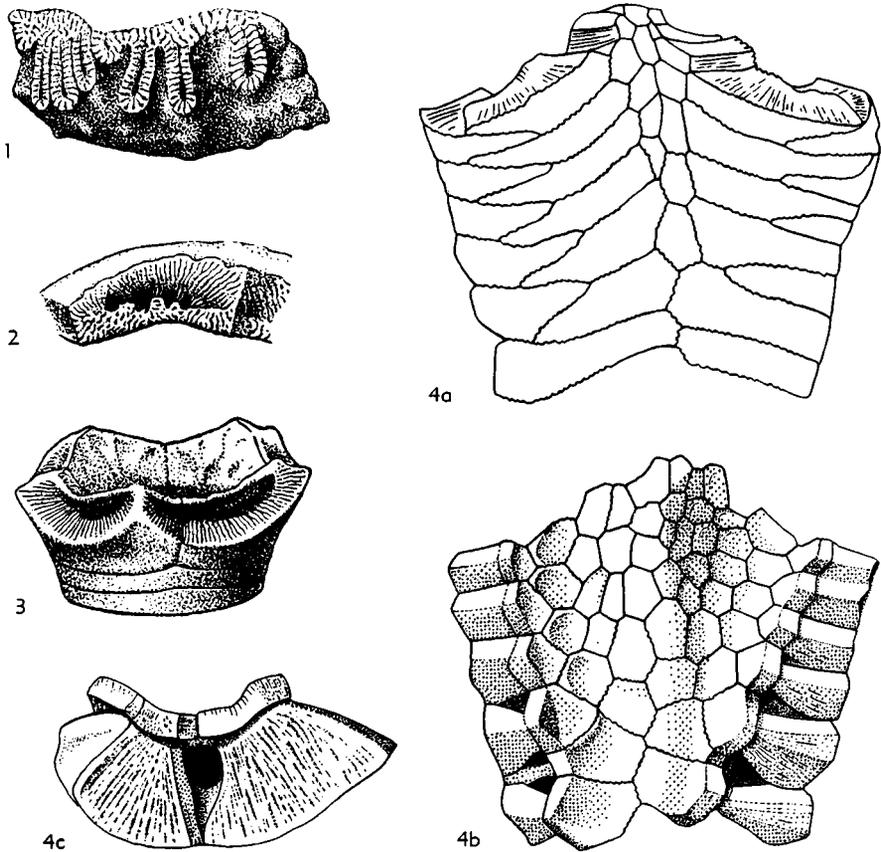


FIG. 103. Articula on selected cup plates of the camerate *Scyphocrinites* ZENKER, ?L.Sil., U.Sil.-L.Dev., Eu., N.Am., N.Afr., Asia,  $\times 4$ .—1. Distal face of primibrach (Springer, 1917).—2. Proximal face of radial.—3. Distal face of basals.—4a-c. Aboral (outer), adoral (inner), and proximal views of distal fixed brachials and pinnulars (Ubaghs, n).

allowed the radial portion of the calyx to erect itself upon the basal portion (Fig. 104). This peculiar conformation—unique among crinoids—facilitated back-and-forth

movements of the recumbent crown in a plane that coincides with the strongly marked bilateral symmetry of these disparid inadunates.

## ARMS

### GENERAL FEATURES

An arm or brachium is a jointed outgrowth of the central body mass (Fig. 105,1). Its aboral skeleton—a direct prolongation of the calycinal skeleton—carries extensions of the food grooves, water-vascular, ectoneural, hyponeural, entoneural, hemal, and genital systems, as well as

adoral and aboral coelomic canals. These soft parts are directly connected with the organs and coelomic cavities of the theca. All or most of them penetrate into it through an orifice at the base of each arm (**arm opening**) (Fig. 105,1,2). A second but smaller orifice may be present; it serves for passage of the aboral motor nerve. Thus, a most intimate connection exists between

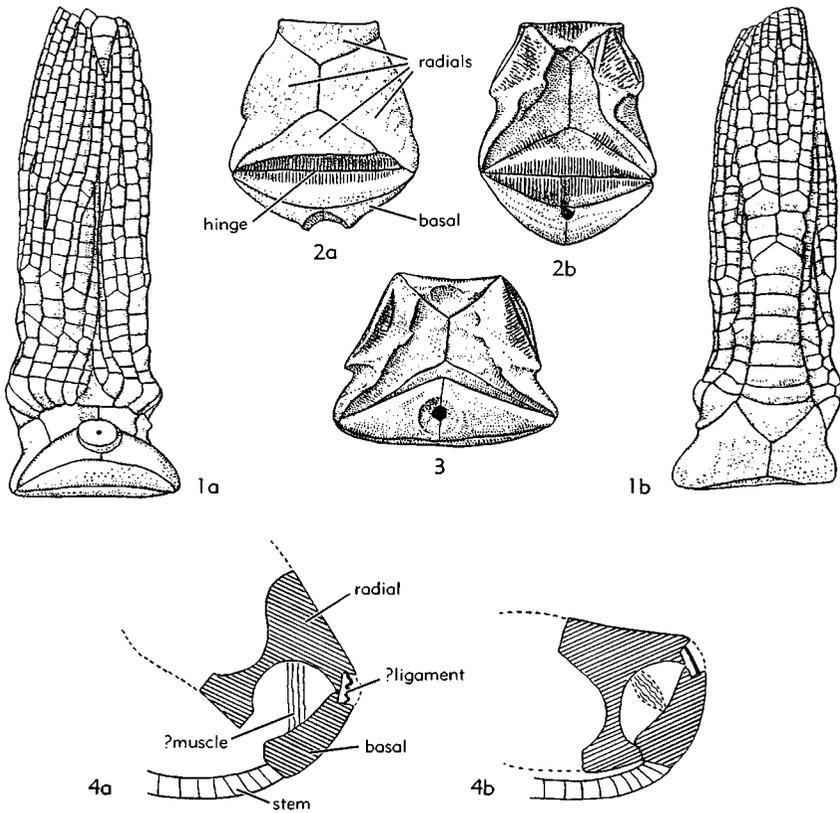


FIG. 104. Hingement in cup of calceocrinid inadunates.

1a,b. *Halysiocrinus nodosus* (HALL), Miss., USA; BC and E-ray views of crown,  $\times 1$  (Springer, 1926a).

2,3. *Halysiocrinus perplexus* (SHUMARD), Miss., USA; 2a,b, outer and inner aspects of calyx with hinge between basals and radials fully

extended; 3, inner aspect of calyx with hinge partially closed (Springer, 1926a).

4a,b. *Calceocrinus* HALL, M.Ord.-U.Sil., Eu., N. Am.; sagittal section of calyx and proximal part of stem, illustrating articulation of base with radials and manner of erection of crown (Ringueberg, 1889, mod.).

brachia and theca—a feature judged to be highly distinctive of the Crinoidea.

In most other pelmatozoan echinoderms, the food-gathering appendages are exothecal processes, and not evaginations of the theca. Their skeletal support does not prolong the thecal series of plates, and there is no special opening at their base. They had no direct connection with the interior of the theca, and hence, could not have carried extensions from the main coelomic cavities, and from the hemal, genital, and entoneural systems (Fig. 105,3).

An arm of a crinoid is not necessarily equivalent to the free part of a ray. In

allagecrinids, anamesocrinids, and parahexacrinids a varying number of independent arms may belong to a single ray (Fig. 84, 1-3,4,8). In some batocrinid and coelocrinid camerates, two (rarely 3 or 4) arms (paired) commonly share a single arm opening (Fig. 106). In many camerates and flexibles, as well as in the articulate *Uintacrinus*, the divisions of the ray-plate series within the calyx increase the number of free arms per ray (Fig. 90, 91). Also, the major branches resulting from one or even several bifurcations of the ray just above the calyx are commonly considered arms. Interpreted in this way, some articulate and inadunate

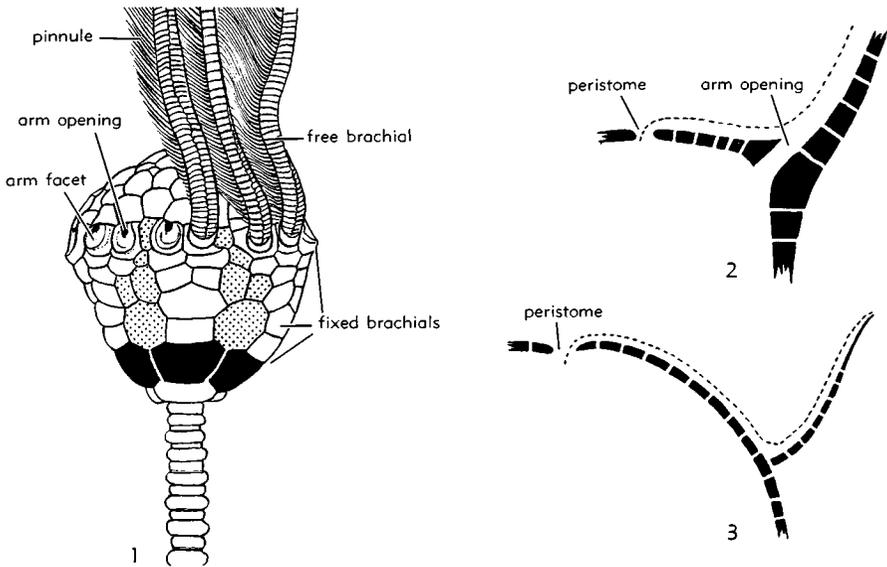


FIG. 105. Relationship of free arms with theca.—1. *Uperocrinus longirostris* (HALL), Miss., USA; theca with parts of free arms and column,  $\times 1.3$  (Ubahgs, n). [Explanation: radials black; interbrachials stippled.]—2,3. Diagrammatic vertical sections of parts of theca and arm or armlike appendage in a crinoid (2) and a noncrinoid pelmatozoan echinoderm (3) (mod. from Jaekel, 1898a).

genera are said to have 30 or more arms. Such practice is justified on the premise that an arm and its branches (including pinnules) have essentially the same constitution.

The aboral skeleton of the arms consists of a single or double series of ossicles, termed **brachials** or **brachs**. It is supported directly by the radials (e.g., most inadunates and articulates, but also some flexibles and camerates), or a variable number of arm ossicles are incorporated in the calyx (fixed brachials, see p. T119). The passage from the fixed to the free part of the ray may be gradually progressive or abrupt. If it is abrupt the attachment of each free arm to the theca is effected by means of an articulate surface called **arm facet** or, in case of attachment directly on a radial, **radial facet**. This facet will be described as **angustary**, **penplenary**, or **plenary**, according to whether it is much narrower than, almost as wide, or as wide as the distal margin of the arm-bearing plate.

The arm ossicles of the free part of the arms (**free brachials**) are generally rounded on the outer or aboral (dorsal) face and

grooved on the inner or adoral (ventral) face. This **ventral** or **adoral groove** contains all the extensions of the organic structures and coelomic canals that have been mentioned above, except that in some cases the entoneural cord lies in a special groove on the floor of the main groove or is included in a distinct, generally single, canal (**axial canal**) perforating the brachial ossicle longitudinally (Fig. 107). A brachial provided with an axial canal is said to be **perforate**. (The adoral groove of the arm skeleton is not to be confused with the ambulacral or food groove that is located on the adoral surface of the soft tissues of the arms. The ambulacral groove is but a minor structure housed by the adoral skeletal groove.)

The arms may remain undivided, but generally they bifurcate once or several times. There are various modes of arm branching (see below, p. T143). The most advanced condition occurs in crinoids that have a small undivided branch, called a **pinnule**, borne by each brachial. Such crinoids are said to be **pinnulate**, and the individual plates that form the aboral skeleton of the pinnules are termed **pinnulars**.

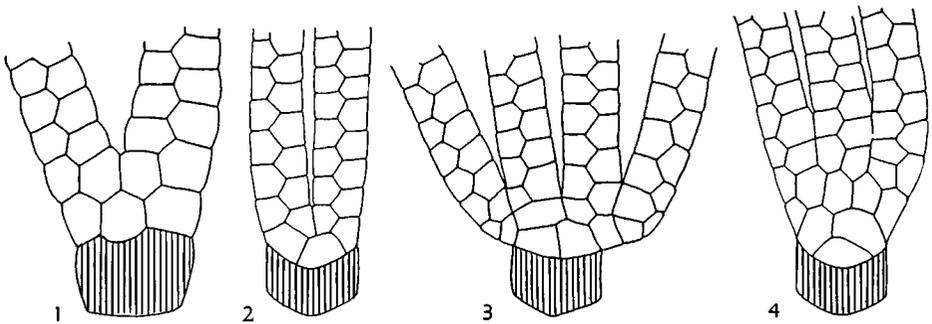


FIG. 106. Occurrence of two or several arms from a single arm-bearing fixed brachial (vertically ruled), to which a single arm opening corresponds (Van Sant in Van Sant & Lane, 1964).—1. *Abatocrinus grandis* (LYON & CASSEDAY), Miss., USA.—2-4. *Dizygocrinus indianensis* (LYON & CASSEDAY), Miss., USA.

The soft structures of the arms and of the pinnules are ordinarily protected by **covering plates**, also named **ambulacrals** (not homologous with ambulacral plates of echinozoan echinoderms). The covering plates belong to the adoral skeleton of the crinoid body and will be described subsequently.

For descriptive purposes, the two lateral sides of an arm may be distinguished as right and left, "right" and "left" corresponding to the right and left of the observer when the arm is viewed from its aboral surface with its distal end directed upward. In a branching arm the adradial branches are termed interior; those to the sides, exterior. The length of an arm (or a branch, or a pinnule) is defined as the distance from its proximal attachment to its distal tip; the width, as the distance from one lateral side to the other, perpendicular to length; the depth is equal to the diameter in an aboral-adoral direction and perpendicular to length and width.

### INEQUALITY OF ARMS

The arms of a crinoid are generally alike in size, form, and mode of branching, albeit a certain amount of variability may be observed in almost every individual. Marked inequalities of arms appear, however, as a diagnostic feature of some families, genera, or species. Conspicuous examples are furnished by 1) the Holopodidae, with their arms arranged in a bivium and trivium; 2) the Calceocrinidae, in which one or com-

monly two arms have disappeared, whereas two of the remaining three are greatly developed (Fig. 87, p. T114); 3) the Silurian flexible *Cholocrinus*, which has two dwarfed rays (*B* and *E*) (Fig. 108, I); 4) the Mississippian inadunates *Anartiocrinus* and *Pentaramicrinus bimagnaramus*, in which half-rays are hypertrophied in *B* and *E* rays (Fig. 108, 2, 3); and 5) various reef-inhabiting forms, the morphology of which depend largely on ecology, and other factors. In many cases, such inequalities contribute to render planes of bilateral symmetry particularly obvious in the crown.

### NUMBER OF ARMS

The number of free arms is primitively and normally five. This five-armed condition characterizes most disparids, some hybocrinids, cladids, and flexibles, and is still preserved in various articulate. On the other hand, in all camerates and many flexibles and articulate the number of free arms is equal to or greater than ten. If, however, some camerates seem to have only five arms, it is because each of their rays comprises two arms that either have fused together longitudinally (as in *Melocrinites*) or are so unequally developed that one of them is reduced to the size of a branchlet and does not look like an arm (as in *Cytidocrinus*).

The ten-armed or multiple-armed forms result generally from the bifurcation of the brachial-plate series within the calyx or at its upper limit or just above it. But it

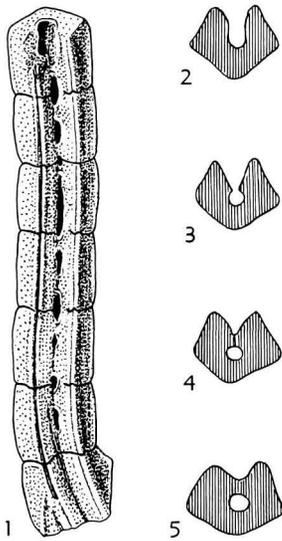


FIG. 107. Differentiation of axial canal from ventral groove.—1. *Gissocrinus* sp. cf. *G. goniodactylus* (PHILLIPS), Sil., Gotl., part of an arm in adoral view, showing axial canal still partly confluent with ventral groove,  $\times 6$  (Bather, 1893a).—2-5. *Gissocrinus goniodactylus* (PHILLIPS), Sil., Eng., Gotl.; stages in separation of an axial canal,  $\times 8$  (Bather, 1900a).

may also be produced by 1) occurrence of more than five arm-bearing plates in the radial circlet (as in *Calycanthocrinus*) (Fig. 84,1); 2) development of multiple-arm-bearing radials (as in Allagecrinidae, Anamesocrinidae, Parahexacrinidae) (Fig. 85); 3) fusion, with each radial, of a recumbent arm carrying a small arm on the free side of each of its component ossicles (as in *Agostocrinus*) (Fig. 84,8); 4) augmentative regeneration, as demonstrated by MINCKERT (1905a) for some comatulids; 5) sudden deviations from pentamerous symmetry affecting some individuals in normally five-rayed species.

The opposite condition, i.e., the tendency to reduction of the number of arms to four, three, two, one or even their complete disappearance, occurs in various families. This has already been illustrated in connection with the elimination of some radials in the Codiocrinacea (Fig. 86, p. T112). Another well-known example is furnished by the hybocrinid inadunates. Some of them have five radials but only three arms, or no arms at all (*Cornocrinus*, *Tripatocrinus*); in these crinoids the atrophy and loss of arms seem to have been more or less compensated by the extension of the ambulacral grooves across the plates of the calyx or on the

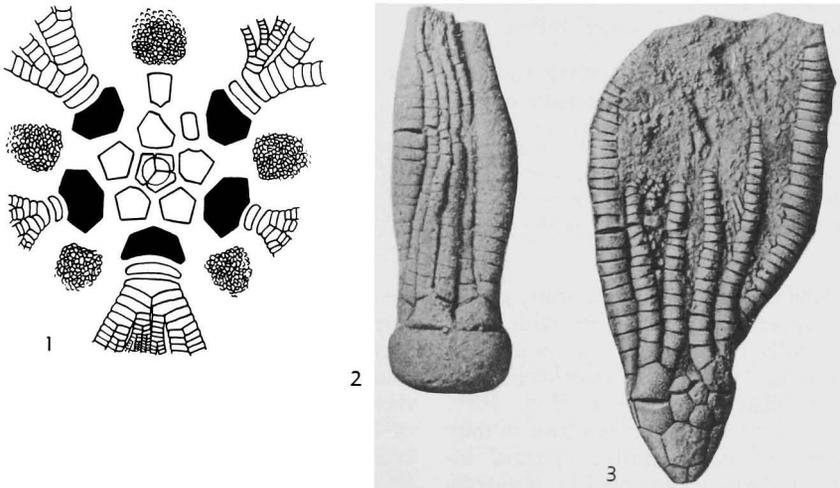


FIG. 108. Unequal development of arms.—1. *Cholocrinus* SPRINGER, Sil., Gotl.; plate diagram of calyx and proximal part of arms, showing enormously enlarged *A*, *C*, and *D* rays, and dwarfed *B* and *E* rays (Springer, 1920).—2. *Pentaramicrinus bimagnaramus* BURDICK & STRIMPLE, Miss., USA; crown in *A*-ray view, with greatly enlarged arms in *B* and *E* rays,  $\times 1.3$  (Burdick & Strimple, 1971).—3. *Anartiocrinus lyoni* KIRK, Miss., USA; crown in *CD* interray view, with hypertrophied arms in *B* and *E* rays,  $\times 1.5$  (Kirk, 1940).

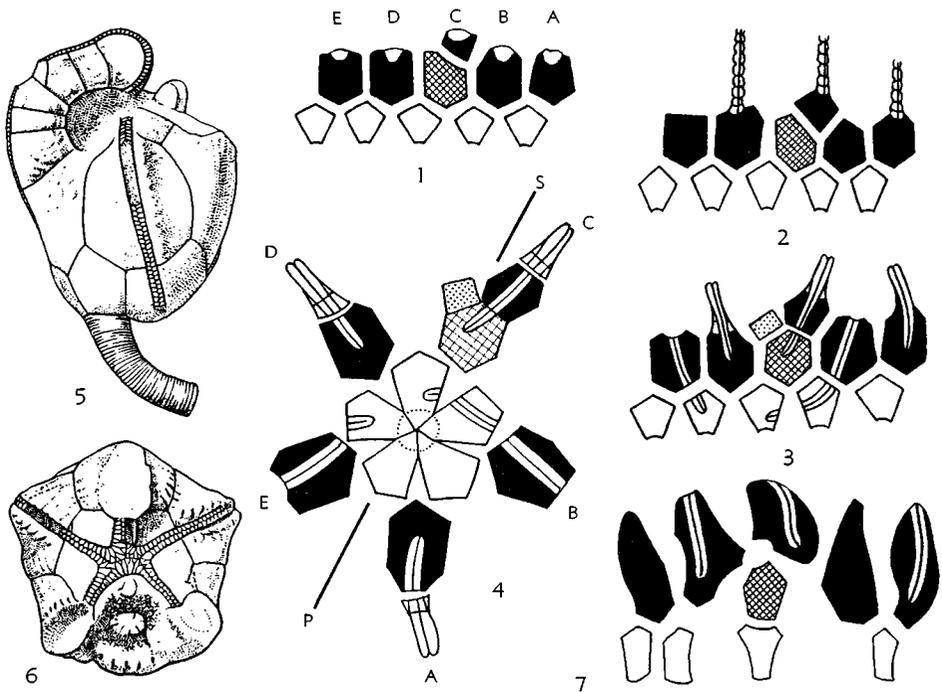


FIG. 109. Reduction of numbers of arms illustrated by hybocrinid inadunates. [Explanation: *P-S*, plane of bilateral symmetry; rays identified by letter symbols of the CARPENTER system; anal *X* stippled; radials black; radialian cross ruled.]

1. *Hoplocrinus* GREWINGK, M.Ord., Swed.; plate diagram of cup, five radials bearing arms (Regnéll, 1948a, mod.).
2. *Baerocrinus* VOLBORTH, M.Ord., USSR (Leningrad distr.); plate diagram of cup and parts of arms, only three arms (Regnéll, 1948a).
- 3,4. *Hybocystites* WETHERBY, Ord., N.Am.; 3, plate diagram of cup and arms, showing three reduced arms, and five ventral grooves extending onto radials and basals (Regnéll, 1948a); 4, plates radially arranged to show eustenocrinoidal plane of bilateral symmetry (Moore, 1962b).
- 5,6. *Hybocystites eldonensis* (PARKS), M.Ord., Ont.; 5, crown and part of column, in *B*-ray view; 6, cup in adoral view, arms not preserved,  $\times 2$  (Springer, 1911b).
7. *Cornucrinus* REGNÉLL, M.Ord., Swed.; plate diagram of cup, no arm, but ventral grooves on *A*, *C*, and *D* radials (Regnéll, 1948a).

aboral side of greatly reduced arms, giving them a superficial resemblance with some cystoids; to be noted is the relation of these modifications with the eustenocrinoidal plane of bilateral symmetry (Fig. 109). Equally noteworthy is the existence of only four arms in the primitive disparid inadunates *Eustenocrinus* and (?) *Ramseyocrinus*, the fifth arm of which is replaced by an anal tube (Fig. 93, p. T122). Many other examples could be cited, such as the four-rayed *Tiaracrinus*, *Nanocrinus*, and *Tetrapleurocrinus* (Fig. 110,1a,b), and the two-rayed *Scoliocrinus* (Fig. 110,2a,b), all from

the Middle Devonian of Germany; the three-rayed *Holynocrinus* from the Middle Devonian of Bohemia (Fig. 110,3a,b); the four-armed *Parindocrinus* (Fig. 110,4) and three-armed *Sundacrinus* from the Permian of Timor; and the usually four-rayed *Tetraacrinus* (which, however, may have 3 or 5 to 8 rays) from the Jurassic of Western Europe (Fig. 110,5). In these instances, the diminutive deviation from pentamerous symmetry appears mostly as a generic feature, but it may also occur as an individual variation in species normally provided with five rays.

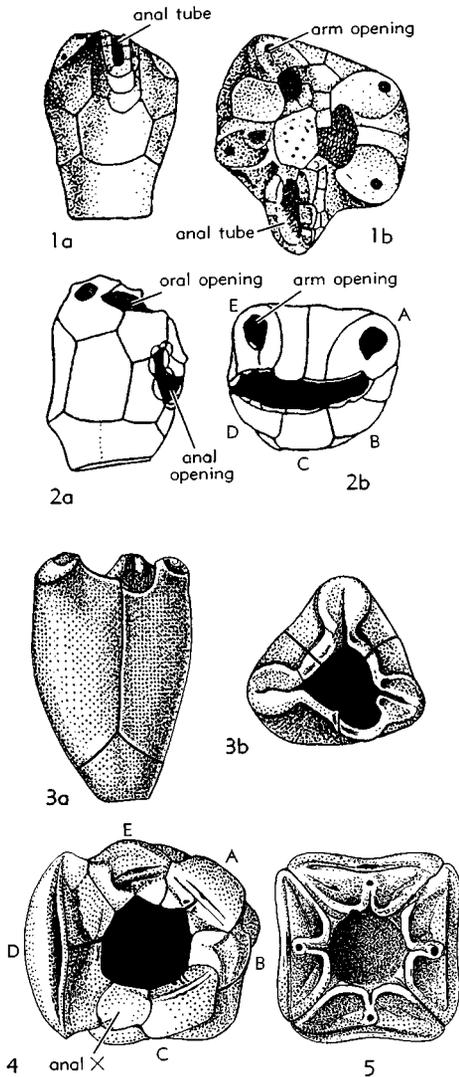


FIG. 110. Reduction of number of arms. [Explanation: rays identified by letter symbols of the CARPENTER system.]—1. *Tetrapleurocrinus eifelensis* WANNER, M.Dev., Ger.; four arm-bearing radials; 1a, CD-interray view; 1b, adoral view,  $\times 2$  (Wanner, 1943).—2. *Scolioocrinus eremita* JAEKEL, M.Dev., Ger.; five radials but only two arm-bearing; 2a, lat. view; 2b, adoral view,  $\times 2$  (Jaekel, 1895).—3. *Holynocrinus moorei* BOUŠKA, M.Dev., Boh.; three arm-bearing radials; 3a, CD-interray view; 3b, adoral view,  $\times 20$  (Bouška, 1948).—4. *Parindocrinus oyensi* WANNER, Perm., Timor; five radials, all of them arm-bearing except B radial; D radial hypertrophied,  $\times 2.6$

In many families, genera and species of crinoids, the number of free arms is fixed and therefore characteristic. But, in some cases, it varies, even within a species or a single specimen. This has been well shown by SPRINGER (1920), LANE (1963b), and others, who have demonstrated that the nonrecognition of this fact has led to the distinction of an illogical number of species in some genera. Figure 111 illustrates examples of such infraspecific variation, the coefficients of which may range from almost zero to seven or eight in different species. There is generally little consistent tendency for the number of arms to increase or decrease systematically through time within a genus. Within a species, the number of arms may be related to size of the specimen, or it may not; in the first instance, the increase in number of arms seems to be a growth phenomenon, in the second, it is either determined at an early ontogenetic stage or genetically controlled (LANE, 1963b). Within a specimen, the number of arms may vary from ray to ray; such variation may be at random, that is, without any definite order or system, or it may show a definite relation to the bilateral symmetry of the crinoid. For instance, in the camerate *Macrocrinus verneuilianus*, 12-armed specimens have two arms in each of the A, B and E rays, and three arms in each of the C and D rays; in 14-armed specimens, the arrangement is 2-3-3-P-3-3, and in 16-armed specimens it is 2-4-3-P-3-4 (P meaning posterior or CD interrayer).

### ARM GROWTH

If the mode of growth of the arms in extant crinoids is rather well known (see p. T56, T134), it remains largely conjectural in fossil crinoids. It seems clear, however, that in most fossil crinoids the arms grew through addition of new brachials at their distal end and subsequent enlargement of the newly secreted brachials. Primary interpolation of new elements between those already formed seems to have occurred very rarely, if ever. WARN (1973) has recently described what looks like plate

(Wanner, 1937).—5. *Tetracrinus moniliformis* (MÜNSTER), Jur., Eu.; only four radials, all of them arm-bearing,  $\times 4$  (de Loriol, 1882-84).

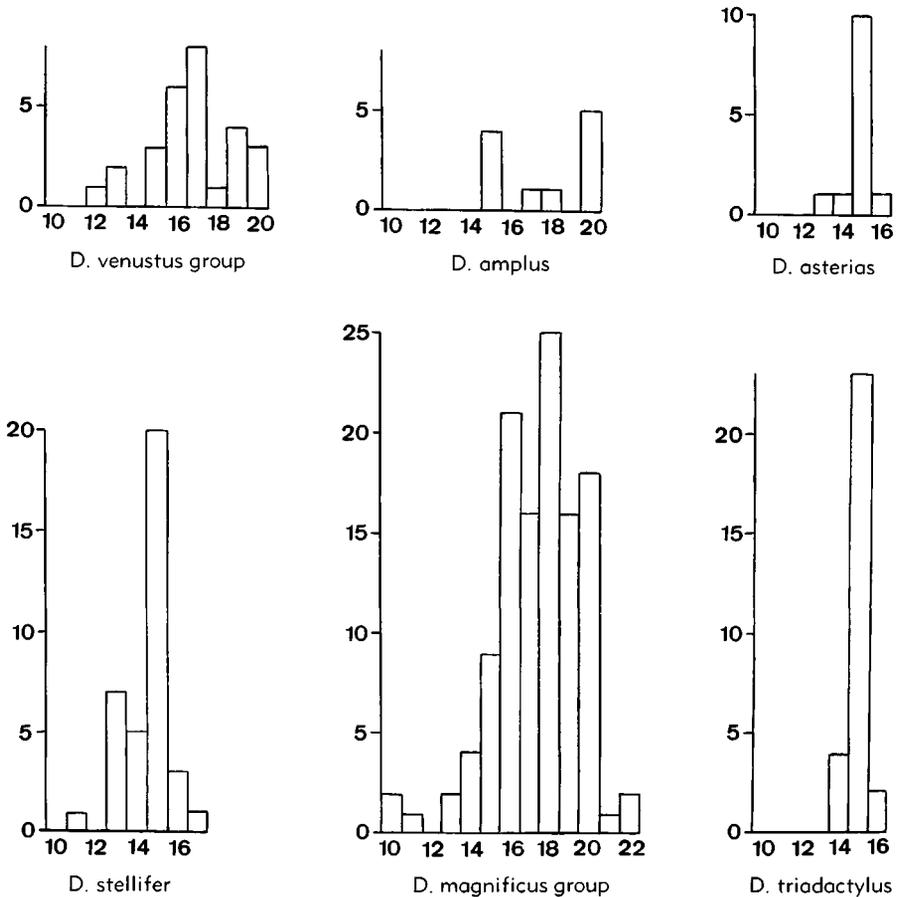


FIG. 111. Histograms of frequency distribution of arm openings in four species and two species groups of *Dolatocrinus* (abscissa, number of arm openings; ordinate, frequency in number of specimens) (Lane, 1963b).

intercalation in the brachial series of *Heterocrinus* cf. *H. tenuis*, but this is probably not the only possible explanation of such facts.

In many fossil crinoids—mainly camerates and flexibles—the growing tip of the arms is coiled upon itself (Fig. 112). Not infrequently its growth appears to have been slower than that of the adjoining branchlets or pinnules, so that it was more or less concealed and protected by these appendages.

Many fossil crinoids exhibit an increase in the number of arm branches per ray during growth. How these additional arm branches developed is not known. Presumably in most cases the mode of forma-

tion was direct or continuous, that is, new branches were produced by division of the growing tip of the arms. Possibly, the differentiation of some pinnules into armlets may also have occurred in some individuals; for instance, specimens of the camerate genera *Compsocrinus*, *Gaurocrinus*, and *Glyptocrinus* have been reported as having the first pinnule replaced by an arm. The existence of a discontinuous mode of formation as in living multibrachiate comatulids is another but yet unproved possibility; it would consist of the casting off of a series of distal arm plates by autotomy and their replacement by two branches.

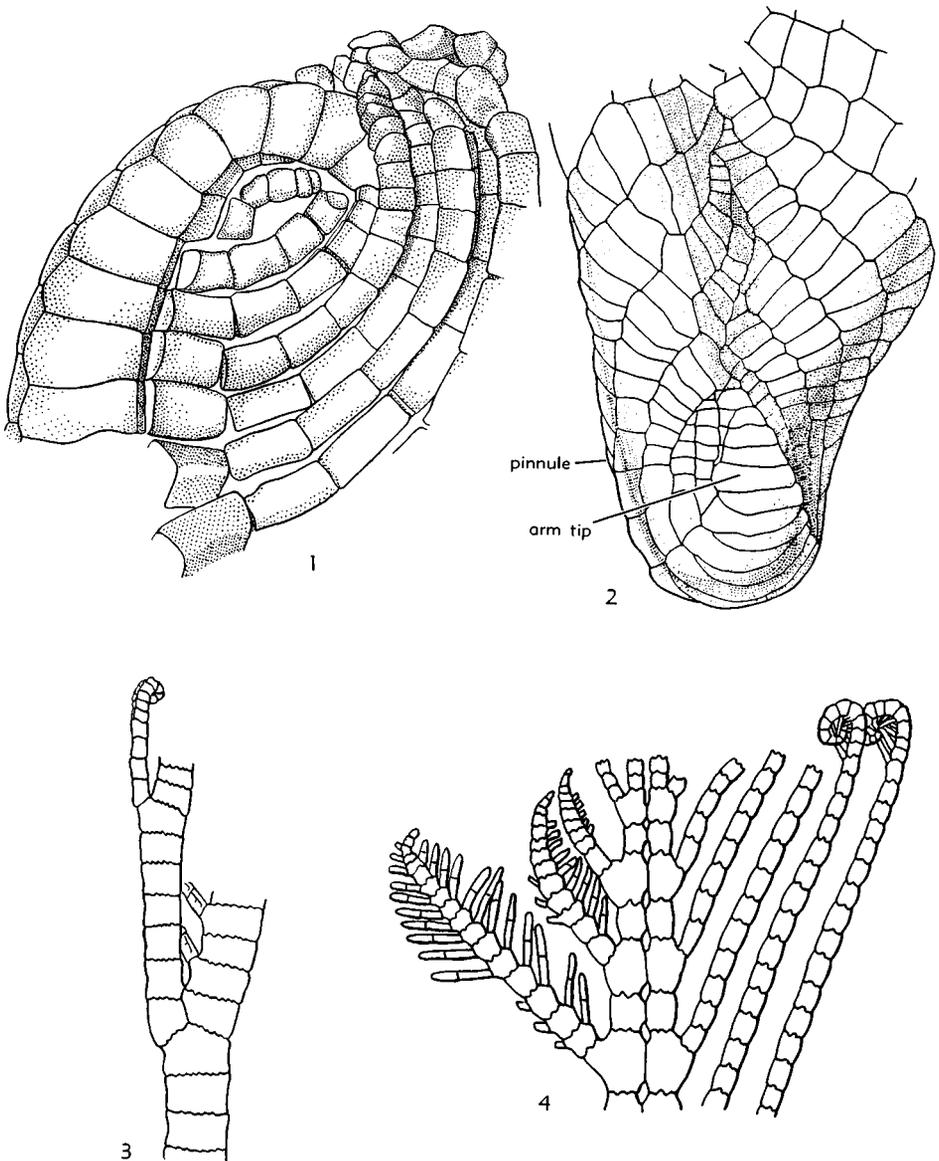


FIG. 112. Distal ends of arms in camerates.—1. *Clonocrinus* sp., U.Sil., Gotl.; lat. view, coiled tip protected by pinnules,  $\times 20$  (Ubaghs, n).—2. *Barrandeocrinus sceptrum* ANGELIN, U.Sil., Gotl.; adoral view, coiled arm tip with interlocking pinnules forming pavement,  $\times 15$  (Ubaghs, 1956).—3. *Ctenocrinus gottlandicus* (PANDER), U.Sil., Gotl.; aboral view, coiled arm tip much smaller than adjacent ramules,  $\times 10$  (Ubaghs, 1958b).—4. *Melocrinites pulcher* (SPRIESTERSBACH), M.Dev., Ger.; aboral view, main arm growing more slowly than adjacent ramules, enl. (Spriestersbach, 1919).

In most fossil crinoids, the arms, like those of recent forms, grew in an upward direction (away from the stem), and are commonly preserved close together (Fig.

113,1). This attitude is particularly well exemplified by the Flexibilia, which are usually found with the arms tightly coiled upon themselves over the tegmen (Fig.

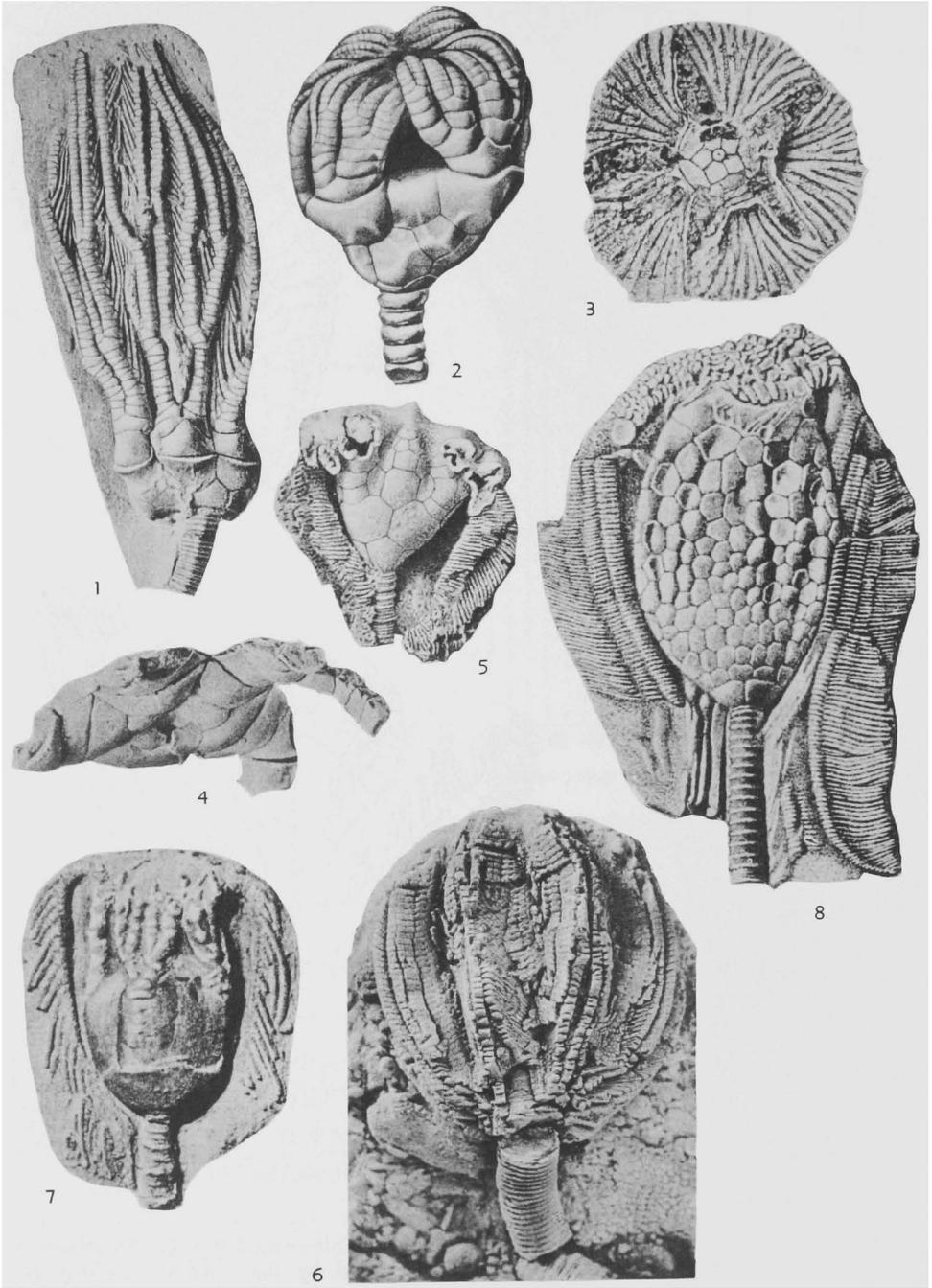


FIG. 113. Various directions of growth in the arms. (*Explanation on facing page.*)

113,2). In some crinoids, however, the arms developed outward, spreading out more or less horizontally around the theca (Fig. 113,3), and in others they grew downward, assuming a permanent pendent or recumbent position during life (Fig. 113,4-8). This last arm type evolved independently in several camerate families (i.e., Acrocrinitidae, Desmidocrinitidae, Patelliocrinitidae, Platycrinitidae, and Rhodocrinitidae), but it is rare among inadunate crinoids (e.g., *Oklahomacrinus*) and unknown in flexible and articulate crinoids. This unusual arm habit is ordinarily associated with special structural features such as a projecting tegmental edge that gave a firm anchorage to the suspended arms, the downward orientation of the arm-facets, a particular shape and thickness of the calycinal plates supporting the arms, the fusion of proximal free brachials, and others.

Regeneration of arms or parts of arms occurred rather commonly among fossil crinoids. Many examples have been recorded, most of them of a reproductive type (Fig. 114,1). Augmentative regeneration seems to have occurred more rarely. In the example illustrated here (Fig. 114,2), the four inner arms of the *A* ray have been broken and the remaining portion of each of them has regenerated two arms, bringing to 10 the number of arms in this ray instead of six or seven as in the other rays.

## ARM BRANCHING

The free arms of crinoids may be simple (**atomous**) or branched. Several types of arm-branching are known (Fig. 115). The simplest, and probably the most primitive,

consists of the division of the arm into two branches (**dichotomy**). If the branches are equal or subequal, the division is called an **isotomy**. An arm affected by such bifurcation, constantly repeated in a regular manner, is said to be **regularly dichotomous** or **isotomous** (Fig. 115,1). The suppression of a bifurcation at definite points produces an **irregular dichotomy** or **heterotomy** (Fig. 115,2). In heterotomous arms the branches resulting from a bifurcation are commonly unequal in size. Such inequality leads to the formation of a main branch (**ramus**), which carries smaller branches (armlets or **ramuli**). The ramules may be borne on both sides of a main branch (**bilateral heterotomy**) (Fig. 115,3), or on one side only (**unilateral heterotomy**), and either on the inner (adradial) side (**endotomy**) (Fig. 115,4) or on the outer (abradial) side (**exotomy**) (Fig. 115,5). The ramules themselves may undergo a similar, but generally less elaborate, process of division. When they remain unbranched, and are regularly placed on alternate sides of successive brachials (**holotomy**), they are called **pinnules** (pl., **pinnulae**) and the arm is "pinnulate" (Fig. 115,6). This succession of stages, effectively traced in some fossil inadunate families, such as the Botryocrinitidae and the Mastigocrinitidae, suggests that the pinnules are the ultimate products of arm division. This interpretation is probably correct as far as it concerns most inadunates and articulates, but whether it is equally relevant for all pinnulate crinoids is still a matter of debate, as we shall see later.

A special type of arm structure, which seems to result from the hypertrophy and the very unequal heterotomous branching

1. *Abrotocrinus unicus* (HALL), Miss., USA (Ind.); complete crown in *A*-ray view, with arms erect,  $\times 1$  (Springer, 1926b).
2. *Pycnosaccus bucephalus* (BATHER), M.Sil., Eng.; complete crown in *CD*-interray view with arms tightly coiled upon tegmen,  $\times 1$  (Springer, 1920).
3. *Petalocrinus mirabilis* WELLER, M.Sil., Ia.; complete crown in aboral view with arms spreading out horizontally,  $\times 2$  (Springer, 1926a).
4. *Oklahomacrinus loeblichii* MOORE, U.Penn., USA (Okla.); oblique view of crown, indicating pendent nature of arms,  $\times 1.5$  (Moore, 1939c).
5. *?Macrostylocrinus recumbens* SPRINGER, L.Dev., USA (Md.); crown with pendent arms partly removed, uncovering calyx and proxistele, *CD*-interray view,  $\times 1$  (Springer, 1926b).
6. *Barrandeocrinus sceptrum* ANGELIN, U.Sil., Gotl.; crown with recumbent arms completely enveloping the theca,  $\times 1.5$  (Ubaghs, 1956).
7. *Dichocrinus recurvibrachiatus* VAN SANT, Miss., USA (Ind.); calyx with pendent arms and proxistele, lat. view,  $\times 2$  (Van Sant, in Van Sant & Lane, 1964).
8. *Amphoracrinus amphora* (WACHSMUTH & SPRINGER), Miss., USA (Ala.); calyx with downhanging arms and proxistele,  $\times 1.5$  (Wachsmuth & Springer, 1897).

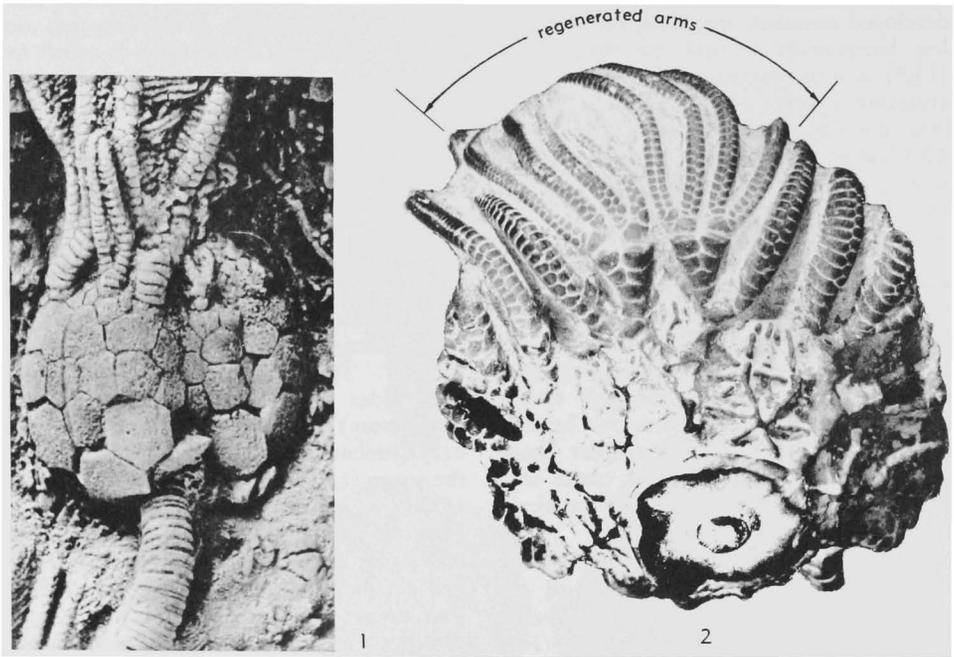


FIG. 114. Regeneration of arms.—1. *Rhodocrinites watersianus* (WACHSMUTH & SPRINGER), Miss., USA (Ia.); crown with two regenerated arms (reproductive regeneration),  $\times 2.5$  (Strimple & Beane, 1966).—2. *Gennaeocrinus mourantae* GOLDRING, M.Dev., Ont.; U.S. Natl. Museum S. 4533, oblique view of a crown that has regenerated 8 arms (instead of 4) in A ray (augmentative regeneration),  $\times 2.4$  (Ubaghs, n).

of the main arms, has been repeatedly produced among camerates. It consists of the occurrence of one or two powerful rami in each ray. These "arm trunks," as they are called, carry relatively slender ramuli, that are pinnulate, whereas the trunks usually (if not invariably) lack pinnules (Fig. 116). In advanced melocrinitids, the two arm trunks of each ray coalesce along their adradial margin—a phylogenetical process repeated in ontogeny that produces a compound ramule-bearing appendage (Fig. 117).

The pattern of the arm branching may be constant and diagnostic for a family or a genus, or it may vary. For instance, among dichocrinid camerates, the arms of *Dichocrinus* are isotomous, while those of *Paradichocrinus* are exotomous. In some forms different ray structures occur in a single individual. Thus, some calceocrinid inadunates have isotomous arms in the E ray and strongly heterotomous arms in the A and D rays.

## AXILLARIES

In a branching arm, each brachial that supports two branches is an axillary (Fig. 118,1). An axillary, therefore, has two upper (distal) sloping shoulders or articular faces (facets), each notched by the adoral groove and pierced by the axial canal (if any), for the groove and the axial canal branch with the arm. The distal facets of an axillary may be equal or unequal, according to the relative sizes of the branches produced by a bifurcation. If the inequality is very important, as for instance when an axillary gives rise to an unbranched ramule or a pinnule on one facet and to a continuation of the arm, of which it is part, on the other, the brachial on which such unequal division takes place may be conveniently designated as a subaxil (Fig. 118,2). A pinnulate arm is made up of a succession of subaxils. It must be clearly understood, however, that a subaxil, as

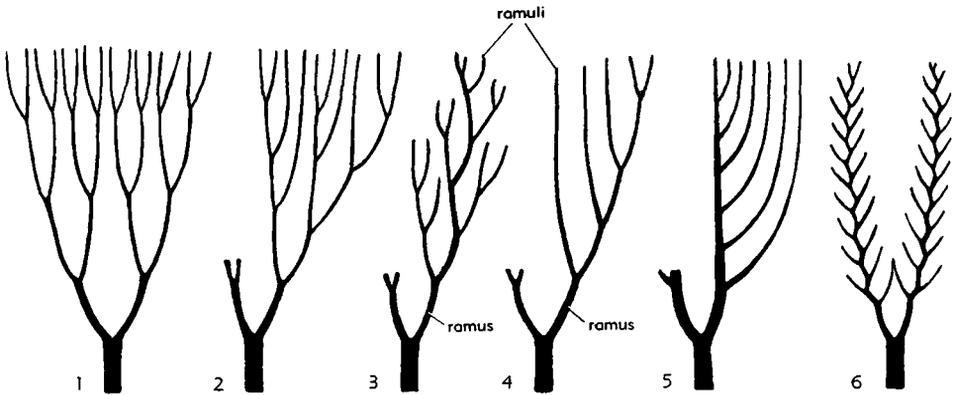


FIG. 115. Various types of arm branching.—1, isotomy; 2, heterotomy; 3, bilateral heterotomy; 4, endotomy; 5, exotomy; 6, holotomy (mod. from Bather, 1900a).

here interpreted, is morphologically equivalent to an axillary. A pinnulate arm or a ramuli-bearing arm may bifurcate as a simple arm, though generally not to the same extent. The axillaries on which the rami or main branches of such pinnulate or ramule-bearing arms fork are similar to ordinary axillaries. In order to distinguish them from subaxils, they may be referred to as **main axils** (Fig. 118,2,3).

In a number of mainly Pennsylvanian and Permian cladid inadunates, the axillary plates are conspicuous; they are considerably larger than the other brachials and commonly bear nodes or spines (Fig. 119,1). Furthermore, in a number of species, the five axillaries corresponding to the first bifurcation of each arm are unequal; generally, the longest belongs to the *A* ray, and the shortest to the *B* ray (WANNER, 1949a) (Fig. 119,2,3).

As a rule, axillaries occur in all crinoids in which the arms bifurcate; however, in camerates with arms composed of two alternating series of brachs the axillaries are generally lacking, and the divisions result from the mere splitting of the rows of brachs immediately below each point of bifurcation (Fig. 120,1). On the contrary, in inadunates with similarly built arms, distinct axillaries are invariably present (Fig. 120,2). Another difference lies in the fact that as a rule in inadunates and articulates the axillary plates do not give off a pinnule, whereas in camerates axillary-like

ossicles commonly bear such appendages (Fig. 120,3,4).

### BRACHITAXIS

The terminology of the series of brachials that compose an arm has already been partially discussed under the treatment of fixed brachials in the calyx (p. T118). The general term **brachitaxis** is used for designating any undivided series of brachs that terminates in an axillary plate or remains undivided up to its distal extremity (Fig. 120,2). The plates of the proximal brachitaxis up to and including the first axillary or **primaxil** (if any) are termed **primibrachs** (also **primibrachials** or **primibrachialia**), those of the following brachitaxis with a **secundaxil** (if any) are **secundibrachs**, then succeed **tertibrachs**, **quartibrachs**, and so on. Numbering of brachials in any brachitaxis starts from the most proximal ossicle. Brachials of the distal rami that do not fork again are called **finials**.

Ordinarily such terminology is easily applied to nonpinnulate arms. In a pinnulate arm that branches, the primibrachs as a rule do not bear pinnules, and are therefore homologous with the primibrachs of a nonpinnulate arm. The pinnules generally begin with the next series. Of the brachs composing this series only the proximal one is strictly homologous with the secundibrach of a nonpinnulate arm with regard to the pinnule borne by it, and the next brachial

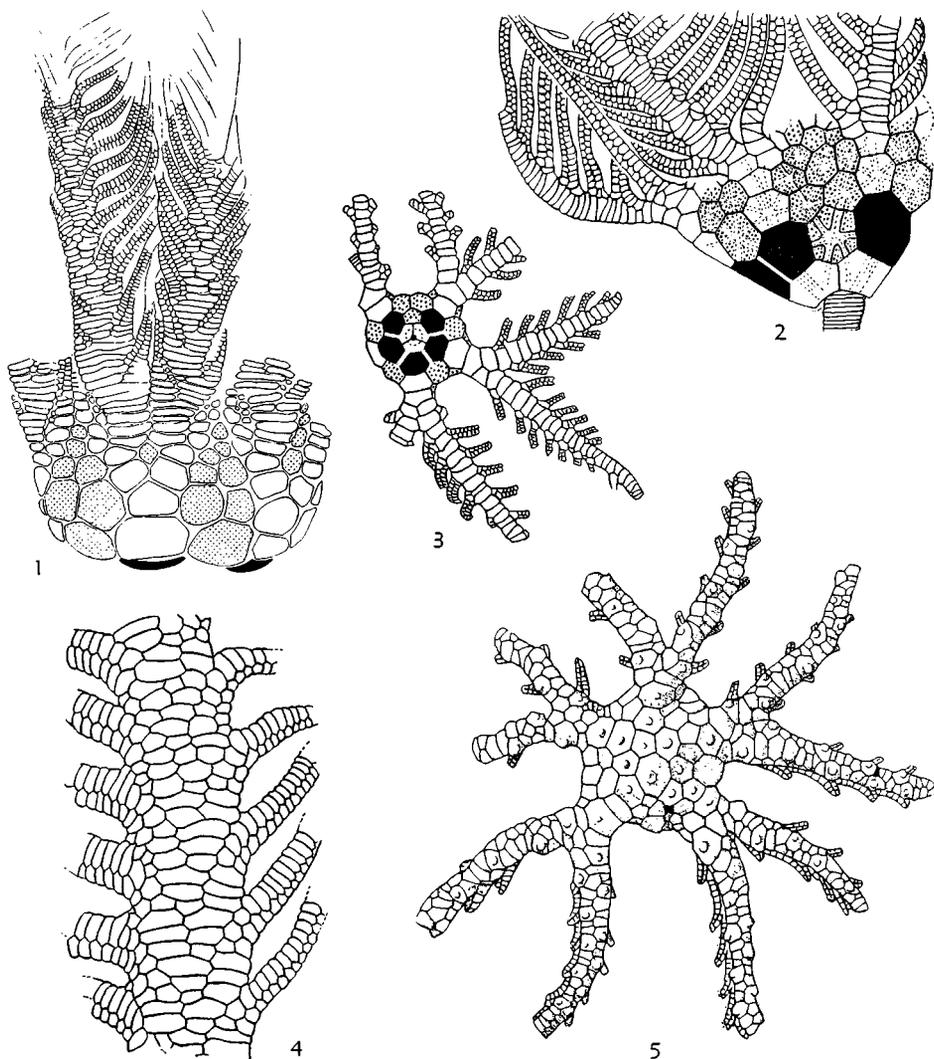


FIG. 116. Arm trunks in camerates.—1. *Rhipidocrinus* sp. cf. *R. perloricatus* W. E. SCHMIDT, M.Dev., Ger.; calyx and arm trunks of *E* ray, ca.  $\times 1$  (Breimer, 1960).—2. *Cytidocrinus sculpus* (HALL), Miss., N.Am.; calyx and proximal portions of arm trunks, in CD-interray view,  $\times 1$  (Kirk, 1943a).—3. *Steganocrinus pentagonus* (HALL), Miss., N.Am.; calyx and parts of arm trunks, aboral view,  $\times 1$  (Kirk, 1943a).—4. *Trybliocrinus flatheanus* GEINITZ, L.Dev., Spain; part of an arm trunk,  $\times 3.3$  (Breimer, 1962).—5. *Eucladocrinus millebrachiatus immaturus* WACHSMUTH & SPRINGER, Miss., USA (Ia.); adoral side of theca and arm trunks,  $\times 1$  (Wachsmuth & Springer, 1897). [Explanation: interbrachials and anals stippled; radials black.]

represents the tertibrachs of a nonpinnulate arm. This makes extremely difficult the task of formulating a consistent terminology for pinnulate and nonpinnulate arms. An attempt made in that direction by BATHER (1892a) never gained acceptance. It is

more practical, though unquestionably incorrect (if the pinnules are really the ultimate product of arm division), to consider the pinnule-bearing brachials of an arm not as markers of successive arm-divisions but as equivalent to nonpinnulate components.

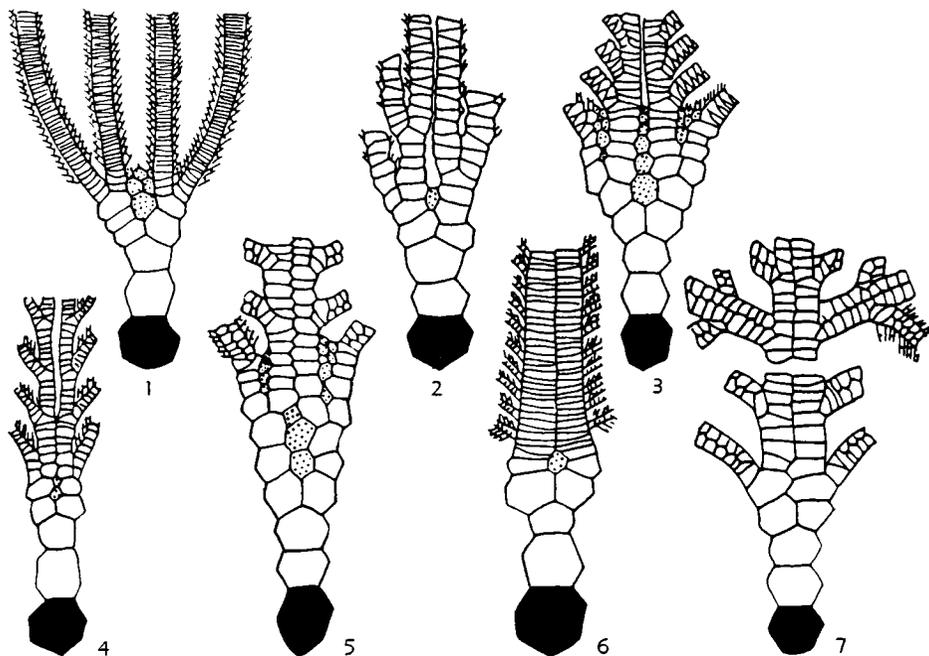


FIG. 117. Evolution of ray structure in Melocrinidae, representation diagrammatic and not to scale (Ubaghs, 1953). [Explanation: interbranchials stippled; radials black.]—1. *Alisocrinus*, U.Ord.-U.Sil., N.Am.—2. *Promelocrinus fulminatus* (ANGELIN), U.Sil., Gotl.—3. *Promelocrinus anglicus* JAEKEL, M.Sil., Eng.—4. *Ctenocrinus gottlandicus* (PANDER), U.Sil., Gotl.—5. *Ctenocrinus nobilissimus* (HALL), L.Dev., USA(N.Y.)—6. *Melocrinites splendens* (GOLDRING), U.Dev., USA(N.Y.)—7. *Trichotocrinus harrisi* OLSSON, U.Dev., USA(N.Y.). (From *Traité de Paléontologie*, v. 3, copyright 1953, courtesy Masson & Cie, Paris.)

A similar procedure may be conveniently applied to arms that bear numerous unbranched ramules on every two or three brachs.

The complexity of arm branching in some crinoids is so great that a special nomenclature may be needed to designate any particular division in a clear manner. An example is furnished by the Calceocrinidae—a highly specialized disparid family characterized by the recumbent position of the crown along the stem and the consequent progressive acquisition of a bilateral symmetry (Fig. 87,2, p. T114). Each lateral (*A* and *D*) ray of most genera comprises a proximal ramus that is reduced to a series of axillaries (main axils), each one of which carries an arm, called an **axil-arm** (Fig. 121). The first (most proximal) axil-arm is the **primaxil-arm**, the next one, the

**secundaxil-arm**, and so on. Each axil-arm forks at least once and generally several times. In any axil-arm the brachials of the proximal series are known as **alphabrachs**, those of the next series as **betabrachs**, of the third as **gammabrachs**, and so on. The axillary alphabrach of each axil-arm carries an unbranched ramule (**alpha-ramule**) on its abanal shoulder and a betabrach series on the other. In its turn the axillary betabrach bears a **beta-ramule** on its adanal facet and, on the other side, a gammabrach series that gives off a **gamma-ramule** on its abanal facet, and so on. This heterotomous pattern of branching extends to the distal end of the main ramus, the last axillary of which bears a branching axil-arm on its abanal side and an unbranched ramule (called **omega-ramule**) on its adanal side. This nomenclature has been devised by

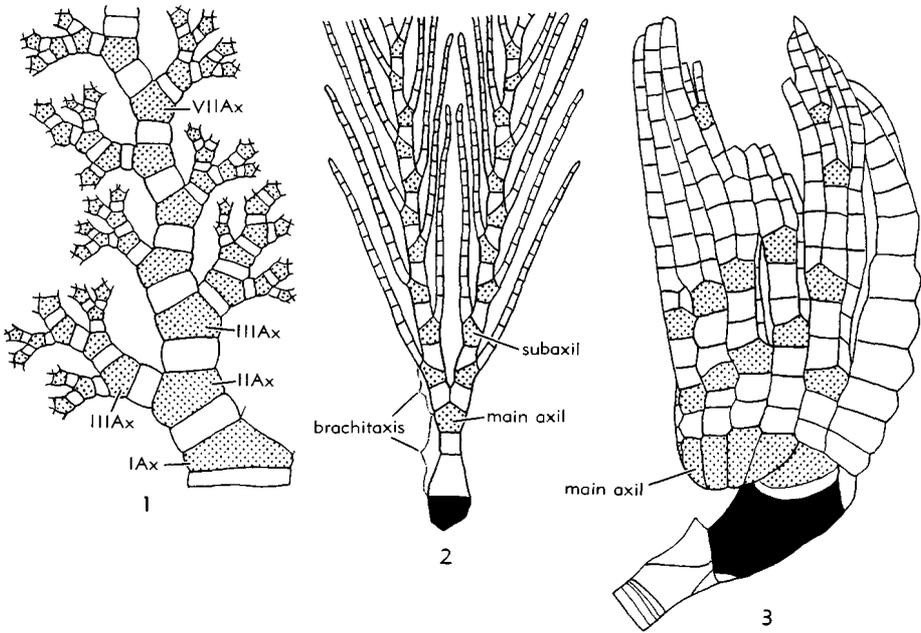


FIG. 118. Diagrammatic and not to scale representations of axillary brachials. [Explanation: *I Ax*, *II Ax*, *III Ax* . . . , axillaries of successive orders; radials black; axillaries stippled.]—1. *Barycrinus asteriscus* VAN SANT, Miss., USA (Ind.) (Van Sant in Van Sant & Lane, 1964).—2. *Logocrinus brandoni* SIGLER, WHITE, & KESLING, M.Dev., USA (Ohio);  $\times 1$  (Sigler, White, & Kesling, 1971).—3. *Halysiocrinus nodosus* (HALL), Miss., USA (Ind.) (drawn from Springer, 1926a).

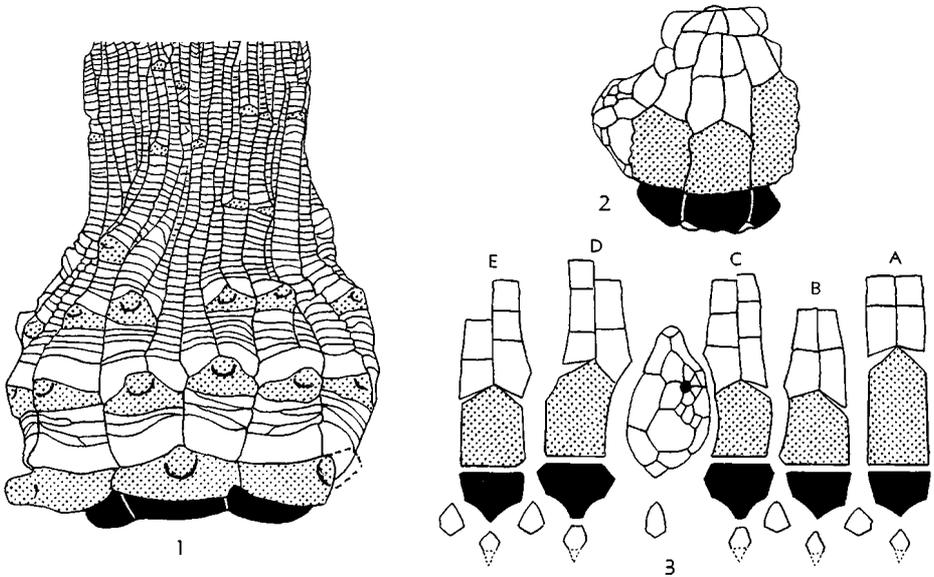


FIG. 119. Morphology of axillaries (axillaries stippled; radials black).—1. *Eirmocrinus grossus* STRIMPLE & WATKINS, Penn., USA (Texas); a species with conspicuous spiniferous axillaries, in B-ray

BATHER (1893a) and expanded by MOORE (1962a) (Fig. 121).

The number of primibrachs is an important taxonomic feature. Most camerate crinoids have two primibrachs per ray but some genera have three, four, or even five in each ray, whereas others have only a single one or even none. This reduction in the number of primibrachs in camerates has a quite different taxonomic value according to the group considered. In some families, it characterizes the whole assemblage; in others, some genera only. It may have a purely specific significance or be just a matter of individual variation; it may even be restricted to a ray or two in a single specimen. The reduction in the number of primibrachs in camerates does not seem to result, as sometimes suggested, from the ankylosis of the component ossicles, but mainly from the atrophy of the first one, more rarely of the second one (primaxil), and in some cases of both (Fig. 84,7, p. T110).

In flexible crinoids, all Ordovician and Silurian members (except *Meristocrinus*), most Devonian, and some Carboniferous genera have two primibrachs per ray, but from the Carboniferous onward three becomes the predominant number.

Among inadunate crinoids, the number of primibrachs per ray varies to a much larger extent than in other subclasses. In forms having branched arms, it may be as high as 12 or as low as one (possibly in some cases as a consequence of fusion of two elements). In Devonian and Mississippian genera, it is commonly two, but most Pennsylvanian and Permian inadunates have only one primibrach in each ray.

In articulate crinoids, the first brachitaxis commonly contains two primibrachs, but a much higher number occurs in several genera.

### ARRANGEMENT OF BRACHIALS

Arms, arm branches, and pinnulae in which the component ossicles are arranged

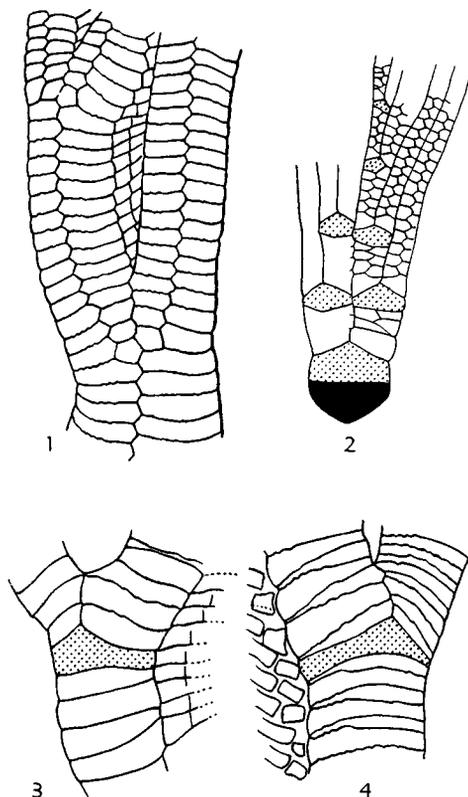


FIG. 120. Bifurcation of arms in camerates (1, 3, 4) and inadunates (2) (axillaries stippled; radial black).—1. *Abacocrinus* sp., U.Sil., Gotl.; no distinct axillaries,  $\times 5$  (Ubaghs, n).—2. *Hydreionocrinus gomiodactylus* (DE KONINCK & WOOD), U.Carb., Eng.; conspicuous axillaries present,  $\times 1$  (Bather, 1911-12).—3, 4. *Scyphocrinites* sp., U.Sil., Alg.; pinnule-bearing axillaries,  $\times 7$  (Ubaghs, n).

in a single series are said to be **uniserial**. Uniramous brachia and pinnulae are invariably uniserial. Their component elements have more or less parallel articular facets. In pinnulate arms the brachials tend to slope alternately to the right and left and thence to become wedge shaped (Fig. 122). Eventually, the brachials come to lie in two alternating rows with their pointed lateral sides meeting midway along a zig-

(Continued from facing page.)

view,  $\times 1$  (Strimple & Watkins, 1969).—2, 3. *Prolobocrinus permicus* WANNER, Perm., Timor; a species with unequal primaxils; 2, B-ray view,  $\times 2$ ; 3, plate diagram of cup and proximal parts of arms (Wanner, 1943).

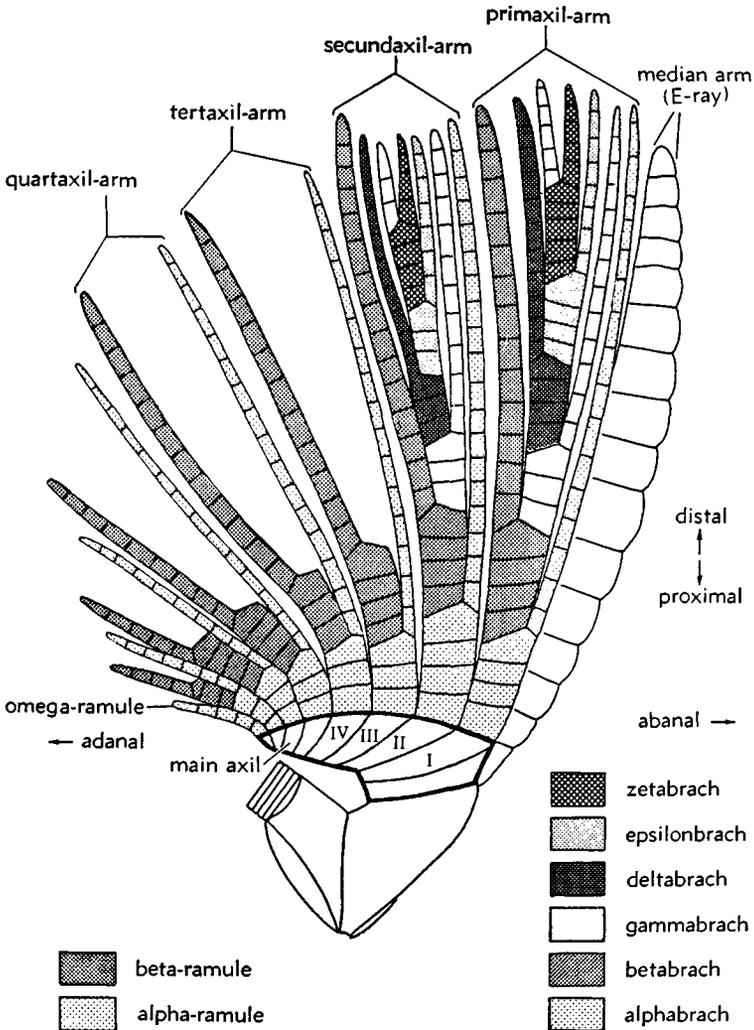


FIG. 121. Nomenclature applied to arm branching in lateral (A and D) rays of Calceocrinidae (Moore, 1962a).

zag suture line. Arms with such arrangement of the brachials are called **biserial**.

A ray is never entirely biserial. Its proximal portion is invariably uniserial, and the change, ordinarily progressive, into a biserial arrangement takes place at varying distances above the radials or the primaxils (Fig. 123,3). Also the few available data on the growing tips of biserial arms suggest that their short distal brachials preserve a uniserial arrangement (Fig. 123,3).

The change from uniserial to biserial arrangement of the brachials may be advantageous in at least one respect; as it approximately doubles the number of pinnules in a given length, it serves to increase the food-gathering and other functions accomplished by the brachial system.

The above interpretation of the origin of biserial arms has gained almost general acceptance. It implies that the brachia of crinoids were primitively uniserial. This

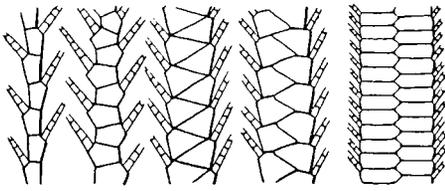


FIG. 122. Evolution from uniserial (left) to biserial arrangement of brachials, diagram. (Bather, 1900a).

conclusion is supported by the following evidence: 1) Most Ordovician crinoids have uniserial arms, and the number of species with biserial arms, both in camerates and in inadunates (the arms of flexibles are invariably uniserial), increased progressively during Paleozoic times. 2) Study of the phylogeny of some lineages, such as the melocrinitid camerates, shows that the uniserial condition precedes the biserial one. 3) Study of the ontogeny of

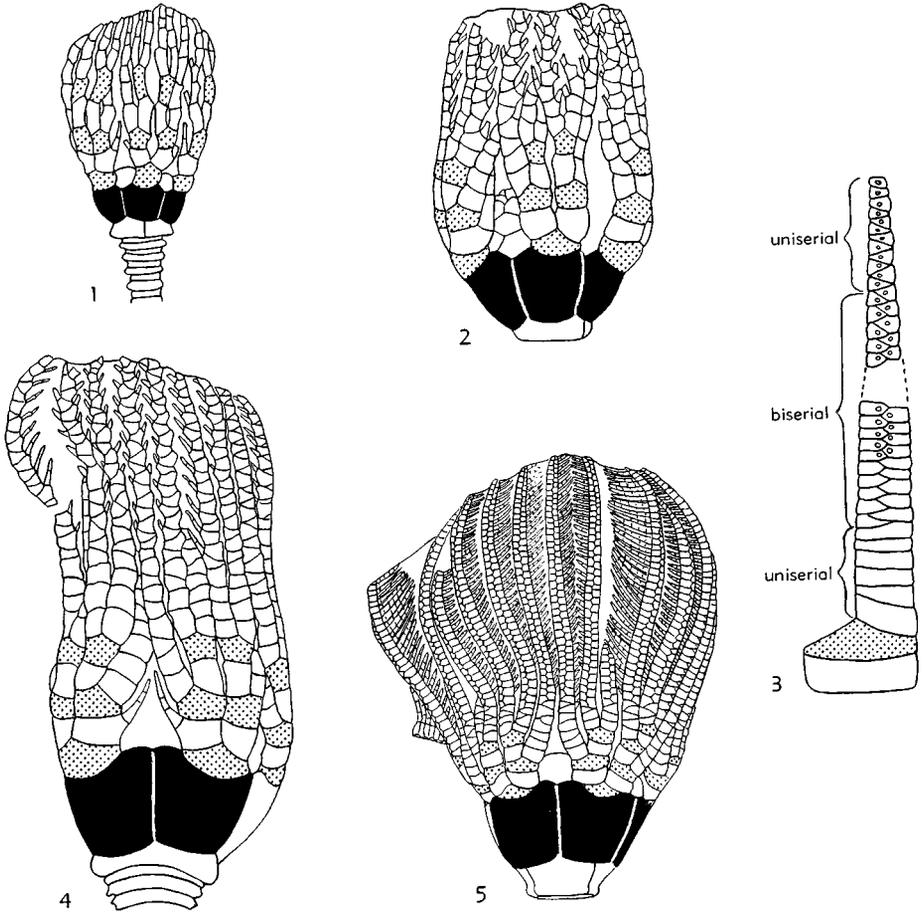


FIG. 123. Progressive change from uniserial to biserial arrangement of brachials in a single arm (3) and in ontogeny (1,2,4,5) (axillaries stippled; radials black).—1,2,4,5. Growth stages in *Platycrinites bozemanensis* (MILLER & GURLEY), Miss., N.Am.; 1, very young specimen with elongate uniserial brachials, ca.  $\times 8$ ; 2, young specimen with brachials becoming cuneiform distally, ca.  $\times 7$ ; 4, somewhat older specimen with strongly cuneiform brachials in distal parts of arms, ca.  $\times 7$ ; 5, adult specimen, with compactly biserial brachials, ca.  $\times 3$  (Laudon, 1967).—3. *Encrinus liliiformis* MILLER, Trias., Eu.; diagram. (Grabau, 1903).

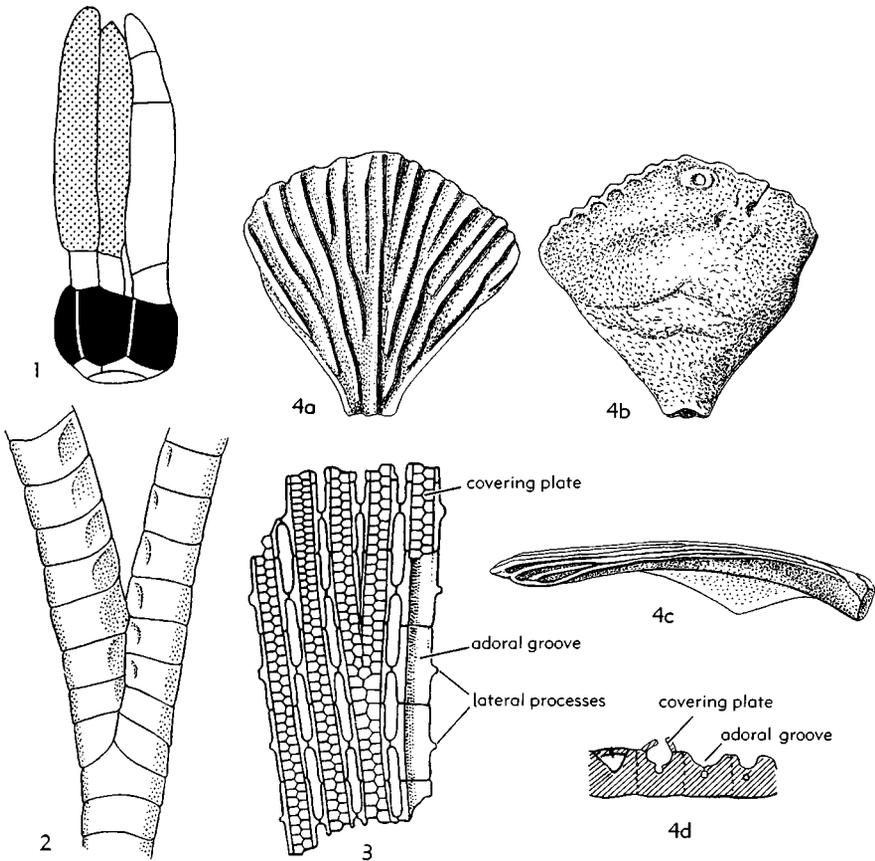


FIG. 124. Fusion of brachials.

1. *Isoallagecrinus strimplei* (KIRK), Penn., USA (Okla.); complete crown; with very long second brachial (stippled) in two arms, each such elongated ossicle possibly resulting from fusion of several elements, still distinct in other arms,  $\times 4$  (Strimple, 1972).
2. *Aethocrinus moorei* UBAGHS, L.Ord., France; part of a free arm showing partial lateral union of two branches, aboral side,  $\times 6$  (Ubaghs, 1969).
3. *Crotalocrinites rugosus* (MILLER), U.Sil., Eu.; adoral view of portion of arms united by lateral processes at repeated intervals, ca.  $\times 4$  (Wachsmuth & Springer, 1889a).
4. *Petalocrinus visbycensis* BATHER, U.Sil., Gotl.; 4a-d, one arm-fan resulting from complete lateral fusion of arm branches, in adoral (4a), aboral (4b), and lat. (4c) views,  $\times 3$  (Bather, 1898); 4d, sec. across four grooves of an arm-fan,  $\times 5$  (Bather, 1900a).

Paleozoic species with biserial arms reveals that an early uniserial stage develops before the biserial growth pattern is acquired (Fig. 123, 1,2,4,5). 4) In full-grown individuals, the new brachials introduced at the growing tip of the arms appear to have generally, if not invariably, a uniserial arrangement (Fig. 123,3). All this suggests that the evolutionary sequence among crinoids is from a uniserial to a biserial con-

dition. Or, in other words, that uniseriality is a primary—not a secondary—feature of the crinoid brachium.

It is a rule that in the pinnulate part of a ray the pinnules are borne on alternate sides of each brachial. However, in a number of camerate and inadunate species two or several pinnules may be inserted on a single brach. It has been generally accepted—though perhaps never clearly demonstrated

—that such **hyperpinnulation** results from the fusion of two or several adjacent right and left ossicles in a biserial arm, forming compound brachials. Thus, an arm comprising compound brachials, though uniserial in appearance, might be equivalent to a biserial one in reality. According to another explanation, the occurrence of two or more pinnules on a brach could have been produced through hypertrophy of this brach and development of one or several supplementary pinnules (W. E. SCHMIDT, 1942). This last interpretation implies, of course, a different origin for the pinnules than would result from the division of the arm on each brachial.

Fusion of brachials into large units certainly occur among crinoids. For instance, the brachials of the Devonian inadunate *Cupressocrinites* are reported to be composed each of several thin, discoid elements (SIEVERTS, 1934); those of the Pennsylvanian inadunate *Exocrinus* are commonly united by ankylosis; the allagecrinid *Isallagecrinus strimplei* (KIRK) has in some rays a very long second primibrach, which may result from the fusion of two or three ossicles, still distinct in other rays (Fig. 124,1); the pendent arms of some Mississippian species of the camerate genus *Dichocrinus* are supported by coalesced proximal free brachials (Fig. 113,7, p. T142). Brachials belonging to adjacent arms may also fuse laterally. This happens commonly in Paleozoic crinoids when the two branches resulting from a bifurcation do not separate immediately (Fig. 124,2). In advanced Melocrinitidae, the main rami of each ray fuse laterally and give rise to powerful arm trunks (Fig. 117, p. T147). Still more remarkable appears to be the lateral union of the arms in the Crotalocrinitidae and Petalocrinitidae. In these inadunates there is a marked tendency of the arm branches to be united by lateral processes from each brachial and to form a network (Fig. 124,3) or, in case of complete lateral union, compact blades (Fig. 124,4a-d).

## PINNULES

Pinnules generally appear as slender, unbifurcated, appendages of the arms typically borne on alternate sides of successive brachials. Their aboral skeleton consists of

uniserially arranged ossicles called **pinnulars**. So far as known, highly movable articulations generally connect brachials and first pinnulars, even in crinoids that possess only ligamentary articulations between brachials. A groove (ventral or adoral groove) is typically present on the adoral side of each pinnule; in extant crinoids it contains an ambulacral groove and extensions of water-vascular, nervous and coelomic systems, so that the pinnules have a constitution similar to that of the arms.

The basic rule of the arrangement of pinnules along the arms or **pinnulation** is that they are borne on alternate sides of each successive brachial. Many exceptions to this rule are known. 1) One or two newly added brachials at tip of arms lack pinnules. 2) In a number of camerates and inadunates more than one pinnule may be attached to a single brach (hyperpinnulation, see above). 3) In pinnulate branched arms, when there are no more than two elements in a brachitaxis, these elements generally (but not invariably) lack pinnules. 4) Axillary brachials have no pinnules, though in camerates brachs that have the appearance and function of axillary plates may carry pinnules (Fig. 120,3,4). 5) In articulate crinoids, pairs or triplets of brachs united by ligamentary (instead of muscular) articulations give rise to a single pinnule from their distal component, and never from their proximal or intermediate elements (see section on recent crinoids, p. T41). 6) At base of the arms (and commonly of the main branches) of many camerates, pairs or triplets of brachs occur that carry a pinnule on their distal ossicle only (Fig. 125); in spite of similarity with the preceding case, there is no evidence that such lack of pinnules in camerates is connected with a particular type of brachial articulation.

Pinnules may also be absent in places when their presence would be normally expected, a feature known as **defective pinnulation** and observed in many recent crinoids (see section on recent crinoids, p. T41). Defective pinnulation may also occur in fossil crinoids. For instance, in a number of poteriocrinitine genera, the proximal pinnules were suppressed, possibly as a consequence of the bulging of the tegminal pavement between the arms.

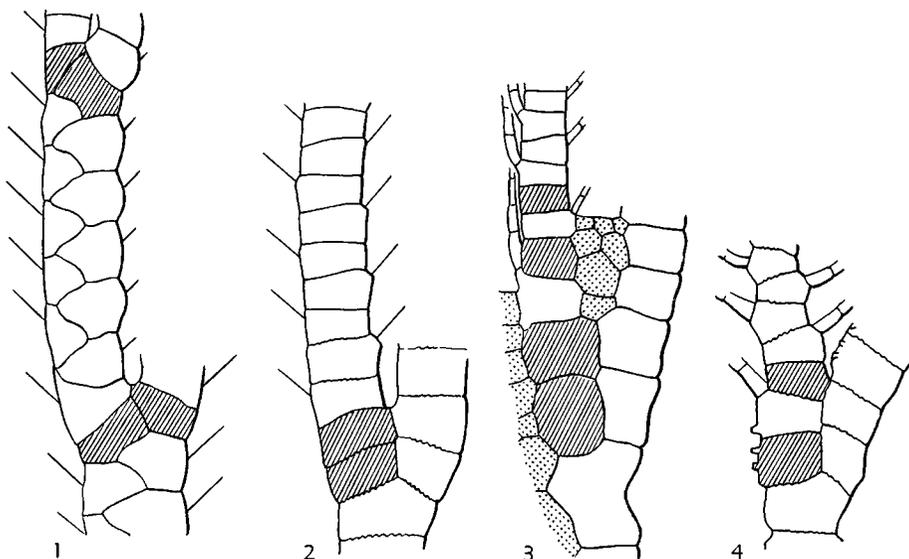


FIG. 125. Brachial units in camerates composed of two or three ossicles with the distal one alone provided with a pinnule (mod. from Ubaghs, 1958b). [Explanation: interbrachials stippled; single or double proximal ossicles without pinnule obliquely ruled. In fig. 1 and 2, places of pinnules indicated by short oblique lines.]—1. *Paramelocrinus angelini* UBAGHS, U.Sil., Gotl.,  $\times 10$ .—2,3. *Promelocrinus radiatus* (ANGELIN), U.Sil., Gotl.,  $\times 10$ .—4. *Ctenocrinus gottlandicus* (PANDER), U.Sil., Gotl.,  $\times 10$ .

Among camerates, pinnules are generally (if not invariably) lacking on these hypertrophied rami called arm trunks; they fail also to develop on the inner (adradial) rami of the melocrinitid *Promelocrinus*, and on the widened, flattened, paddle-shaped distal portion of the arms of *Eretmocrinus* and allied genera (Fig. 126). These examples show that defective pinnulation may affect various parts of the arms and are probably caused by different inhibiting factors.

The pinnules may be subcylindrical, laterally flattened, or prismatic, with cross sections respectively subcircular, elliptical, or U-shaped (rarely subtriangular). Their ornamentation, extremely diversified, consists of spines, nodes, longitudinal median keel, comblike structures, and other features. Generally, the two lateral faces of a pinnule are similar, so that the transverse section is symmetrical. But it may also be asymmetrical, particularly in species provided with strongly imbricating pinnules. In such cases, it may be useful in descriptions to recognize a lateral **abthecal** side directed away from the theca and an oppo-

site lateral **adthecal** side directed toward the theca.

The pinnules of some crinoids are set more or less wide apart, but usually, particularly in biserial arms, they are closely spaced. In some camerates, they are imbricate and provided with lateral and (or) aboral expansions or spines that overlap adjoining pinnules and served to compel these organs to move together (Fig. 127). Pinnules are generally inserted obliquely on the arms and directed upward and outward, but they may also be set at right angles to the arms and interfinger with pinnules of adjacent arms. In some fossil crinoids, as well as in some recent forms, they could be folded inward and laid back along the arms so that they formed a protecting covering over the soft brachial structures. The pinnules of each row of the Silurian camerate genus *Barrandocrinus*, characterized by pendent arms, were attached together, their pinnulars interlocking and building an outer, probably rigid, pavement around the crown; water was introduced into this almost entirely

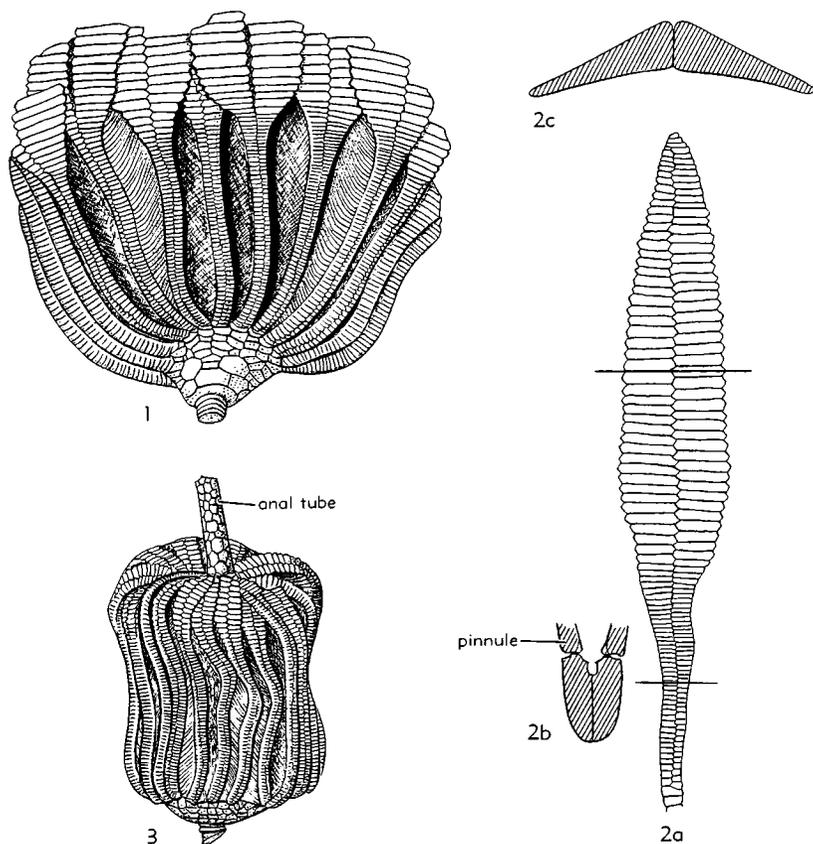


FIG. 126. Defective pinnulation in batocrinid camerates which have no pinnule on paddle-shaped distal portions of arms.—1,2. *Eretmocrinus remibrachiatus* (HALL), Miss., USA (Ia.); 1, complete crown in lat. view, with distal portion of arms folded inward,  $\times 0.67$  (Wachsmuth & Springer, 1897); 2a, aboral side of a fully extended arm; 2b,c, two cross sections (enlarged), showing occurrence of pinnules on proximal normal brachs but lack of them on distal widened ossicles,  $\times 0.67$  (Ubaghs, n).—3. *Dizygo-crinus cantonensis* WACHSMUTH & SPRINGER, Miss., USA (Ind.); complete crown with arms curving inward,  $\times 0.67$  (Wachsmuth & Springer, 1897).

closed system through tiny passageways between the distal portions (which remained free) of the pinnules, and expelled through a common aperture located at the apex of the crown (Fig. 128).

In recent crinoids, there are commonly very marked differences in the aspect of the pinnules of different parts of the arms. In comatulids especially, one or several proximal pinnules (oral pinnules) are modified and lack an ambulacral groove; they are followed by several pairs of genital pinnules that bear the gonads and have a rudimentary ambulacral groove, while the distal pinnules of the remaining part of each arm

serve mainly as food-catching organs. In most fossil crinoids, such diversification of the pinnules along the arms does not occur, and all the pinnules are fundamentally alike. In some species, however, the proximal pinnules differ somewhat from the others. This may result from their total or partial incorporation in the calyx, the fixed pinnulars (see above, p. T153) tending to approach the adjacent cup plates in appearance and probably in function, or from specific modification of the first pinnule of each ray, as illustrated by some species of the camerate genera *Carpocrinus* (Fig. 129, 1,2) and *Batocrinus* (Fig. 129,3). In at

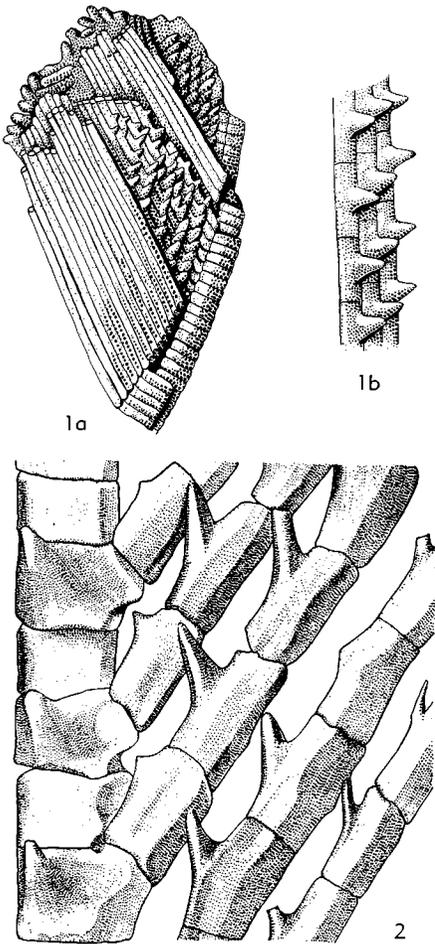


FIG. 127. Spines or hooks on pinnules.—*1a,b*, *Cactocrinus proboscidalis* (HALL), Miss., N.Am.; *1a*, portion of arms showing hooks on aboral face of pinnules,  $\times 3$ ; *1b*, aboral aspect of part of three adjoining pinnules greatly enl. (Wachsmuth & Springer, 1897).—*2*, *Ctenocrinus gottlandicus* (PANDER), U.Sil., Gotl.; portion of arms with spines on pinnules,  $\times 35$  (Ubaghs, 1958b).

least one species of the latter genus (*B. icosidactylus*), the two proximal ossicles of the first pinnule were considerably enlarged and served as a covering flap to the aperture through which the ambulacral groove and associated structures of the pinnule penetrated into the theca (Fig. 129,3). According to SPRINGER (1917), the huge tubular appendages of the rhodocrinitid camerate genus *Gilbertocrinus* (Fig. 129,4) repre-

sented enormously enlarged and modified proximal pinnules—an opinion not accepted unreservedly (VAN SANT, in VAN SANT & LANE, 1964). As to the existence of genital pinnules in fossil crinoids, no unquestionable indication of it has been discovered as yet. JAEKEL (1895) thought that the enlarged distal portion of the pinnules of the Devonian camerate *Acanthocrinus rex* lodged the gonads, but neither the shape, structure, nor position of the ossicles composing this region made them appropriate to serve such a function. The proximal pinnules of another Devonian camerate *Hapalocrinus elegans* may show an undivided, variously wide, lateral extension that has been regarded by JAEKEL (1895) as a gonad receptacle, but this interpretation was rejected by W. E. SCHMIDT (1934).

In any pinnule, the pinnulars are never exactly similar. Ordinarily, the proximal pinnular is shorter and wider than the succeeding ones, and its proximal face differentiated into an articulation that serves to move the whole pinnule. In some crinoids, particularly the recent ones, it is the two first pinnulars that are specialized in this way and accomplish this function. The next pinnulars generally do not differ from one another except in size and proportions along the pinnule, which usually tapers gradually from the base to the tip. Distal pinnulars may be similar to the preceding ones (Fig. 130) or, relative to fulfillment of some special function, very different and specialized. Such is the case of the distal pinnulars of the oral pinnules of the comasterids. These are provided with tooth-like projections that collectively form a terminal comb whose function is probably to aid fixation. Another example is furnished by various camerates (Fig. 131): their distal pinnulars are short, wide, and massive; they have a flattened or slightly rounded, sometimes spiniferous, aboral face and a strongly convex opposite side, which lacks a ventral groove; their transverse section is subtriangular, and they are perforated by an axial canal that ends blindly in the last segment. As a rule, the part of the pinnules that is composed of such differentiated pinnulars is flexed adorally in such a way that the two rows of pinnules of each arm coming into contact form a sort of

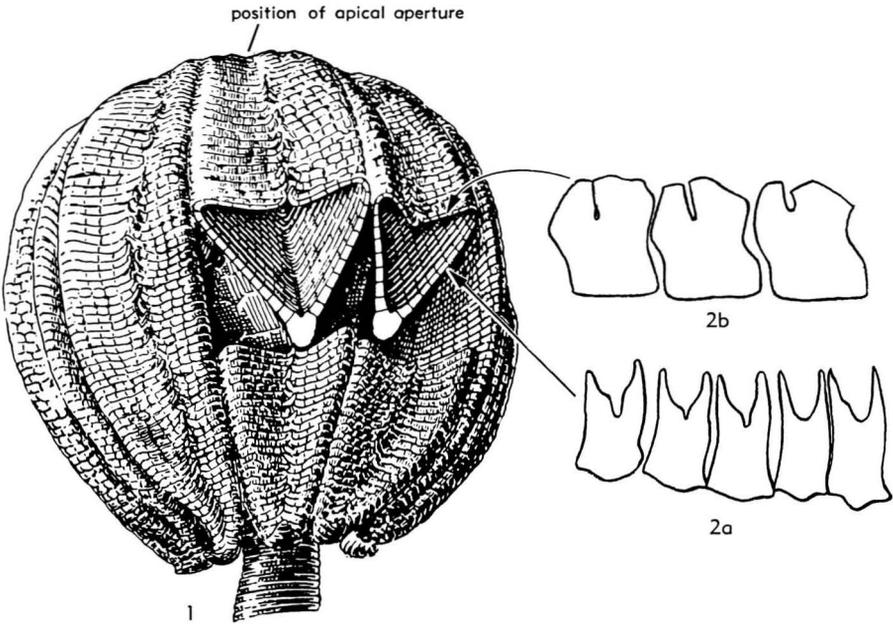


FIG. 128. *Barrandeocrinus sceptrum* ANGELIN, U.Sil., Gotl.—1. Reconstruction of crown in side view, with two arms and attached pinnules cut away,  $\times 2.25$  (MOORE, 1952a).—2. Sections across proximal (2a) and distal (2b) portion of adjoining pinnules,  $\times 20$  (UBAGHS, 1956).—3. Aboral aspect of outer pavement of crown showing interlocking, rigidly joined pinnulars and free distal ossicles,  $\times 14$  (UBAGHS, 1956).

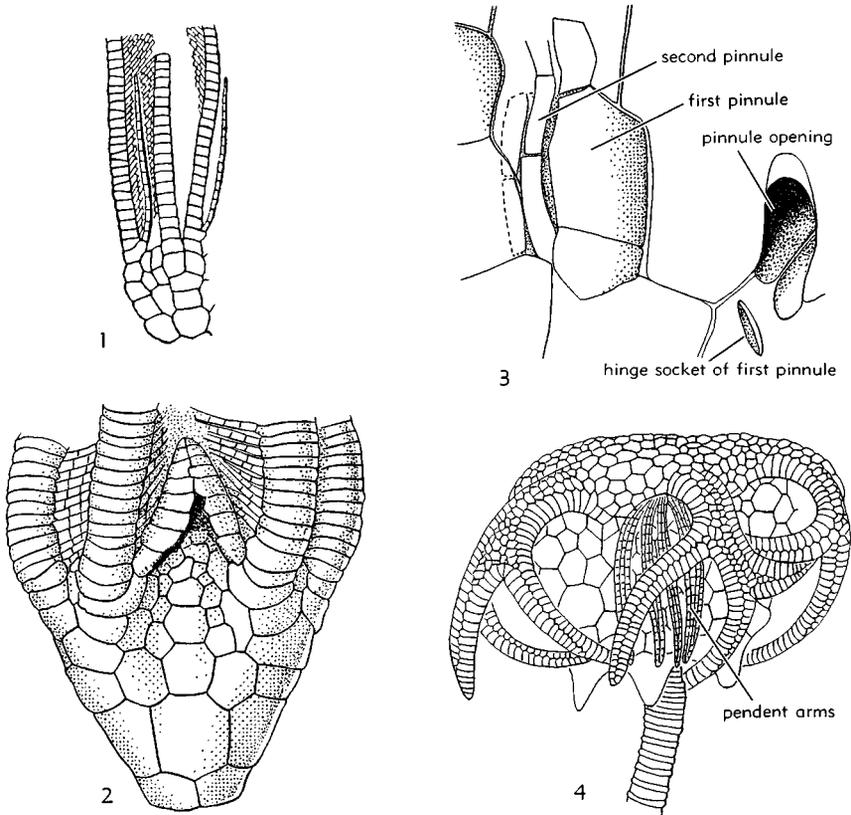


FIG. 129. Modified proximal pinnules in camerates.

1. *Carpocrinus simplex* (PHILLIPS), U.Sil., Eng.; large proximal pinnule (or atrophied ramus ?),  $\times 1.3$  (Bather, 1900a).
2. *Carpocrinus ornatus* (ANGELIN), U.Sil., Gotl.; Stockholm Mus. Ec. 11300, short and wide proximal pinnules on each side of CD interray,  $\times 3$  (Ubaghs, n).
3. *Batocrinus icosidactylus* CASSEDAY, Miss., USA (Ind.); two first pinnulars of first pinnule transformed into cover flap sealing pinnule aperture (shown at right side of figure),  $\times 15$  (Haugh, 1973).
4. *Gilbertocrinus tuberosus* (LYON & CASSEDAY), Miss., N.Am.; diagram. sketch of crown and proxistele, showing large, tubular appendages (? proximal pinnules),  $\times 0.8$  (Van Sant, in Van Sant & Lane, 1964).

roof, which presumably protected the soft structures of the brachial system.

The pinnules of crinoids are typically undivided. A few cases of division into smaller branches have been reported, however, but they are not sufficiently numerous to invalidate the rule. Small, apparently uncalcified, threads occur along the adoral grooves of the pinnules of the Lower Devonian camerate *Macarocrinus semelfurcatus* (W. E. SCHMIDT, 1934), but they probably represent preserved tentacles or podia and not branchlets. MOORE & LAUDON

(1943) have described, and called "pinnulets," long, articulated structures, seemingly attached on the pinnules (or ramules ?) of another camerate, the early Middle Ordovician rhodocrinitid *Trichotocrinus terranovicus*; they resemble cystoid brachioles, and apparently several of them arise from the adoral surface of each pinnular. Their exact nature and function are unknown.

In extant crinoids ambulacra are typically present on all of the pinnules, as well as on the arms. In some comatulids, however, they are absent on the oral pinnules and

rudimentary on the genital pinnules; they may also be lacking in some of the arms of several comasterid species (see section on recent crinoids, p. T43). In fossil crinoids, their presence may be inferred from the existence of a groove on the pinnulars. Most pinnulars have such a groove, and therefore probably carried ambulacral extensions from the main ambulacra of the arms. The only significant exception to this rule concerns the massive pinnulars forming the distal differentiated portion of the pinnules of many camerates (Fig. 131). As described above, these ossicles have no ventral groove, and apparently served a protective rather than a food-collecting function.

The pinnules of the recent crinoids have a constitution very similar to that of the arms. This fact, the way these organs develop, and the occasional replacement of a pinnule by an arm indicate that the pinnules of the extant crinoids and more generally of all articulates are morphologically equivalent to the arms, which in many respects they duplicate on a small scale. The evolutionary development of the pinnulate condition from the closely spaced armlet condition observed in advanced dendrocrinine inadunates (particularly in the Bothryocrinidae and Mastigocrinidae) leads to the same conclusion concerning the pinnules of most cladid inadunates. It is not certain, however, that the pinnules of all fossil crinoids have arisen through a similar process of progressive specialization of arm branching (see above, p. T153). For instance, the arms of the Silurian dendrocrinine genus *Cyliocrinus* are provided with appendages that outwardly resemble pinnules and probably had the function of pinnules, but which are given off from the middle of brachials and occur in pairs instead of alternately, as if they were articulate outgrowths from the brachials rather than the products of an arm division (Fig. 132). Very surprisingly, also, the camerates from their earliest appearance have pinnulate arms, whereas this feature, which never occurred in flexibles or in monocyclic inadunates (with the possible exception of the highly specialized disparid genus *Chiropinna*), was acquired by cladid inadunates only at a late phylogenetical stage. One may therefore question whether all crinoid appendages designated as pinnules

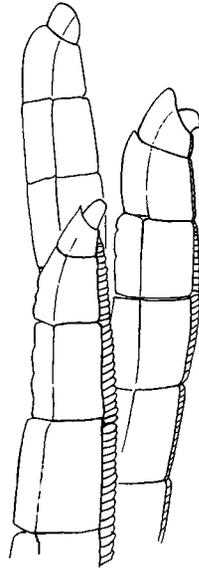


FIG. 130. *Carpodocrinus ornatus* (ANGELIN), U.Sil., Gotl.; Stockholm Museum Ec. 11265, distal ends of three pinnules,  $\times 20$  (Ubaghs, n).

have the same origin and morphological significance.

### ADORAL GROOVE

As seen above, the inner or adoral face of the brachials and pinnulars typically carries a furrow that in life contains extensions of the ambulacral grooves (food grooves), coelom, and nervous, water-vascular, and (at least in recent crinoids) reproductive systems. This furrow (often erroneously called ambulacral groove) is here termed **adoral groove**. It is variously deep and wide, V- or U-shaped in transverse section. Ordinarily it preserves no trace of the soft structures it housed, though, in some fossils, a special groove on its floor or an underlying axial canal perforating the plates indicate the former presence of an entoneural nerve cord (Fig. 107, p. T137). In some camerates, the arm ossicles have two ridges, one along each side of the adoral groove; these ridges have been interpreted as indicating the former location of the hyponeur system (HAUGH, 1937). In the floor of the groove of some inadunates pits disposed at regular intervals may be observed. Thus, between successive

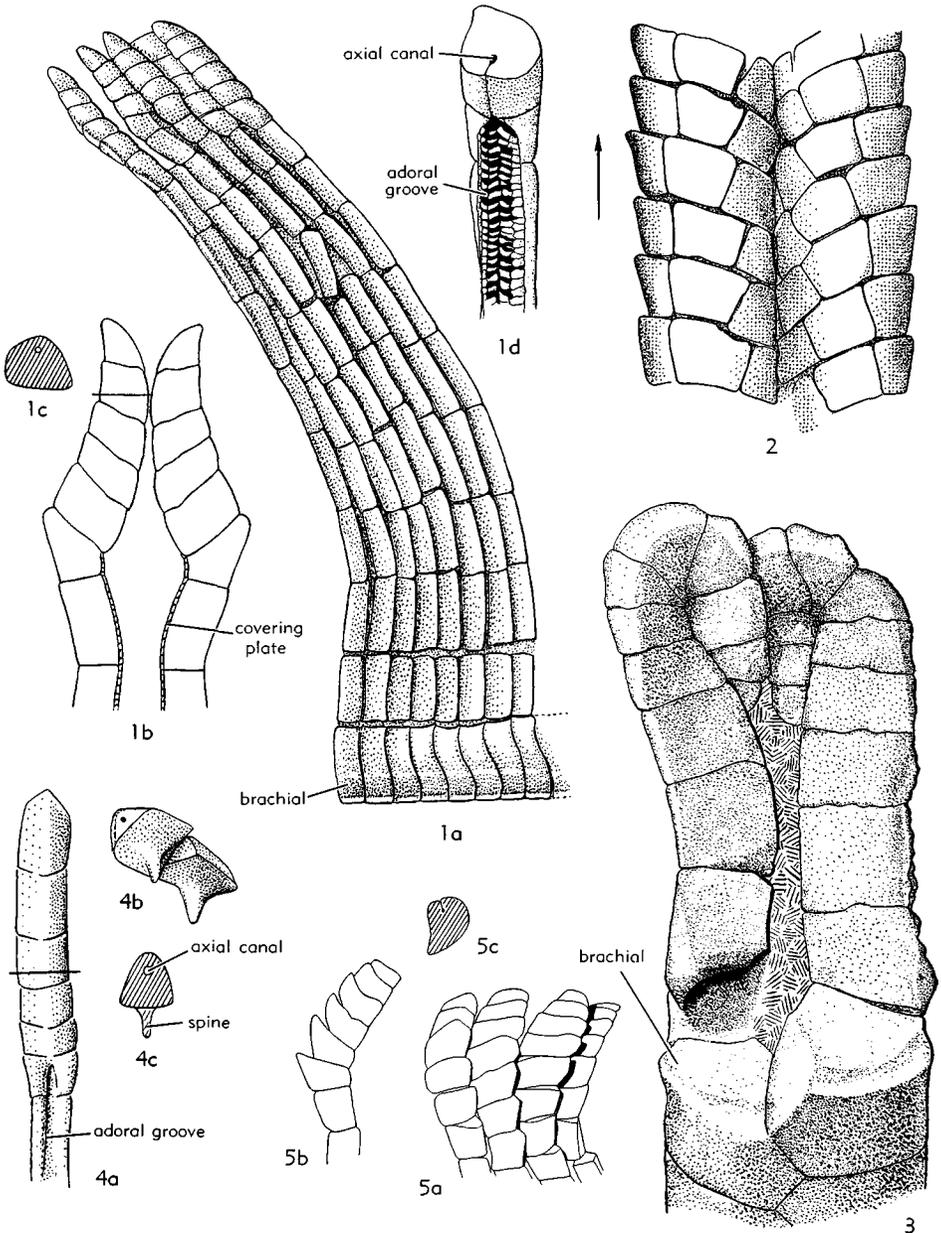


FIG. 131. Modified distal pinnulars in camerates.

1. *Clonocrinus* sp., U.Sil., Gotl.; Stockholm Museum Ec. 6156; 1a, part of arm with complete pinnules, aboral side,  $\times 10$ ; 1b, lat. aspect of distal portions of two pinnules in adoral contact, with section (1c) of distal pinnular,  $\times 20$ ; 1d, distal end of adoral groove at base of modified distal portion of a pinnule,  $\times 25$  (Ubaghs, n).
2. *Abacocrinus* sp., U.Sil., Gotl.; Stockholm Mus. Ec. 6153, aboral aspect of modified distal pinnulars folded inward so as to protect soft structures; arrow indicates distal direction,  $\times 20$  (Ubaghs, n).
3. *Abacocrinus tasseracontadactylus* (GOLDFUSS), U. Sil., Gotl.; Stockholm Museum Ec. 10855, im-

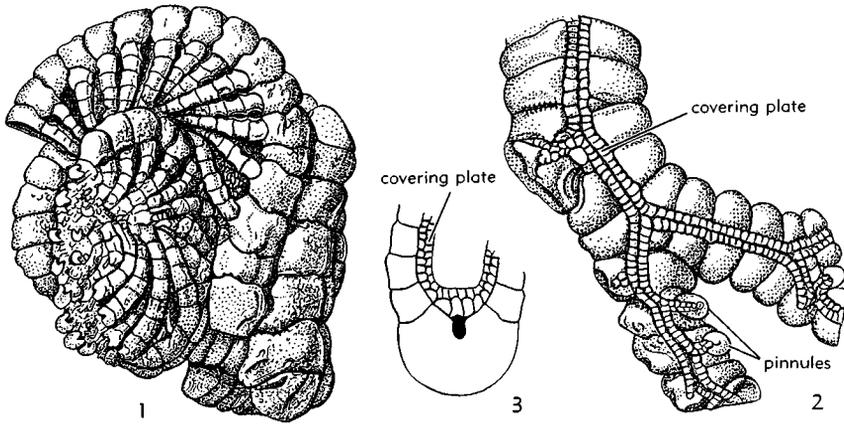


FIG. 132. *Cyliocrinus scolopendra* (BATHER), U.Sil., Gotl. (redrawn from Bather, 1893a).—1. Lat. view of arm,  $\times 3$ .—2. Adoral aspect of part of arm, in which only the bases of the pinnules are preserved,  $\times 3$ .—3. Transverse section of a brachial with two pinnules,  $\times 3$ .

brachials of the crotalocrinitid *Pernerocrinus discus*, three canals link the groove with the axial canal (Fig. 133). In several poteriocrininine inadunates with biserial arms (e.g., *Cromyocrinus simplex*, *Erisocrinus* sp., *Proallosocrinus glenisteri*) pits occur at the level of each suture between the two series of brachials; they end blindly at some distance from the bottom of the adoral groove and do not appear to connect with any canal (see Fig. 138, p. T167). The exact function of these pits is unknown, but they probably served as passageways for nutrient fluids and aboral nerve branches.

### BRACHIAL AND PINNULAR ARTICULATIONS

The mode of union between crinoid plates has been systematically treated by various authors (CARPENTER, 1884a; BATHER, 1900a; MINCKERT, 1905a; REICHENSPERGER, 1912; A. H. CLARK, 1915a; SPRINGER, 1920; GISLÉN, 1924; VAN SANT in VAN SANT and LANE, 1964). We have already described the articulation uniting the columnals (p. T74) and those connecting the calycinal plates, in-

cluding the fixed brachials (p. T130). Following this will be considered only the arm-bearing articular facets, the articulations between free brachials, the articulations for attachment of pinnules on brachials (pinnule socket or facet), and the articulation between free pinnulars.

These articulations, as any others in crinoids, fall into one of two categories, the muscular articulations and the ligamentary articulations. In the first type, the connection between ossicles is effected by a combination of ligament and muscle fibers. In the second one, ligaments alone intervene in union of skeletal pieces.

The ligamentary and muscular tissues are clearly distinct histologically, but not so much physiologically. The muscles, it is well known, have active contracting power. Ligaments, on the other hand, which are primarily composed of collagenous fibers, are reputed to have no contractile power, but elastic properties; they serve to bind the plates together, to oppose the action of the muscles and to provide cirri, arms, and pinnules with the stiffening required for maintaining the crinoid in position and

(Continued from facing page.)

- mature brachials and pinnules, distal portions strongly folded,  $\times 30$  (Ubaghs, n).  
4. *Acanthocrinus* sp., L.Dev., Belg.; 4a, adoral side of distal portion of a pinnule; 4b, two modified distal pinnulars; 4c, cross section of

- distal pinnular,  $\times 16$  (mod. from Ubaghs, 1947).  
5. *Polypeltes granulatus* ANGELIN, U.Sil., Gotl.; 5a-c, aboral, lat., and cross section of distal pinnulars,  $\times 14.5$  (Ubaghs, 1956).

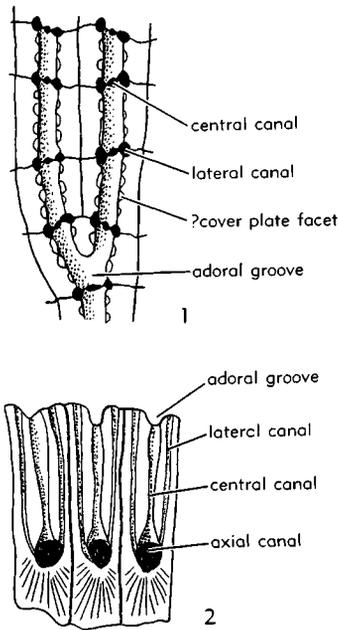


FIG. 133. *Pernerocrinus discus* BATES, L.Dev., AUS. (Bates, 1972).—1. Portion of adoral surface of adjacent arms, showing sutural pits in adoral grooves,  $\times 6$ .—2. Articula of three contiguous brachials,  $\times 6$ .

feeding in moving waters (MEYER, 1971). It appears, however, that some parts of the body, such as the stalk and the cirri, which have so-called ligamentary articulations only, may also accomplish generally slow but active movements, as if the ligaments, activated by the nervous system, had some contractile power, too. [For a review on this subject, see BROWER, 1973, p. 286-287.]

The microstructure of the crinoid endoskeleton reflects the type of the tissues that are bending the ossicles. The meshwork of the stereom in the ligament fields is markedly coarse and galleried, allowing deep penetration of the ligament fibers into the skeleton. In sharp contrast, the sites of muscle attachment are fine meshed, for the muscle fibers do not extend into the stereom. Thus, the stereomic microstructure furnishes a reliable criterion for the paleobiological interpretation of the articulations in fossil crinoids (MACURDA & MEYER, 1975; LANE & MACURDA, 1975).

### MUSCULAR ARTICULATIONS

The surface of a typical muscular articulation bears a more or less straight ridge (**transverse ridge**) and five depressions or fossae (Fig. 134). The transverse ridge is a prominent, generally sharp-crested elevation that extends from near one outer lateral edge to the other. It may be marked by minute teeth, or denticles, normal to its axis. Slightly adorally to the middle of the transverse ridge, on a raised calcareous platform and on a level with it, is located the axial canal through which passes the axial cord of the aboral nervous system. The transverse ridge acts as a fulcrum upon which the motion of the articulation is accommodated. For this reason, it may also be called the **fulcral ridge**.

On the aboral (outer) side of the transverse ridge lies a single narrowly semicircular depression serving for attachment of ligament fibers. It is termed the **dorsal or aboral ligament fossa**. It usually contains a (generally) well-marked excavation (**ligament pit**) that adjoins the midportion of the transverse ridge. The dorsal ligament probably serves to counteract the muscles on the opposite side of the transverse ridge and, therefore, serves as extensor of the arms and pinnules, to which, as described above, it may also provide rigidity over more or less long periods.

On the adoral (inner) side of the transverse ridge, lies a pair of more or less triangular depressions (**interarticular ligament fossae**), one on either side of the axial canal. These fossae lodge ligaments of uncertain function. According to authors, they may serve merely to connect adjacent arm segments (CARPENTER, 1866), or to serve as antagonists of the muscles (BOSSHARD, 1900; VAN SANT in LANE and VAN SANT, 1964), or to oppose the dorsal ligament (GISLÉN, 1924). These fossae are bounded adorally by strong, oblique ridges that separate them from the two **muscular fossae**, in which are inserted the paired flexor muscles of the arms and pinnules. Between the muscular fossae runs a narrow ridge or a groove (**intermuscular ridge or groove**) from the platform about the axial canal to the inner (adoral), generally concave, margin of the facet.

Muscular articulations are of two types.

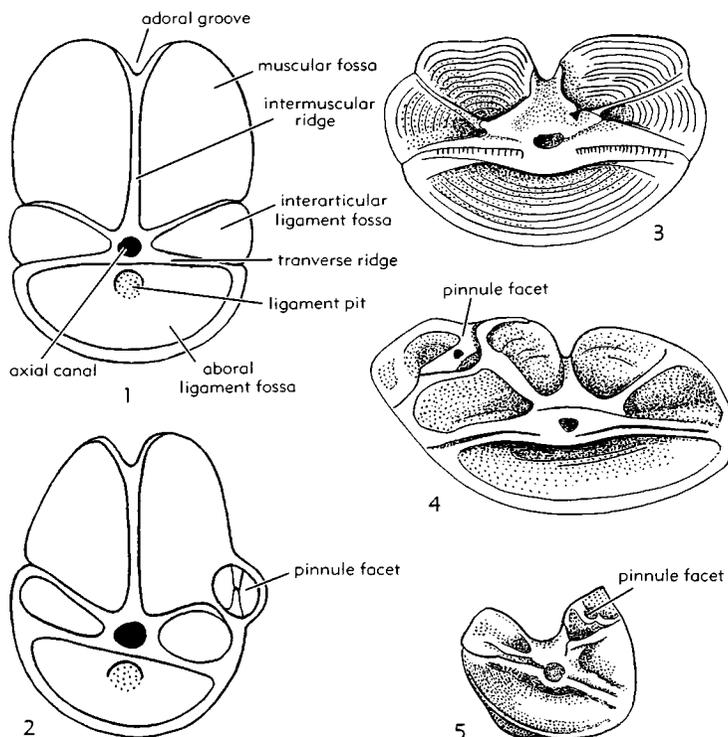


FIG. 134. Muscular articulations.—1. Diagram sketch of a straight muscular articulation (Clark, 1915a).—2. Diagrammatic sketch of an oblique muscular articulation (Clark, 1915).—3-5. *Marsupites testudinarius* (SCHLOTHEIM), U.Cret., Eu.; 3, radial facet; 4, second secundibrach; 5, 25th secundibrach, all  $\times 6$  (redrawn from Sieverts, 1927).

In one type, known as the **straight muscular articulation**, the transverse ridge is perpendicular to the adoral-aboral axis of the facet, the right and left halves of which are alike and symmetrical (Fig. 134,1,3,4). The plane of such a facet is normal to the longitudinal axis of the arm, and its edge, viewed from the outer (aboral) or inner (adoral) side of the ossicle, cuts the arm transversely.

In the second type, termed **oblique muscular articulation**, the transverse ridge and the adoral-aboral axis meet at an angle so that the two parts of the facet on either side of the intermuscular ridge or groove are unequally developed (Fig. 134,2,5). In that case, the plane of the facet, and its edges in outer (aboral) and inner (adoral) views are more or less oblique to the longitudinal axis of the arm. The slope of succeeding

articulations is alternately to the right and to the left, so that each brachial, as seen from its aboral or adoral sides, offers a high lateral side and a low lateral side. Usually (but not invariably; see reversion in chapter on recent crinoids, p. T37), the socket for attachment of the pinnule is located on the high lateral side.

In arms provided with muscular articulations, the distal face of axillary brachials bears two muscular articulations separated by a projecting median ridge. The apposed sides of these articulations, which are usually intermediate between straight and oblique muscular articulations, are more or less reduced.

Typical muscular articulations such as those just described, are well developed between radials and primibrachs and between most brachials of recent and fossil articu-

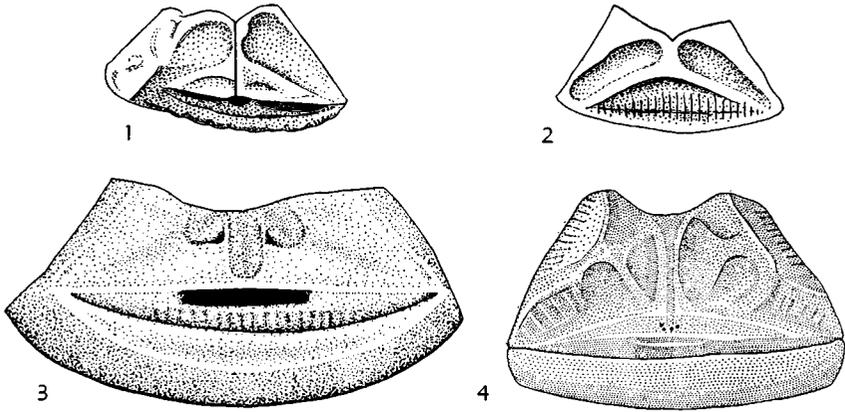


FIG. 135. Muscular articular radial facet of various inadunates.—1. *Synbathocrinus texasensis* MOORE & EWERS, Miss., USA (Texas); a disparid inadunate,  $\times 10$  (Moore & Ewers, 1942).—2. *Parapisocrinus ollula* (ANGELIN), U.Sil., Eu., N.Am.; a disparid inadunate,  $\times 6$  (Bather, 1893a).—3. *Goleocrinus mangeri* BURDICK & STRIMPLE, Miss., USA (Ark.), a poteriocrinine cladid inadunate,  $\times 10$  (Burdick & Strimple, 1973b).—4. *Graphiocrinus timoricus* WANNER, Perm., Timor; a poteriocrinine cladid inadunate,  $\times 6$  (Van Sant, in Van Sant & Lane, 1964).

lates. They are also present, but slightly modified, between the brachials and first pinnulars and between the two first pinnulars of these crinoids. In the remaining portion of their pinnules, the articulations are generally characterized by the presence of a small adoral muscular fossa and a large aboral ligamentary depression on each side of a median fulcral ridge running in an adoral-aboral direction.

Muscular articulations seem to have evolved independently in several groups and between different parts of the crinoid body. We have seen above (p. T132) that in Calceocrinidae the basals and the radials were probably connected during life by ligaments and muscles (Fig. 104, p. T134). The radial facets of disparid inadunates like *Allagecrinus*, *Pisocrinus*, and *Synbathocrinus* have a straight transverse ridge or a sharp-crested angulation separating a single, rather small, ligamentary depression on the outer (aboral) side from a much larger inner part composed of a pair of flat or gently concave symmetrical (?) muscular areas (Fig. 135, 1, 2). It is, however, within the Poteriocrinina that the muscular articulation appears to have more generally evolved during late Paleozoic times. In many Pennsylvanian and Permian representatives of these advanced inadunates, the

radial and, but perhaps in a lesser degree, the brachial facets show a prominent, generally sharp-crested denticulate transverse ridge and three large depressions, an outer (aboral) ligament area (commonly with a distinct ligament pit), and two inner (adoral) large fields separated by a narrow groove (intermuscular furrow) normal to the transverse ridge and leading into a V-shaped indentation (intermuscular notch) of the inner edge of the facet (Fig. 135, 3, 4). To these basic elements are usually added small ridges, furrows and pits, but interarticular ligament fossae are rarely clearly defined. It seems highly probable that in that sort of articulation muscles, which could flex the arms inward, occupied at least a part of the inner (adoral) fields, while extensor aboral ligaments served to pull them outward.

The socket serving for attachment of pinnules on brachials in most pinnulate Paleozoic crinoids seems also to represent an antagonistic system of articulation. Although our knowledge of such a small and delicate articulum is very limited, it appears that, in spite of a certain amount of diversity, its basic structure remains approximately the same. In both camerates and inadunates, it consists of two or three unequal fossae separated by a ridge or an

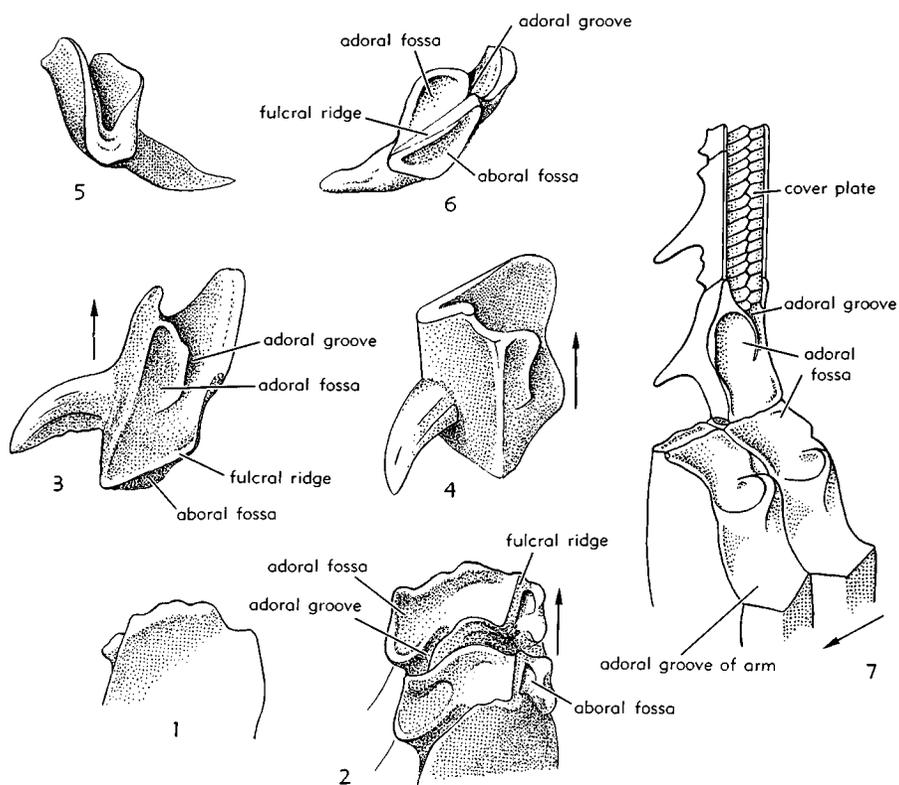


FIG. 136. Pinnule facet and first pinnular of an actinocrinitid camerate, *Actinocrinites* sp., L.Carb., Belg.; all figures  $\times 20$  (Ubaghs, n). [Explanation: arrows indicate distal direction.]—1,2. Pinnule facet in 1) proximal lateral view, 2) oblique adoral aspect.—3-6. First pinnular seen from 3) adoral face, 4) ext. lat. face, 5) distal face, 6) proximal face.—7. Diagram. reconstr. of adoral aspect of two brachials with proximal part of a pinnule.

elongated swelling, which manifestly acted as a fulcrum (Fig. 136-138). On the outer (aboral) side of the latter, there is usually one (in some cases two) shallow ligamentary fossa, provided in many inadunates with a distinct ligament pit. On the other side of the fulcrum, there is generally a large and deep, probably muscular fossae that ordinarily slopes rather strongly toward the oral groove of the arm. In the inner (adoral) edge of the pinnule facet, a notch prolonged downward by a straight or contorted furrow may occur, indicating the position of the proximal end of the ambulacral tract of the pinnule. All these features find their counterparts on the most proximal pinnular (Fig. 136, 137). In this ossicle, the depression corresponding to the

outer fossa of the pinnule socket is located on the proximal face, whereas the concavity corresponding to the inner fossa covers a more or less large part of the adoral side; as to the edge that separates these two faces, it rested against, and had the same function as the fulcral ridge of the pinnule facet.

#### LIGAMENTARY ARTICULATIONS

Ligamentary articulations (called non-muscular articulations by some authors) occur in brachia of both living and fossil crinoids. In Paleozoic forms they are the commonest mode of union between radials and arms, and between arm plates. Some of them allow a certain amount of differential movement between apposed joint faces. They are termed **movable ligamen-**

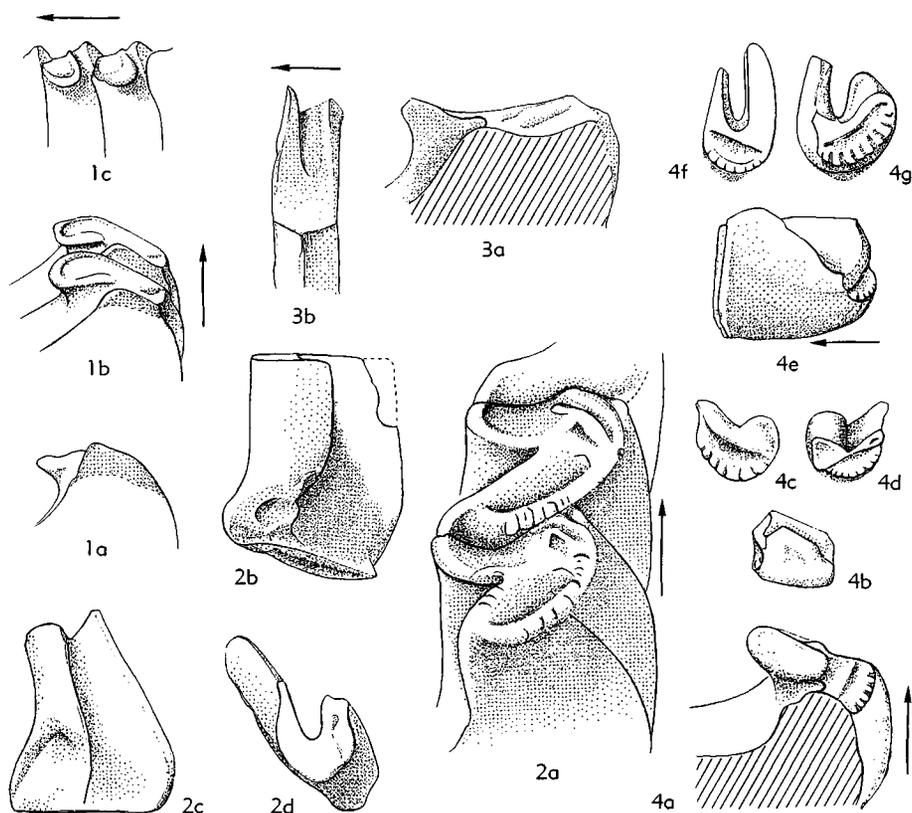


FIG. 137. Pinnule facet and first pinnular in various camerates (Ubaghs, n). [Explanation: arrows indicate distal direction.]

- Abacocrinus tesseracontadactylus* (GOLDFUSS), U.Sil., Gotl.; 1a, pinnule facet seen from proximal side; 1b, in oblique adoral view; 1c, from inner side facing ventral groove of arm,  $\times 20$ .
- Platycrinites* sp., L.Carb., Belg.; 2a, pinnule facets in oblique adoral view; 2b-d, first pinnular showing int. lat. face, adoral face, and distal face,  $\times 20$ .
- Eucalyptocrinites* sp., U.Sil., Gotl.; pinnule facet showing (3a) proximal side, and (3b) inner side facing ventral groove of arm,  $\times 20$ .
- Scyphocrinites* sp., U.Sil., N.Afr.; 4a, pinnule facet in oblique adoral view; 4b-d, first pinnular showing int. lat., distal, and proximal faces; 4e-g, second pinnular showing int. lat., distal, and proximal faces,  $\times 20$ .

tary articulations. Others, that permit only very slight movement or none at all, are said to be **immovable**.

#### MOVABLE LIGAMENTARY ARTICULATIONS

Several kinds of such articulations are known, between which many intermediates

exist, so that it is not always easy to determine the type of articulation.

*Trifascial Articulations*.—The ligamentary articulation nearest the muscular one, to which it may have been antecedent is termed **trifascial**. It is characterized by the occurrence on each apposed joint face of

FIG. 138. Pinnule facets of some inadunates (arrows indicate distal direction).

- ?*Pentaramicrinus* cf. sp. *bimagnaramus* BURDICK & STRIMPLE, Miss., USA (Ill.); 1a, adoral view of part of arm,  $\times 6$ ; 1b, sketch of two pinnule facets,  $\times 10$  (Ubaghs, n).
- Erisocrinus typus* MEEK & WORTHEN, Penn., N.Am.; sketch of a pinnule facet,  $\times 10$  (Ubaghs, n).
- Erisocrinus* sp., U.Penn., USA (Kans.); 3a, adoral

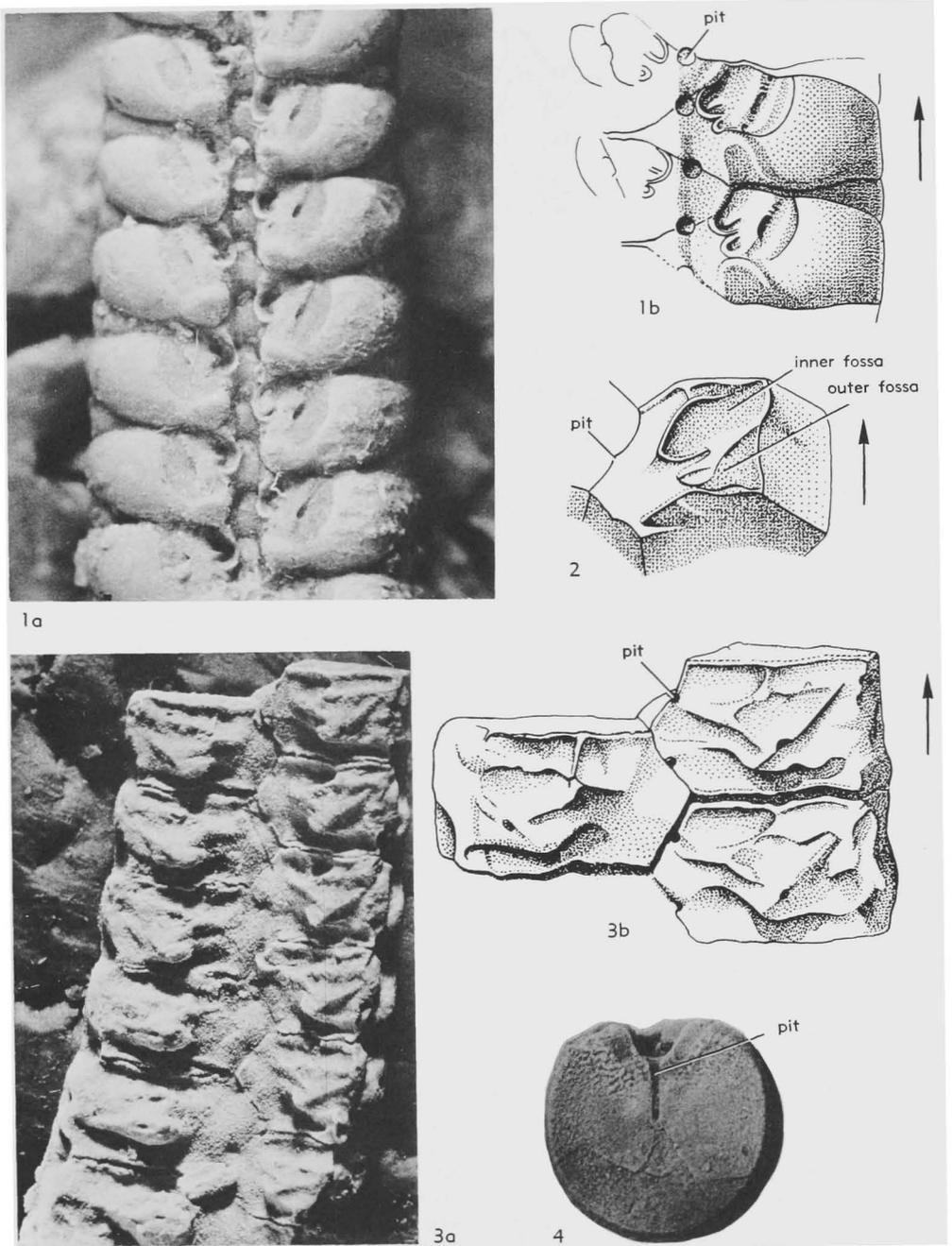


FIG. 138. (Explanation continued from facing page.)  
 view of part of arm,  $\times 6$ ; 3b, sketch of three pinnule facets,  $\times 10$  (Ubaghs, n).  
 4. *Proallosocrinus glenisteri* MOORE & STRIMPLE, L.Penn., USA (Okla.); articular surface of secundibrach with sutural pit,  $\times 4.5$  (Moore & Strimple, 1973).

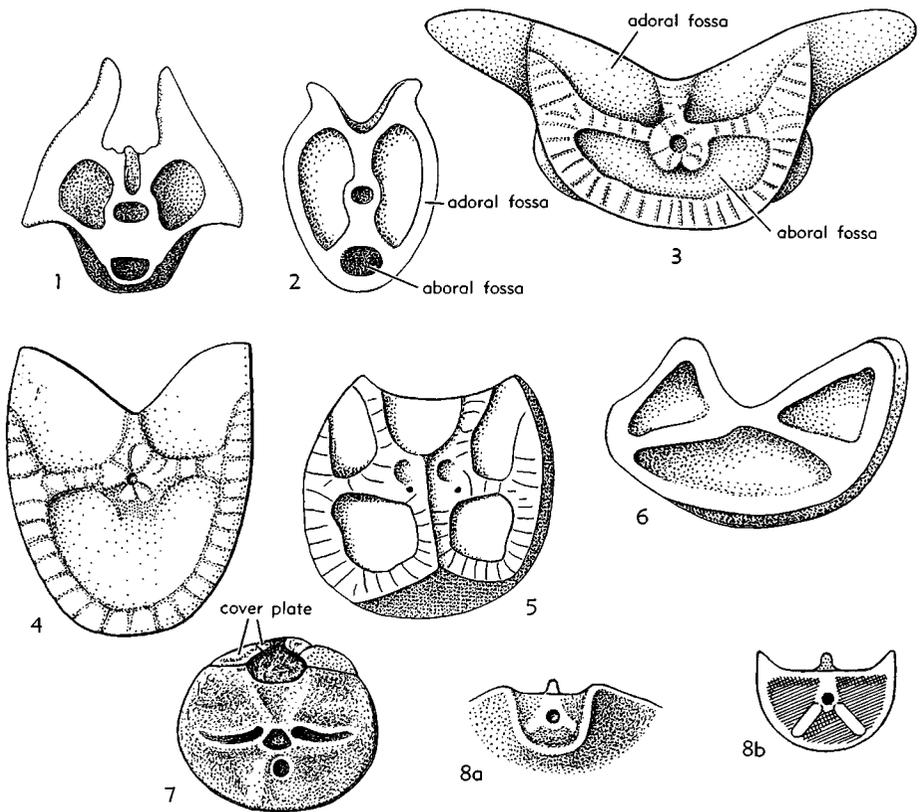


FIG. 139. Trifascial articulations.

1. *Bathyrinus australis* CLARK, recent, Ind.O.; proximal face of fifth brachial,  $\times 20$  (Carpenter, 1884a).
2. *Bathyrinus aldrichianus* THOMSON, recent, Atl.; proximal part of a brachial,  $\times 33$  (Carpenter, 1884a).
- 3-5. *Paradichocrinus polydactylus* (CASSEDAY & LYON), Miss., USA (Ind.); radial, first secondary brachial and primaxial distal facets,  $\times 6$  (Van Sant, in Van Sant & Lane, 1964).
6. *Pellecrinus hexadactylus* (LYON & CASSEDAY), Miss., USA (Ind.); distal facet of a radial,  $\times 4$  (Van Sant, in Van Sant & Lane, 1964).
7. *Botryocrinus ramosissimus* ANGELIN, U.Sil., Gotl.; proximal facet of an axillary,  $\times 4$  (Bather, 1892b).
- 8a,b. *Petalocrinus visbyensis* BATHER, U.Sil., Gotl.; 8a, arm facet,  $\times 4$ ; 8b, diagram of same (Bather, 1898a).

three depressions for attachment of ligaments. These depressions are a single median outer (aboral) fossa, which corresponds to the outer fossa of a muscular articulation, and two inner (adoral) fossae. They are separated by more or less well-defined elevations, which do not act as a fulcrum, but allow distinct though moderate mobility in two directions. The median outer fossa may consist of a small and rather deep depression, as shown by some recent crinoids (Fig. 139,1,2), but, in

Paleozoic genera, it is usually larger and shallower, and may have distinct markings, like crenulae and even a median ligament pit. Such articulations occur in some advanced camerates (Fig. 139,3-5) and in some flexibles (e.g., *Lecanocrinidae*) between radial and brachial plates or between certain brachials. It is probably among Devonian and Mississippian cyathocrinid and dendrocrinitid inadunates (Fig. 139,6-8) that they were commonest, however, though precise and systematic information on that

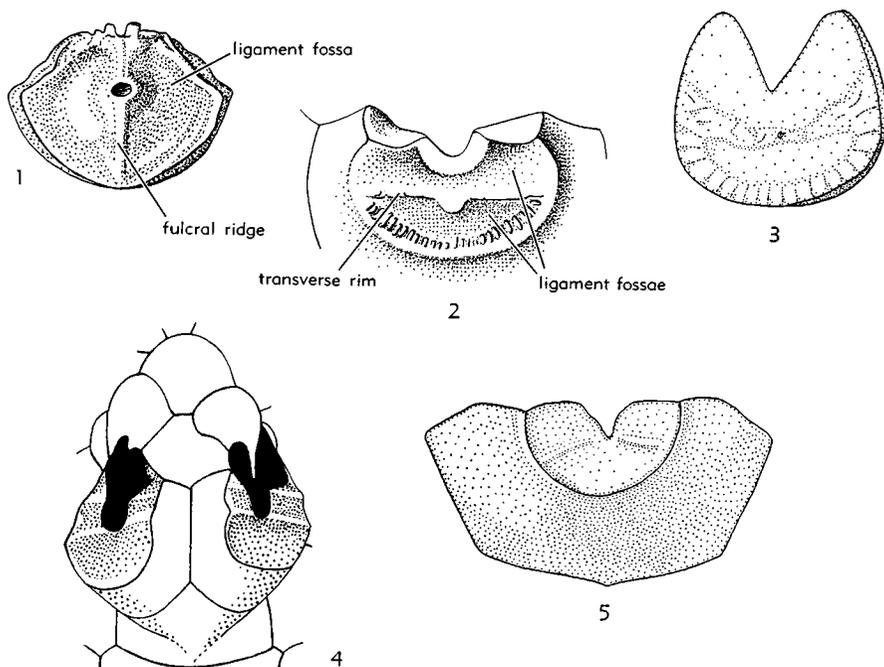


FIG. 140. Bifascial articulations.—1. *Himerometra bassleri* GISLÉN, Eoc., USA (S.Car.); first primibrach,  $\times 6$  (Gislén, 1934).—2. *Platycrinites austinianus* DE KONINCK & LE HON, L.Carb., Belg.; arm facet,  $\times 5$  (Ubaghs, n; unnumbered specimen from collection of Univ. Liège).—3. *Platycrinites hemisphericus* (MEEK & WORTHEN), Miss., USA (Ind.); distal facet of third tertibrach,  $\times 13.3$  (Van Sant in Van Sant & Lane, 1964).—4. *Aacocrinus nododorsatus* BOWSHER, Miss., USA (Mo.); arm facet on first secondibrach,  $\times 1.5$  (Bowsheer, 1955b).—5. *Barycrinus hoveyi* (HALL), Miss., USA (Ind.); radial facet,  $\times 4$  (Van Sant in Van Sant & Lane, 1964).

matter are badly lacking. Besides, it is usually difficult, judging from the shape of depressions and the importance of ridges, to determine the exact nature of the tissues uniting the opposed joint faces in such articulations. For instance, the radial facets of such disparids as *Allagecrinus*, *Pisocrinus*, or *Synbathocrinus* might be classified almost as well as ligamentary trifascial articulations as muscular articulations.

**Bifascial Articulations (Synarthry).**—A synarthry or bifascial articulation is a ligamentary junction in which each apposed joint face bears two fossae separated by a fulcral or articular ridge. In typical brachial synarthry, the two fossae are equal and deep and the ridge is strong and medially located, running in an aboral-adoral direction (Fig. 140, 1). Articulations of this sort occur between some brachials of living and

fossil articulates. They are similar to those found between the cirrals and between the columnals of such crinoids as the *Platycrinidae* of the *Bathycrinidae* (see p. T77), and they allow differential movements in two directions normal to the median ridge.

A synarthry that is modified by a general flattening of the joint faces, together with a reduction in size of the ligament fossae and in distinctiveness of the median ridge, is known as a **cryptosynarthry** (hidden synarthry). Such articulation is found between certain brachials of some post-Paleozoic crinoids. It allows a very small amount of differential movement between opposed ossicles and approaches synostosis (see below). It is practically an immovable articulation.

Articulations more or less similar, at least functionally, to synarthries have evolved

independently in many Paleozoic crinoids between brachials or between arm-bearing thecal plates and free arms. Such facets commonly have two unequal shallow fossae, with or without crenulated margin, and a more or less distinct transverse elevation that allowed slight motion in an aboral-adoral direction (Fig. 140,2-5). The elevation, which may extend from one lateral side to the other, or be shorter, or be reduced to two symmetrical knobs, and which may be straight or incurved, smooth or denticulate, resembles a transverse rim rather than a typical fulcral ridge.

A modified articulation of this type occurs in brachials of many flexibles that possess distinctly arcuate transverse sutures (Fig. 141). In these crinoids the proximal margin of the aboral portion of each ossicle bends downward and forms a rounded process or lip that fits into a corresponding socket in the distal aboral margin of the ossicle next below. Both lip and socket have crenulated marginal contact surfaces, which restricted lateral movement of the plates when the structures were fitted together. Between their apposed faces there is a space, which during life was filled by

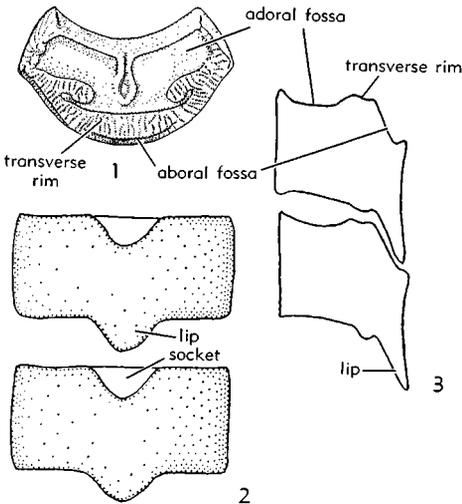


FIG. 141. *Forbesiocrinus nobilis* DE KONINCK & LE HON, L.Carb., Belg. (Springer, 1920).—1. Distal facet of second primibrach,  $\times 2.8$ .—2,3. Diagrammatic representation of a pair of brachials, from aboral side and in long, median section.

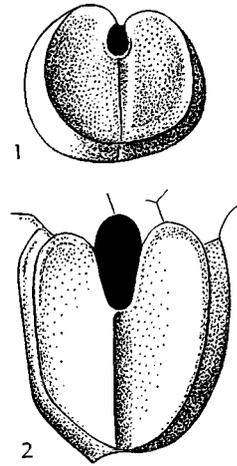


FIG. 142. Compound arm facet (pseudosynarthry) (Ubaghs, n).—1. *Allopsallocrinus conicus* CASSEDAY & LYON, Miss., N.Am.;  $\times 4$ .—2. *Agariocrinus inflatus* (HALL), Miss., N.Am.;  $\times 4$ .

the aboral ligament. The remaining and main part of the articulation is occupied by a single ligament fossa or by paired adoral fossae, separated from the aboral fossa by a transverse crenulated rim. Such articulations could only permit limited folding of the arms inward, but considerably restricted their extension outward. The projecting processes are thin and commonly fractured along their upper margin, so that they take the appearance of separate plates, called "patelloid plates" by HALL (1858). SPRINGER (1920) was the first to recognize their true nature. This type of structure is unknown in other crinoids; however, a few inadunates and camerates, as well as some recent pentacrinids, have similar arcuate sutures (but not necessarily similar articulations) in some parts of their arms.

Different in origin and nature from the above described articulations, though still somewhat synarthrial in function, are the so-called compound facets occurring between fixed and free brachials in some camerates provided with biserial arms (Fig. 142). Each one consists of two slightly concave surfaces borne by two adjacent ossicles, and, as these two surfaces are not on the same level, the lateral admedian edge of the highest one could probably act in some way as a rudimentary fulcrum, allowing

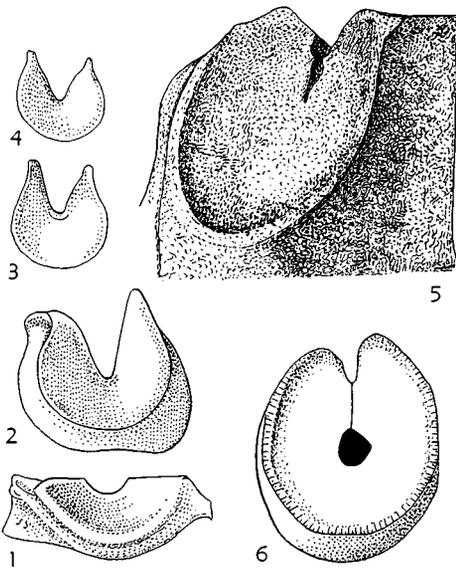


FIG. 143. Synostosomal articulations.—1-4. *Aethocrinus moorei* UBAGHS, L.Ord., France; distal facets of second fixed primibrach, of a free primibrach, and of two secundibrachs,  $\times 10$  (Ubahgs, 1969).—5. *Thetidocrinus piriformis* WANNER, Perm., Timor; a radial facet in oblique view,  $\times 3$  (Wanner, 1937).—6. *Baryocrinus hoveyi* (HALL), Miss., USA (Ind.); distal facet of third primibrach,  $\times 3$  (Van Sant in Van Sant & Lane, 1964).

restricted movements in a lateral direction. Such synarthrial type of articulations, which allowed movements in two directions as in true synarthry, but in which there is no distinct median ridge, has been named **pseudosynarthry** (false synarthry) by VAN SANT (in VAN SANT & LANE, 1964).

**Synostosomal Articulations.**—A **synostosis** is a ligamentary junction in which the apposed joint faces are more or less concave. The surfaces of the facets are smooth or barely rugose and may be surrounded by a low, crenulated rim (Fig. 143). Articulations of this type allow a slight flexibility in all directions. They are common in the distal portions of the arms in many recent and fossil crinoids. They may also occur between all the brachials, as in the early dendrocrinid *Aethocrinus* (Fig. 143,1,4) or the recent *Calamocrinus* and *Ptilocrinus*. The term **synostosis** has been used with different meanings. It is here considered

as synonym of “loose synostosis” of authors, particularly GISLÉN (1924).

#### IMMOVABLE ARTICULATIONS

Many crinoid ossicles are united in such a manner that no differential movements or only very slight ones occur between them. Such articulations have been commonly referred to as “close sutures.” The following types may be distinguished.

**Zygosynostosis.**—In the sort of union termed **zygosynostosis** the apposed joint faces are nearly flat and closely fitted together by short ligament fibers (Fig. 144). They commonly have moderate amounts of calcareous deposits on their faces. They may be smooth or have supplementary structures that strengthen the union of the ossicles, such as radial crenulae in a part of the apposed facets, or irregular vermiculation; there may also be a faint ridge on one facet that fits into a corresponding groove on the opposed facet (Fig. 144,1,3). This type of union between arm plates is certainly the most common among Paleozoic crinoids. It allows very slight differential movements between joined ossicles. However, even in such cases, a limited flexibility of the arms could be achieved merely by multiplication of the ossicles. Commonly, in biserial arms, one may count 20 or 25 transverse sutures per cm. on each side. This number reaches 60 to 70 in some species of *Desmidocrinus*, and this probably is a maximum. The mode of preservation of certain specimens of this genus suggests, indeed, that their arms were remarkably flexible.

**Symplexy.**—A **symplexy** is an articulation in which culmina and crenellae of apposed joint faces interlock, so that the corresponding suture is crenulate (Fig. 145, 1-3). This type of joint is very common in the stem of crinoids, particularly Paleozoic forms. It may also occur in the arms of camerates and between thecal plates. The extremely slight mobility of each articulation may only be partially compensated in arms and stems by reduction in length of the component ossicles and consequent multiplication of the joints. An ill-defined symplectical articulation is known as a **cryptosymplexy**.

**Syzygy.**—A **syzygy** is an articulation in

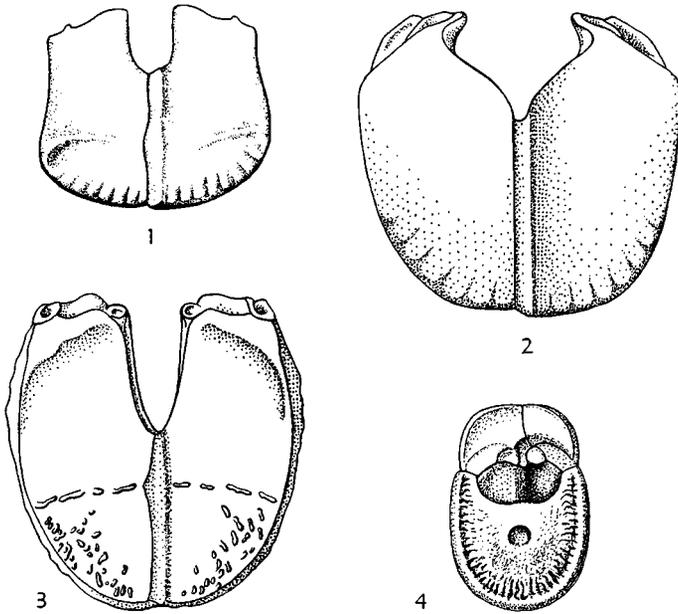


FIG. 144. Zygostostial articulations.—1. *Clonocrinus polydactylus* (McCoy), M.Sil.-U.Sil., Eng., Gotl.; articular facet of two biserial brachials,  $\times 20$  (Ubaghs, n).—2. *Abacocrinus* sp., U.Sil., Gotl.; articular facet of two biserial brachials,  $\times 20$  (Ubaghs, n).—3. *Actinocrinites* sp., L.Carb., Belg.; articular facet of two biserial brachials,  $\times 20$  (Ubaghs, n).—4. *Cyathocrinites acinotubus* (ANGELIN), M.Sil., Eng.; articular facet of a brachial, with covering plates in position,  $\times 10$  (Bather, 1892d).

which the joint faces are flat and covered with radiating ridges and furrows, but instead of interlocking as in symplexies, the ridges of one articulum meet the ridges of the other articulum and the furrows are opposite the furrows (Fig. 145,4,5). Connective tissue fills the furrows. Externally a syzygy is usually readily recognizable; it appears as a fine dotted line that crosses the arm at a right angle to the longitudinal axis. Two brachials united by syzygy form a syzygial pair. In such a pair the proximal ossicle is called **hypozygal**, the distal one **epizygal**. The latter alone bears a pinnule, the former never. It is clear from all this that a syzygy is a very specialized type of ligamentary articulation that occurs only in the arms (never in the stem) of the Articulata, where it represents a preformed place for autotomy (a function performed in some cases by zygostostial articulations). The existence of true syzygies in Paleozoic crinoids is extremely questionable. In most cases what is called syzygy

in these crinoids is synostosis or symplexy or another type of ligamentary articulation. Moreover, the term has been used with several meanings, sometimes serving to designate the articulation, sometimes the pair of ossicles united by syzygy, or even all the brachials located between two succeeding syzygies. But, as stressed by BATHER (1896a), the term "syzygy" must invariably be used in accordance with its original definition by MÜLLER (1843), as a particular type of ligamentary articulation. Articulations of syzygial type, but with very short ridges that may be replaced by rows of tubercles or granules, with tendency toward irregular arrangement and disappearance, are distinguished as **cryptosyzygies**. They occur in the arms of Articulata (e.g., some Isocrinidae) and certainly permit but a very low capacity for movement.

**Symmorphy.**—The term **symmorphy** designates a ligamentary junction in which one or two prominent ridges or toothlike elevations on one face fit into corresponding

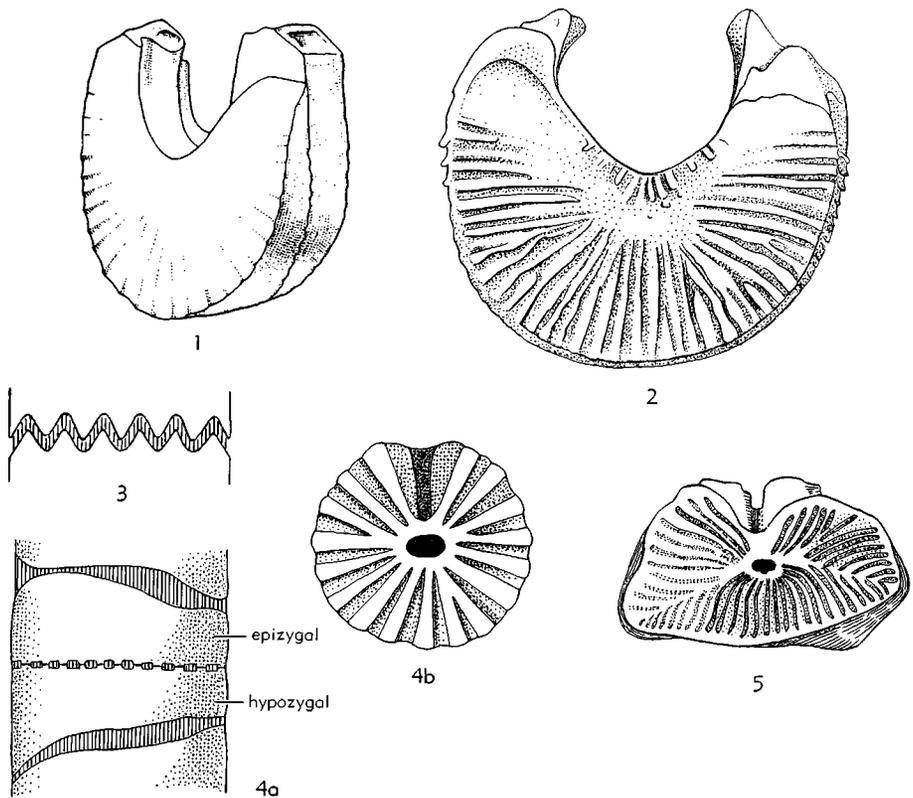


FIG. 145. Symplectial and syzygial articulations compared.

1. *Diamenocrinus stellatus* JAEKEL, L.Dev., W.Eu.; symplectial articulation,  $\times 18$  (Ubahgs, 1947).
2. *Scyphocrinites* sp., U.Sil., N.Afr.; symplectial articulation,  $\times 20$  (Ubahgs, n).
3. Diagrammatic representation of two brachials united by symplectial articulation (Ubahgs, n).
- 4a,b. Diagrammatic representation of (4a) two brachials united by syzygy, and (4b) a syzygial articulation (Minckert, 1905a).
5. *Marsupites testudinarius* (SCHLOTHEIM), U.Cret., Eu.; syzygial articulation,  $\times 6$  (redrawn from Sieverts, 1927).

grooves or sockets on the opposed faces accompanied in some cases by peripheral crenulae (Fig. 146,1,2). With such articulations only very slight differential movement of joined ossicles in two directions seems possible. Symmorphial articulations occur in some recent (e.g., *Neocrinus*, *Hypalocrinus*) and fossil articulates. The presence of similar types of joints in Paleozoic crinoids has also been recorded in a few cases, and even between pinnulars (Fig. 146,3,4).

*Ankylosis*.—An *ankylosis* (also spelled *anchylosis*) is an immovable union of ossicles cemented by a deposit of stereom on

their apposed joint faces. It is commonly accompanied by a partial or complete obliteration of the sutures (Fig. 124, p. T152). Lateral fusion of the arms in some inadunates (e.g., *Crotalocrinus*, *Petalocrinus*) and the formation of hyperpinnulated brachials through fusion of ossicles are well-known examples of this type of union. Ankylosis may also occur between certain brachials normally in some species, or as the result of an adaptive development in other ones. For instance, the support of pendent arms in some camerate species was furnished by fusion of proximal free brachials.

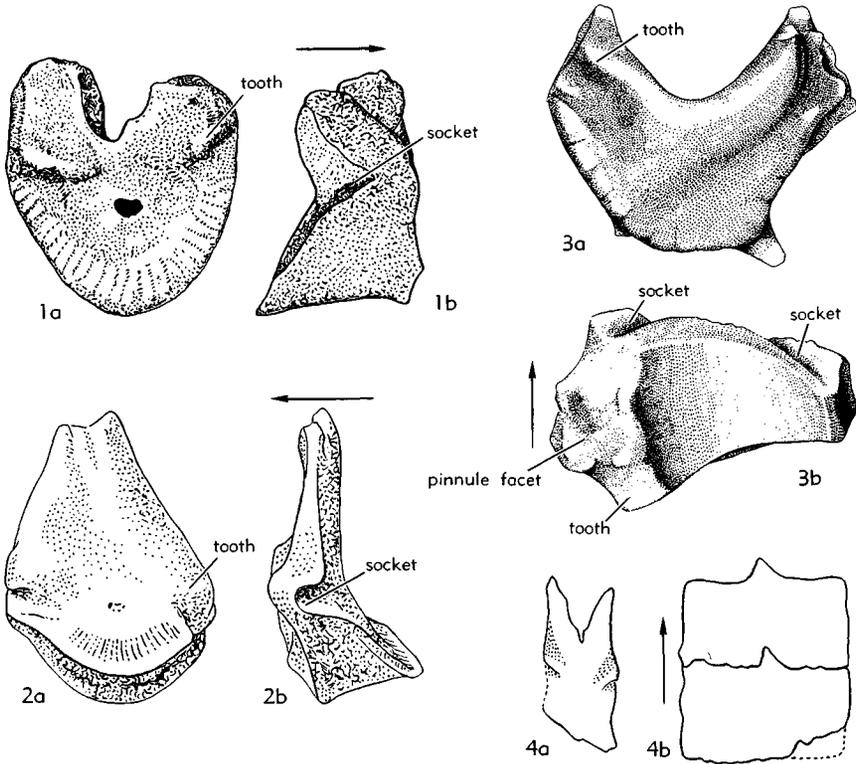


FIG. 146. Symmorphial articulation (arrows indicate distal direction).

1. *Cainocrinus tintinnabulum* FORBES, Eoc., Eng.; 1a,b, distal facet and lat. side of second tertiobranch,  $\times 6$  (Rasmussen, 1972a).
2. *Isocrinus cingulatus* (MÜNSTER), Jur., Eu.; 2a,b, distal facet and lateral side of third secundibranch,  $\times 10$  (Hess, 1972b).
3. *Ctenocrinus gottlandicus* (PANDER), U.Sil., Gotl.;

3a,b, proximal and adoral view of a ramule ossicle,  $\times 70$  (Ubaghs, 1958b).

4. *Barrandeocrinus sceptrum* ANGELIN, U.Sil., Gotl.; 4a,b, distal facet of a pinnular and lat. side of two adjoining pinnulars,  $\times 35$  (Ubaghs, 1956).

## ADORAL SKELETON

The **adoral skeleton**, also called **perisomic skeleton**, includes every skeletal element that may be present in the teguments that 1) surround or cover the mouth, 2) support the ambulacral tracts, and extend along the adoral side of the free arms from their bases to the tips of their smallest branches and pinnules, and 3) in some crinoids pass down the fixed parts of the rays and their divisions, and cover the interbranchial areas of the calyx. The central part of these teguments extending over the visceral mass and forming the roof of the thecal cavity is dis-

tinguished as the **tegmen** (also called "disc" or "vault").

The adoral skeleton consists of plates, ossicles, or spicules of various sizes and shapes. Almost completely lacking in some crinoids, it is fairly well developed in others, forming a thick protective covering over the viscera, and in some cases over the adoral groove of the free brachials. As a rule, it is rather less definite and characteristic than the aboral skeleton. It may even vary in different parts of the same individual. Morphologically it includes the in-

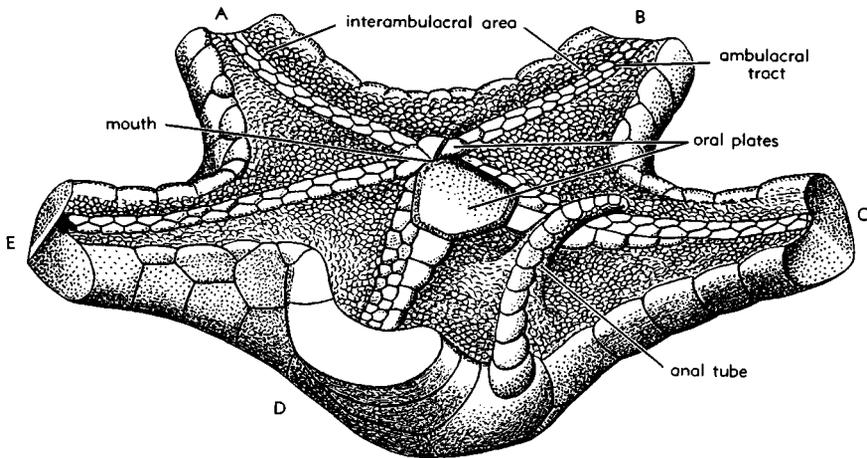


FIG. 147. *Onychocrinus ulrichi* MILLER & GURLEY, Miss., USA (Ind.); reconstr. of calyx, tegmen, and proximal part of arms of a flexible crinoid, oblique adoral view, enl. (Springer, 1920). [Explanation: A, B, C, D, E, letter symbols designate rays according to CARPENTER system.]

terbrachials, but as these plates in the crinoids where they are best developed (Camerata, Flexibilia) occupy areas that under normal conditions are on the aboral side of the body, they have been treated along with elements belonging to the aboral skeleton (see p. T120).

## TEGMEN

### GENERAL FEATURES

The tegmen is the adoral portion of the theca. It differs markedly from the aboral portion or cup (calyx), a feature that is most distinctive of the crinoids.

The shape and relative size of the tegmen are quite diversified. This structure may be low, medium, or high; flat, gently rounded, strongly convex, conical, flask- or mushroom-shaped, or have other form. Its surface, generally simple and regular, may comprise ridges that run from near the center to the arm bases. In a few inadunates (e.g., *Tenagocrinus*) and some camerates (e.g., *Paragazacrinus*, *Methabocrinus*, *Eucalyptocrinites*), outgrowths of some of its plates form vertical partitions that produce alcoves for reception and protection of free arms. On the tegmen of many crinoids stands a variously developed conical to cylindrical structure (anal tube, pyramid,

or cone) that bears the anal opening; in some cladid inadunates this structure acquires an enormous size and forms the so-called "ventral sac" (anal sac). The tegmental plates are smooth or ornamented with pustules, granules, vermiculations, nodes, spines, and so forth.

A typical tegmen is divided into five interambulacral areas by five narrow ambulacral tracts (Fig. 147). The ambulacral tracts radiate from the edges of the central mouth and pass over the tegmen to the bases of the free arms. They are bisected by the radii, and then correspond to the rays of the crinoid. The interambulacral areas correspond to the interrays and they are bisected by the interradii. As the rays may bifurcate within the cup or calyx, so the ambulacral tracts entering the tegmen and prolonging the food grooves of the arms over its surface may divide into as many branches as free arms (and pinnules, if such organs are incorporated in the calyx).

In most crinoids, the main orifices of the body are located on the adoral surface of the body, and this is another characteristic feature of these echinoderms. The mouth is found at the point of convergence of the ambulacral tracts. It is ordinarily central or subcentral, but it may be secondarily dis-

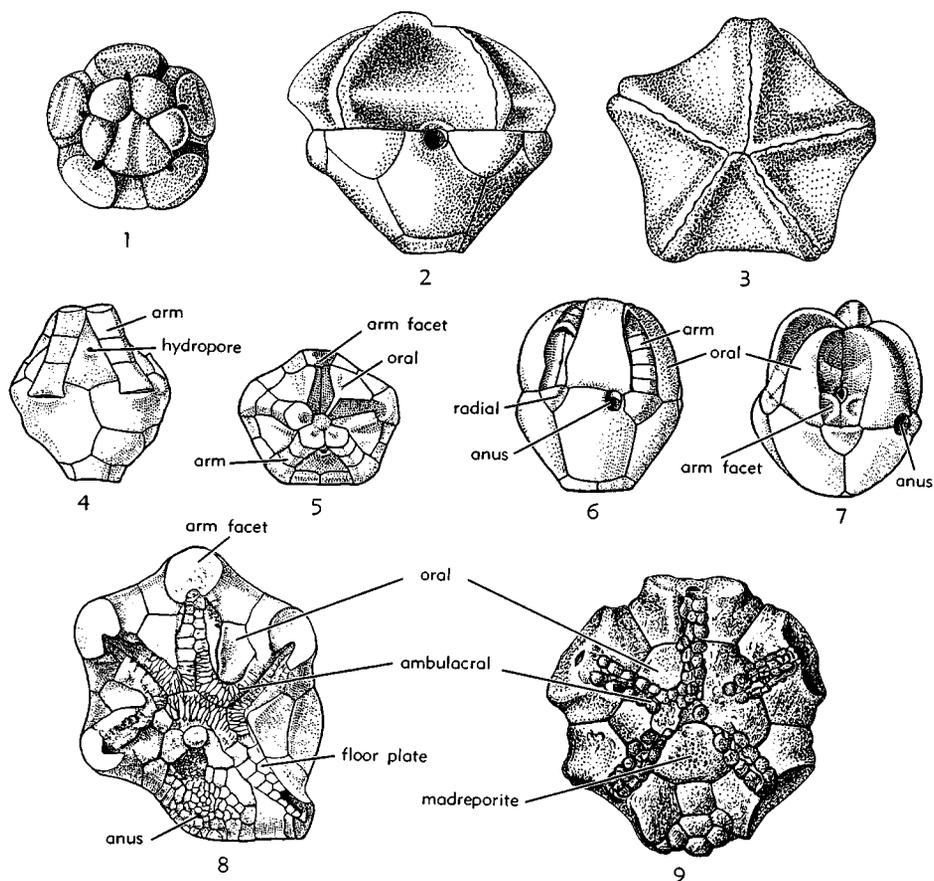


FIG. 148. Tegmens with orals only (1-7), or with orals and ambulacrals (8-9).

1. *Neodichocrinus nanus* WANNER (compsocrinine camerate), Perm., Timor; adoral view,  $\times 5$  (Wanner, 1937).
- 2,3. *Cranocrinus timoricus* WANNER (cyathocrinine inadunate), Perm., Timor; CD-interray and adoral views,  $\times 8$  (Wanner, 1929b).
- 4,5. *Haplocrinites mespiliiformis* (GOLDFUSS) (disparid inadunate), M.Dev., Ger.; CD-interray and adoral views of a specimen with part of 3 arms fitting closely in grooves on apposed edges of orals,  $\times 5$  (Springer, 1926a).
- 6,7. *Tenagocrinus sulcatus* WANNER (cyathocrinine inadunate), Perm., Timor; arms forming niches for reception of arms; 6, CD-interray; 7, oblique adoral view, arms not preserved,  $\times 5$  (Wanner, 1929b).
8. *Hybocrinus conicus* BILLINGS (hybocrinid inadunate), M.Ord., N.Am.; adoral view,  $\times 1$  (Springer, 1911b).
9. *Gissocrinus incurvatus* (ANGELIN) (cyathocrinine inadunate), Sil., Gotl.; adoral view,  $\times 4$  (Bather, 1893a).

placed toward the margin. In a large number of Paleozoic crinoids, it was not exposed on the surface, but it opened beneath the tegmen, so that in order to reach the mouth the food grooves had to be lowered (at least in part) beneath the surface—a position known as **subtegminal**. The anus opens in one of the interambulacral areas designated for that reason as posterior, the opposite ray being anterior. According to

CARPENTER'S nomenclature, this ray is termed *A* ray, and the posterior interray, *CD* interray. Like the mouth, the anus may be secondarily displaced and come to occupy a central or even anterior position. In many forms, it is located on a conical protuberance (anal pyramid, tube, or sac), which may be of considerable height and acquire an extraordinary development. With the mouth and anus, one or several

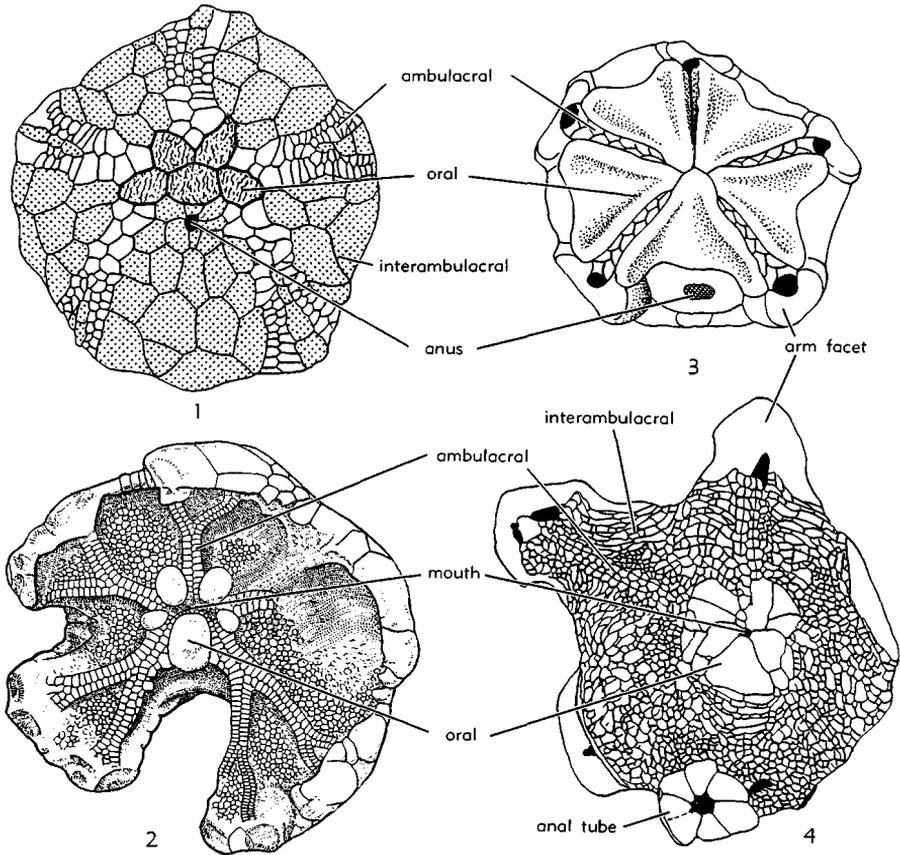


FIG. 149. Tegmens with orals, ambulacrals, and interambulacrals (1,2,4), or with orals and ambulacrals only (3).

1. *Marsupiocrinus striatus* WACHSMUTH & SPRINGER (glyptocrinid camerate), M.Sil., USA (Tenn.);  $\times 1.5$  (Wachsmuth & Springer, 1897).
2. *Taxocrinus intermedius* WACHSMUTH & SPRINGER (flexible), Miss., USA (Iowa);  $\times 1.5$  (Springer, 1920).
3. *Cantharocrinus simplex* BREIMER (glyptocrinid camerate), M.Dev., Spain; ambulacrals lacking in *A* radius,  $\times 4$  (mod. from Breimer, 1962).
4. *Ceratocrinus gracilis* WANNER (cladid inadunate), Perm., Timor;  $\times 3$  (Wanner, 1937).

hydropores may also occur on the tegmen. In extant crinoids these orifices are usually many and scattered over the five interambulacral areas, but in Paleozoic forms, where they exist, they are located in the *CD* interray, between the mouth (or its presumed position, if it is subtegminal) and the anus. A tegminal plate on which the hydropores are concentrated is called **madreporite**.

The tegmen may be formed by a soft integument that contains no skeletal elements except microscopic ones, or may be

supported by closely fitted or loosely imbedded plates. Three different types of plates may enter its composition: the **orals**, which form a central, pentamerous circlet around or above the mouth; the **ambulacrals**, that protect the ambulacral tracts and their branches (if any); and the **interambulacrals**, which are located between the ambulacral tracts and their branches.

### ORALS

The orals (also called deltoids) belong to the primary skeleton. They consist of five

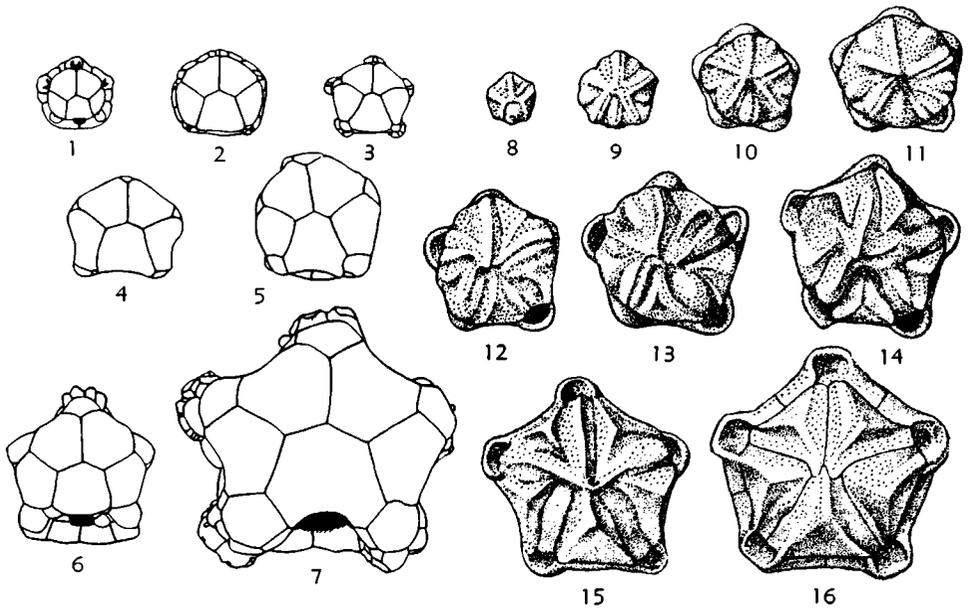


FIG. 150. Growth series of oral plates in a platycrinid (1-7) and a hapalocrinid camerate (8-16).—1-7. *Neoplaticrinus dilatatus* WANNER, Perm., Timor;  $\times 1$  (Wanner, 1937).—8-16. *Cyttarocrinus eriensis* (HALL), M.Dev., USA(N.Y.);  $\times 15$  (Koenig, 1965).

plates interradially disposed, which in the larvae of comatulids develop at the same time as the basals and long before the radials, but are wholly resorbed before maturity in most species. Five triangular plates that cover the mouth and the proximal parts of the ambulacral tracts in some recent crinoids (e.g., *Holopus*, *Cyathidium*, *Hyocrinus*, *Rhizocrinus*) are judged to be homologous with the larval orals of comatulids.

Plates similar in appearance and position to orals, and for that reason also called orals, occur in the tegmen of many fossil crinoids, including articulates, inadunates, flexibles, and camerates. They may rest on the radials and form the whole tegmen (Fig. 148, 1-7), but generally they are associated with ambulacrals (Fig. 148, 8,9) or with ambulacrals and interambulacrals (Fig. 149), or with an undifferentiated pavement of tegminal plates (see Fig. 151,7). In some streblocrinid inadunates, which have no arms and generally no radial plates, the orals have been shifted to a radial position in advanced genera.

The plates called orals in fossil crinoids

are extremely variable in size; they may be very small or remarkably conspicuous. They may carry nodes or even spines, and in some cases appear quite modified. Thus, in Devonian *Cupressocrinites* and *Rhopalocrinus*, they form an annular structure (the so-called "consolidating apparatus") that served at least in part for the attachment of brachial muscles. In the Permian *Tenagocrinus* they had the same function, and also formed niches for the reception of arms (Fig. 148,6,7). They may meet centrally (Fig. 148,1,3), or be disposed around a central space (peristome) that in life remained open and contained the mouth (as in some *Flexibilia*) (Fig. 149,2) or was covered by ambulacrals (see below) (Fig. 148,8,9). They may be laterally in contact or separated by furrows. As to the ambulacral tracts, they passed under the orals (Fig. 149,1) or between them (Fig. 149,2), or they occupied grooves on their apposed edges (Fig. 149,3).

Oral plates of fossil crinoids are equal or unequal in size. When they are unequal, the posterior (CD) one is the largest. Not infrequently, this large posterior plate oc-

cupies a central position between the four others (Fig. 148,1), or, as in many inadunates, it is pierced by a single pore or by many pores (madreporite) (Fig. 148,9)—a feature suggesting that it performed the same basic function as the perforated orals of the extant *Holopus*, *Cyathidium*, or *Hyocrinus*.

The homology of the oral plates of fossil crinoids with those of recent ones is indicated by 1) their resemblance to these plates in shape, number, position, and orientation; 2) the relatively common occurrence of a pore or pores in the posterior one; 3) their location over the mouth or in the five angles of the mouth opening; 4) the location of the anus between the posterior one and the adjacent *C* and *D* rays; 5) the discovery of a growth series showing that these plates were already present in the earliest known stages, as if, like the orals of the larval comatulids, they were among the first plates to be developed in ontogeny (Fig. 150); 6) the chronological sequence of genera or species in some lineages, suggesting that early members had more conspicuous orals than later ones.

### AMBULACRALS

The portions of the ambulacra that enter the tegmen generally do not have any skeletal floor, unless they rest over the apposed edges of the orals. In *Hyocrinus conicus*, however, a double row of large, alternating **floor plates** lies at the bottom of the groove formed by the lateral extensions of the orals—a quite exceptional feature (Fig. 148,8). On the other hand, covering plates or **ambulacral**s are ordinarily present; they protect the food grooves over the surface of the tegmen (Fig. 147; 148,8; 149; 151). They are suturally connected with the orals (if present) and (or) with the plates that occupy the interambulacral areas (i.e., interambulacral)s, where such plates occur. In their simplest form, they are disposed in a single row on either side of each ambulacral tract, meeting medially along a zigzag line resulting from their alternating arrangement (Fig. 149,1-3). To the ambulacral)s may be added side plates or **adambulacral**s, which separate them from the edges of the ambulacral tracts. Ordinarily, the side plates form a single row

on each side of the ambulacral)s (Fig. 151, 2,3), but they may be arranged in a double interlocking series of outer and inner side plates (Fig. 151,4). The ambulacral)s may be very distinct (Fig. 151,1,2). In some crinoids, however, the plating of the tegmental portion of the ambulacra is less regular, and it tends to merge into the plating of the interambulacral areas (Fig. 151,5,6). Eventually, ambulacral)s and interambulacral)s cease to be distinguishable, and the whole tegmen appears to be composed of an undifferentiated pavement (Fig. 151,7).

In flexible, articulate, and inadunate crinoids the plated covering of the ambulacral tracts traverses the perisome from the arm bases to the mouth, and passes between, or on apposed edges of the orals, if such plates are present (Fig. 148,8,9; 149, 2,3; 151,2,3). Such condition is referred to as **suprattegmental** (Fig. 148,8,9). In camerates, the ambulacral)s may also be incorporated in the surface (Fig. 149,1,3; 151, 1,5), but more generally a more or less considerable part of them is lowered beneath the surface. Traces of these subtegmental portions of ambulacral tracts in camerates may consist of 1) impressions of covering plates against the inner surface of the tegmen, 2) tubes composed of several rows of plates that connect the arm openings to the edge of a special inner structure, the so-called convoluted organ (see p. T201) (Fig. 152); these tubes probably contained the food grooves and associated structures, transformed into tubular passages leading to the subtegmental mouth, or 3) grooves on the inner surface of the tegmen or canals within the tegmental plates, which have been interpreted (HAUGH, 1973) as indicating the location and plan of the water-vascular system (see p. T195).

Some ambulacral)s may be considerably modified. In the coronatid *Stephanocrinus*, each ambulacral tract in the tegmen is covered by a single pair of elongate plates, which possibly resulted from fusion of several ambulacral)s (Fig. 153,1). The mouth of the same genus and of some cyathocrinine inadunates is covered by plates that are regarded as proximal ambulacral)s. These plates—here termed **peristomials**—are larger than ordinary ambulacral)s; they tend to assume, and in some cases effectively have

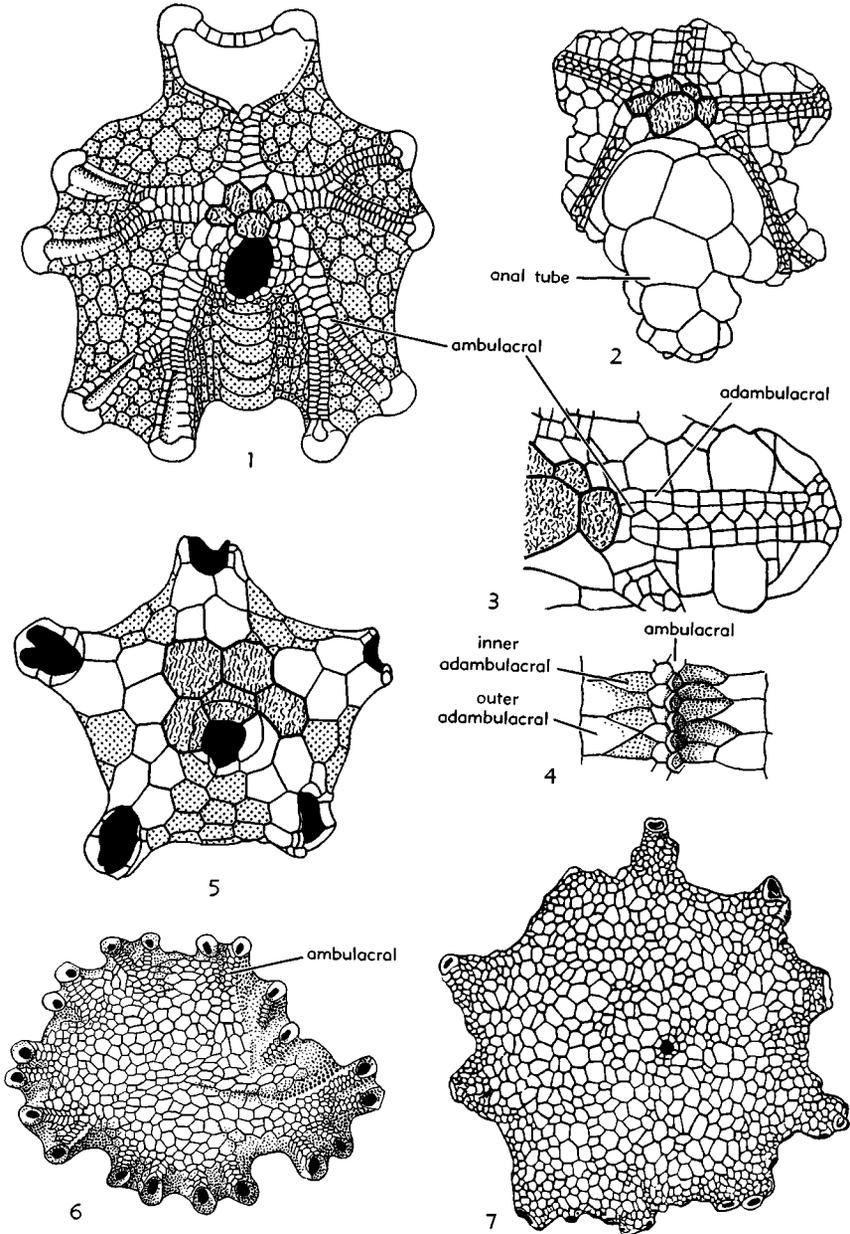


FIG. 151. Various arrangements of ambulacra. [Explanation: orals shaded; interbranchials, interambulacra, and anals stippled.]

1. *Dimerocrinites inornatus* (HALL) (camerate), M.Sil., USA (Ind.);  $\times 3$  (Wachsmuth & Springer, 1897).
- 2,3. *Ceratocrinus exornatus* WANNER (cladid inadunate), Perm., Timor; 2, tegmen,  $\times 1$ ; 3, part of same (B ray),  $\times 2$  (Wanner, 1937).
4. *Hybocystites eldonensis* (PARKS) (hybocrinid), Ord., N.Am.; portion of ambulacrum with two sets of adambulacra, and small arched ambulacra forming median ridge,  $\times 15$  (Springer, 1911b).
5. *Steganocrinus pentagonus* HALL (camerate),

assumed, a pentamer arrangement and an interradial position so that they simulate oral plates, with which they have been sometimes confounded (Fig. 153,1,2). At the same time, in many forms, the true orals are reduced, though the posterior one, commonly recognizable by the fact that it is pierced by hydropores, may remain relatively large (Fig. 153,3).

In a number of camerates, the ambulacra located at the points of bifurcation of ambulacra (i.e., axillary ambulacra) are conspicuous (Fig. 154). Known as **radial dome plates**, they commonly form prominent bosses on the tegmen. In some cases, they are hypertrophied and develop (particularly in the genus *Pterotocrinus*) into an extraordinary variety of forms; according to the species, they may be thick, rounded, club-shaped, or spatulate; they may bifurcate; they may produce knife-like blades, wing-like processes, or gigantic spines (Fig. 154,3,5,6). Radially disposed between the orals (if present) and the arm bases, the radial dome plates may be single (Fig. 154,1-3), or several in each ray (Fig. 154,4); they may be the only ambulacra incorporated into the tegmen (Fig. 154,1), or be accompanied by ordinary ambulacra (Fig. 154,2); in many cases, they are isolated among undifferentiated tegmental plates, presumably because they remained exposed on the surface, after the sinking of the ambulacral tracts below the tegmen (Fig. 154,4), or simply because other ambulacra are not distinct from adjacent interambulacra.

### INTERAMBULACRALS

Plates other than orals that occur in the tegmen between ambulacral tracts and between branches of ambulacral tracts are termed **interambulacra**. They correspond in position and nature to the interbranchials of the calyx. In a large number of crinoids, they are essential skeletal components of the tegmen. In the Flexibilia (Fig. 149,2), some inadunates (Fig. 149,4), and articulated they consist of small plates in a pliant

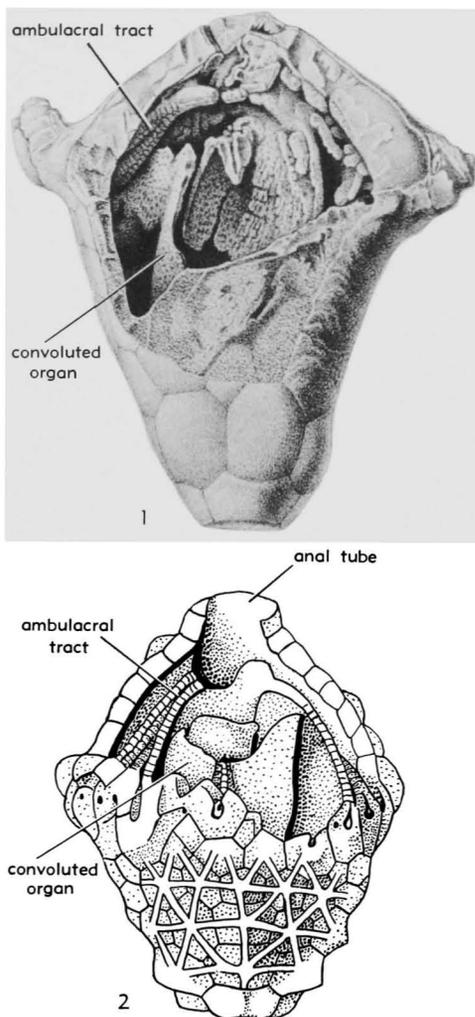


FIG. 152. Subtegmental ambulacral tracts in camerates. Specimens with one side of tegmen broken away, showing partially preserved inner structures. —1. *Cactocrinus glans* (HALL), Miss., USA (Iowa);  $\times 2$  (Wachsmuth & Springer, 1897). —2. *Cactocrinus proboscidalis* (HALL), Miss., USA (Ill.);  $\times 2$  (redrawn from Meek & Worthen, 1873).

integument, which supports the ambulacral tracts, and extends downward and outward

(Continued from facing page.)

- Miss., USA; ambulacra similar to interambulacra,  $\times 1.5$  (Brower, 1965).  
6. *Periechocrinus whitfieldi* (HALL) (camerate), Sil., USA; ambulacra still recognizable at periphery,  $\times 1$  (Wachsmuth & Springer, 1897).

7. *Strotocrinus glyptus* (HALL) (camerate), Miss., USA (Iowa-Mo.); ambulacra unrecognizable,  $\times 1$  (redrawn from Wachsmuth & Springer, 1897).

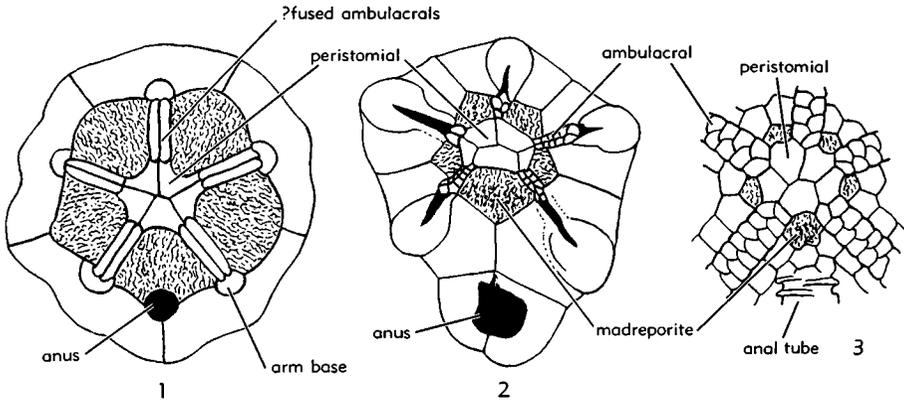


FIG. 153. Modified ambulacrals. [Explanation: orals shaded.]—1. *Stephanocrinus angulatus* CONRAD, M.Sil., USA (N.Y.); diagram of tegmen,  $\times 4$  (adapted from Fay, 1961).—2. *Thetidocrinus piriformis* WANNER, Perm., Timor;  $\times 2.5$  (Wanner, 1937).—3. *Gissocrinus arthriticus* (PHILLIPS), M.Sil., Eng.;  $\times 3$  (Bather, 1900a).

between the rays and their divisions where it may connect the interbrachial areas. Ordinarily the latter are covered with larger and more definite plates, and the distinction between tegmental and interbrachial skeletal elements is plain, but in some forms a gradual passage between the two may be observed. In either case, however, both interambulacrals and interbrachials are judged to have the same secondary origin, and to represent different modifications of a common skeletal component.

Interambulacrals are usually present in Camerata, where with other tegmental plates they form a continuous vault, which, according to its thickness and number of component elements, may be extremely rigid or rather yielding. This vault may even be stratified, as in *Trybliocrinus*, where near the arm bases it is composed of several layers of small plates, a structure called "*Macadam-struktur*" by W. E. SCHMIDT (1937). In some camerates, a clear distinction exists between orals, ambulacrals, and interambulacrals (Fig. 151,1), but in others the whole tegmen appears as made of the same type of plates (Fig. 151,7). The latter condition may result either from the reduction and disappearance of the orals and the lowering of the ambulacral tracts below the surface, with the consequent extension of the interambulacrals over them, or from a loss of differentiation of the various component skeletal elements. Whereas some

camerates (e.g., Hapalocrinidae) have no interambulacrals at all or but a few, others have many such plates. During ontogeny, as more ray and interray plates enter the cup, their number tends to grow. In primitive camerates, they merge gradually into the interbrachial pavement between the arms, but in some more advanced forms they are separated from them by the ray plates in lateral contact. Rather generally indefinite, they may acquire a high degree of specialization; thus, in such genera as *Callicrinus* and *Eucalyptocrinites* they bear vertical partitions to varying heights, which served to protect the free arms.

In most Inadunata, the interambulacrals do not appear to have reached such great development as in Flexibilia and Camerata. They are generally absent or few, and largely confined to the *CD* interray, where they participate in the formation of the anal structures. In some cases, however, they are numerous, covering the largest part of the interambulacral areas (Fig. 149,4).

### ANAL TUBE

In recent crinoids, the anus is generally located in the *CD* interray at the summit of a fleshy conical elevation. This structure, known as the *anal tube* or *cone* or *pyramid*, according to its shape and height, may be of considerable size. A similar organ occurs in many fossil crinoids, though in some forms it is considerably modified

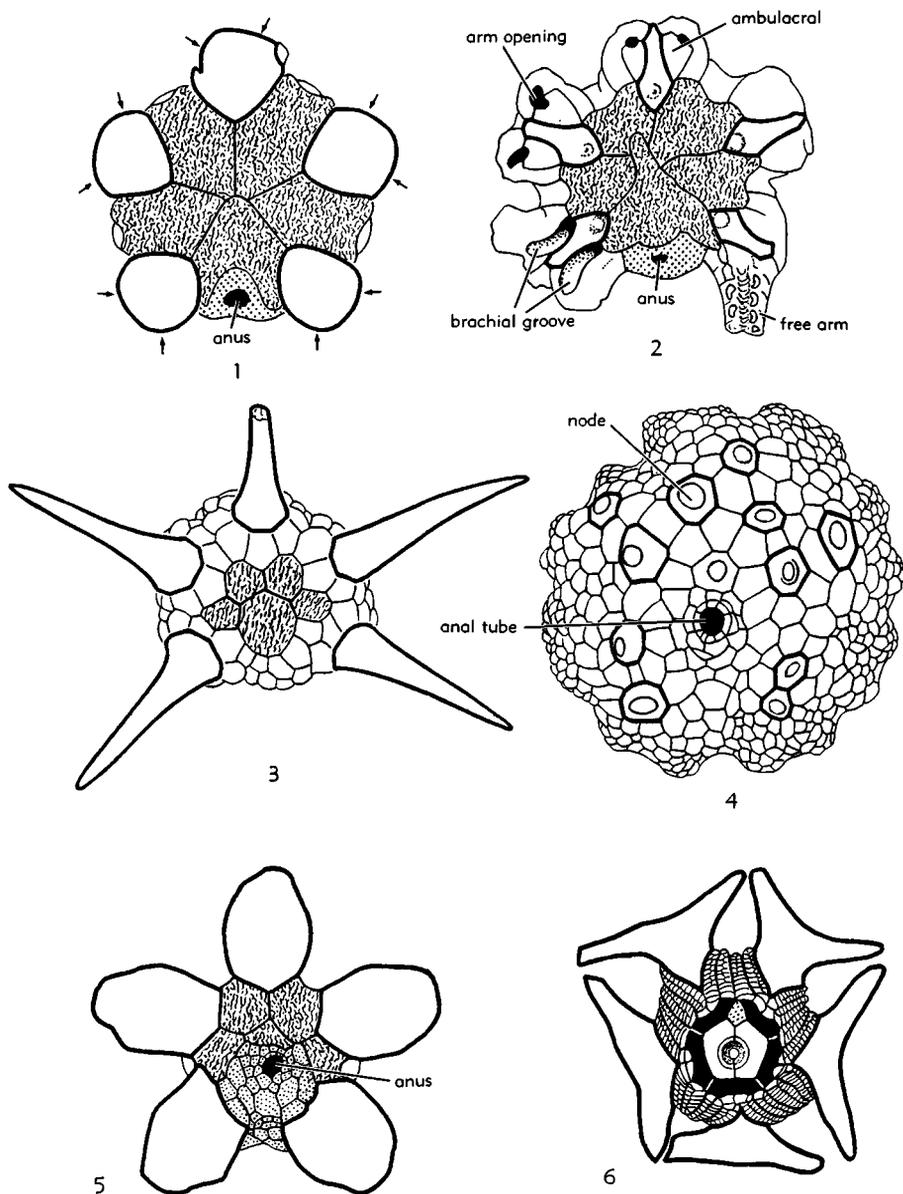


FIG. 154. Axillary ambulacra and radial dome plates in camerates. [Explanation: radials black; anals stippled; orals shaded; axillary ambulacra and radial dome plates with heavy outlines.]

1. *Oenochocrinus pileatus* BREIMER, M.Dev., Spain; arrows indicate positions of arm facets,  $\times 3$  (Breimer, 1962).
2. *Oenochocrinus princeps* BREIMER, Dev., Spain;  $\times 3$  (Breimer, 1962).
3. *Dorycrinus missouriensis* (SHUMARD), Miss., USA (Iowa-Mo.);  $\times 1$  (redrawn from Wachsmuth & Springer, 1897).
4. *Megistocrinus nodosus* BARRIS, M.Dev., USA (Iowa-Mich.);  $\times 1$  (redrawn from Wachsmuth & Springer, 1897).
5. *Pterotocrinus coronarius* (LYON), Miss., USA (Ky.); adoral view,  $\times 1$  (Springer, 1926b).
6. *Pterotocrinus bifurcatus* WETHERBY, Miss., USA (Ky.); adoral view,  $\times 1$  (redrawn from Springer, 1926b).

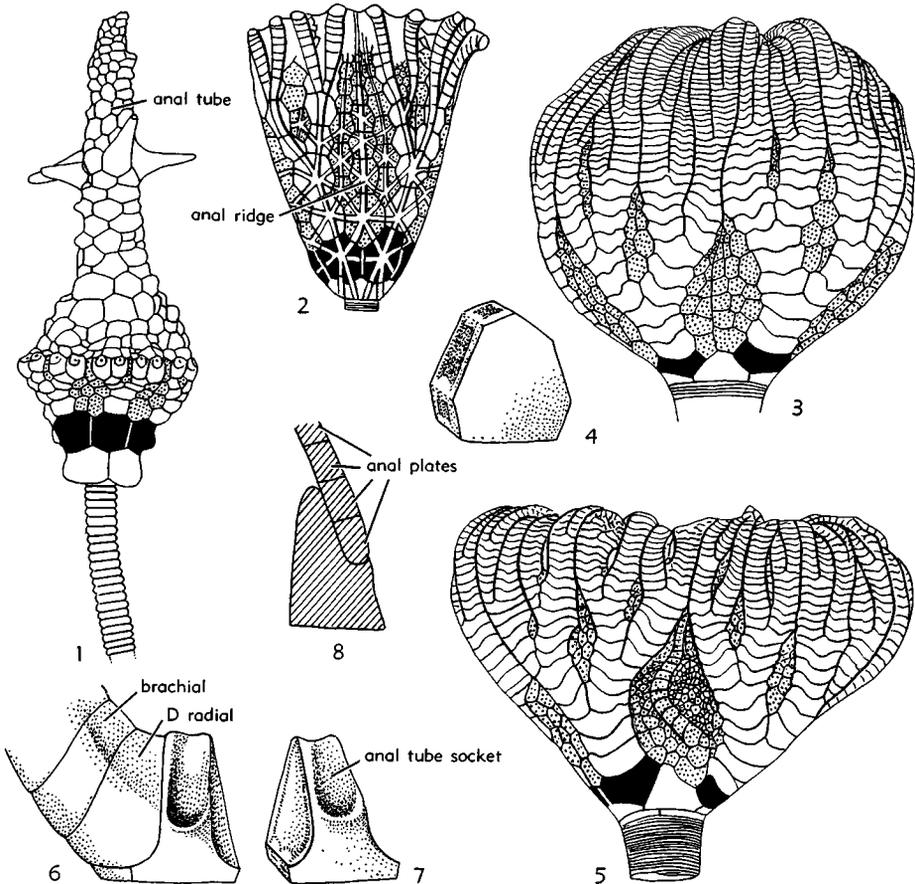


FIG. 155. Morphology and relations of anal tube in camerate (1,2) and flexible crinoids (3-7). [Explanation: radials black; interbrachials and anals stippled.]

1. *Uperocrinus nashvillae* (TROOST), Miss., USA; part of stem, distal end of tube and arms lacking,  $\times 0.45$  (Wachsmuth & Springer, 1897).
2. *Glyptocrinus decadactylus* HALL, Ord., USA; theca seen from CD interrady with clearly differentiated anal ridge,  $\times 1.5$  (Wachsmuth & Springer, 1897).
3. *Forbesiocrinus multibrachiatus* LYON & CASSEY, Miss., USA(Ind.); crown in CD-interrady view,  $\times 1$  (Springer, 1920).
4. *Forbesiocrinus* sp.; CD basal, showing angular distal face, and mode of union (Springer, 1920).
5. *Taxocrinus ungula* MILLER & GURLEY, Miss., USA(Ind.); crown in CD-interrady view,  $\times 1$  (Springer, 1920).
- 6-8. *Taxocrinus* sp.; CD basal showing rounded distal margin and deep socket for anal tube, with adjoining D radial and brachials (6), isolated and exposed articular facets (7), and in vertical section (8) (Springer, 1920).

and acquires an extraordinary development.

An anal tube (sometimes called proboscis) is present in various camerates. It is conical or subcylindrical, and of quite variable size. In some genera it is relatively short, whereas in others it rises well above the distal end of the arms (Fig. 155,1).

It is generally composed of many irregular, commonly nodose or spinose, plates. In various early camerates, such as *Reteocrinus* and *Glyptocrinus*, it is supported by a line of ridged plates continuous with the anal plates of the calyx (Fig. 155,2). This ridge (anal ridge) is connected with the ridges

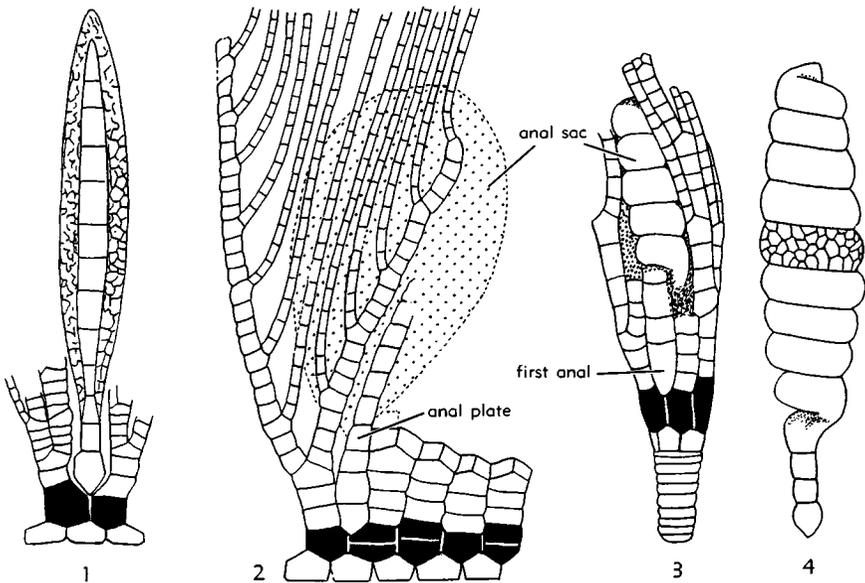


FIG. 156. Morphology of anal tube or sac in disparid inadunates. [Explanation: radials and biradials black.]—1. *Dystactocrinus constrictus* (HALL), U.Ord., USA(Ohio); diagram of part of crown and anal sac (adapted from Ulrich, 1925).—2. *Daedalocrinus kirki* ULRICH, Ord., Can.(Ont.); diagram of part of crown and anal sac (Ulrich, 1925).—3. *Ohiocrinus brauni* ULRICH, U.Ord., USA(Ind.); CD-interray view of crown,  $\times 4.5$  (redrawn from Ulrich, 1925).—4. *Ohiocrinus laxus* (HALL), U.Ord., USA(Ohio); anal series and spiral anal sac, enl. (Ulrich, 1925).

that unite the *CD* basals with adjacent radials, and this suggests that a nerve cord passed up to govern the motion of the tube. In later forms, where the tegmen is more rigid and the plates of the tube are firmly joined together, the anal ridge disappears (BATHER, 1900a). The anal tube of camerates may be regarded as an outgrowth of the *CD* interambulacrum. Secondly it may occupy a central or even an anterior position. Its presence is ordinarily considered to be a generic characteristic, rarely (as in *Platycrinites*) a specific one only. It has been suggested by HAUGH (1973) that it could have contained a respiratory structure in addition to the hind-gut.

In flexible crinoids, as in articulates, the anal tube never acquires gigantic size or marked differentiation (Fig. 147). It is a mere conical protuberance from the *CD* interambulacrum, but may have different relations with the calyx. In some genera like *Forbesiocrinus* its plating prolongs upward the rather solid pavement that fills the *CD* interbrachial area of the calyx, so

that the tube itself originates at some height above the posterior (*CD*) basal, which is not markedly differentiated (Fig. 155,3,4). On the contrary, in such genera as *Taxocrinus* or *Onychocrinus* the anal tube rests directly on the posterior basal, in a socket and a groove that serve for attachment of the proximal ossicle of a series of strong articulated anal plates; these plates support a portion of the pliant tegmen and raise it into an inverted funnel-shaped structure containing the rectum and anal opening (Figs. 147, 155,5-8).

It is among inadunates that the anal tube reaches its highest degree of diversity and specialization. While in some groups like the Hybocrinida (Fig. 148,8), and Coronata (Fig. 153,1), and in such genera as the disparid *Haplocrinites* (Fig. 148,4,5) and *Zophocrinus*, or the Cyathocrinittidae, *Carabocrinus* and *Porocrinus*, it is entirely lacking or reduced to a slight protuberance made of small plates, in most members it is a well-developed and commonly complex structure. In disparid inadunates, it is

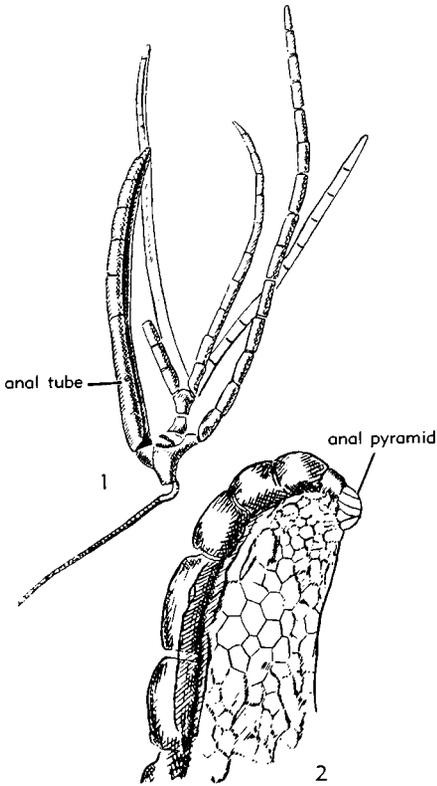


FIG. 157. *Senariocrinus maucheri* W. E. SCHMIDT, L.Dev., Ger.; 1, crown,  $\times 2$ ; 2, distal part of anal tube,  $\times 3$  (W. E. Schmidt, 1934).

closely related to the adjacent *C* ray (Fig. 156). The series of plates that support it may rest directly on the *C* radial or biradial, or on the *B* and *C* superradials, which have fused in a single plate, or on left shoulder of the second or the third *C*-ray plate, taking the place and, in some cases, the appearance of an arm or an arm branch (see anal plates, p. T121). Thus, in *Eustenocrinus* (and probably also in *Ramseyocrinus*) it rests on the whole distal articular facet of the *C* radial or superradial and consists of a single series of brachial-like plates ending in a small anal pyramid (Fig. 93, p. T122). In Calceocrinidae also, the anal tube is the sole appendage borne by the *C* superradial or by the fused *B* + *C* superradials, and its uniserially arranged plates closely resemble brachials: they are massive and crescentic in cross section, with their

hollowed side enclosed by a saclike covering of small, irregular plates (Fig. 87, 1, 5, p. T114); Fig. 157). In other disparids, the anal tube generally consists of an elongate, segmented, armlike appendage that supports a variously expanded wall of small plates, the whole structure being tubelike, saclike, balloon-shaped, or other form, according to the genus (Fig. 156, 1-4). In consideration of these anatomical relations and general appearance, the anal tube of the disparids has been commonly interpreted as representing an evolutionary modification either of the *C*-arm itself or of a branch of this arm.

The anal tube of the cladid inadunates appears to be somewhat different. Primitively, it does not rest on the radial, which

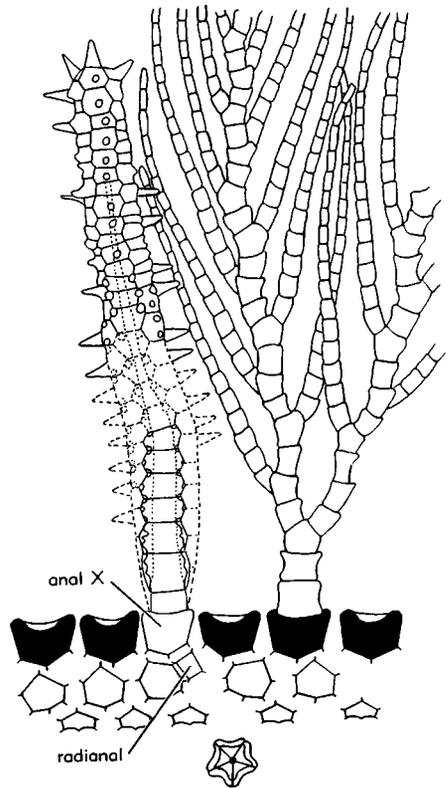


FIG. 158. *Botryocrinus bellensis* KESLING, M.Dev., USA (Mich.); plate diagram of cup, anal sac and *B* ray, showing strong median row of sac plates resting on anal *X* (McIntosh in Kesling, 1973).

[Explanation: radials black.]

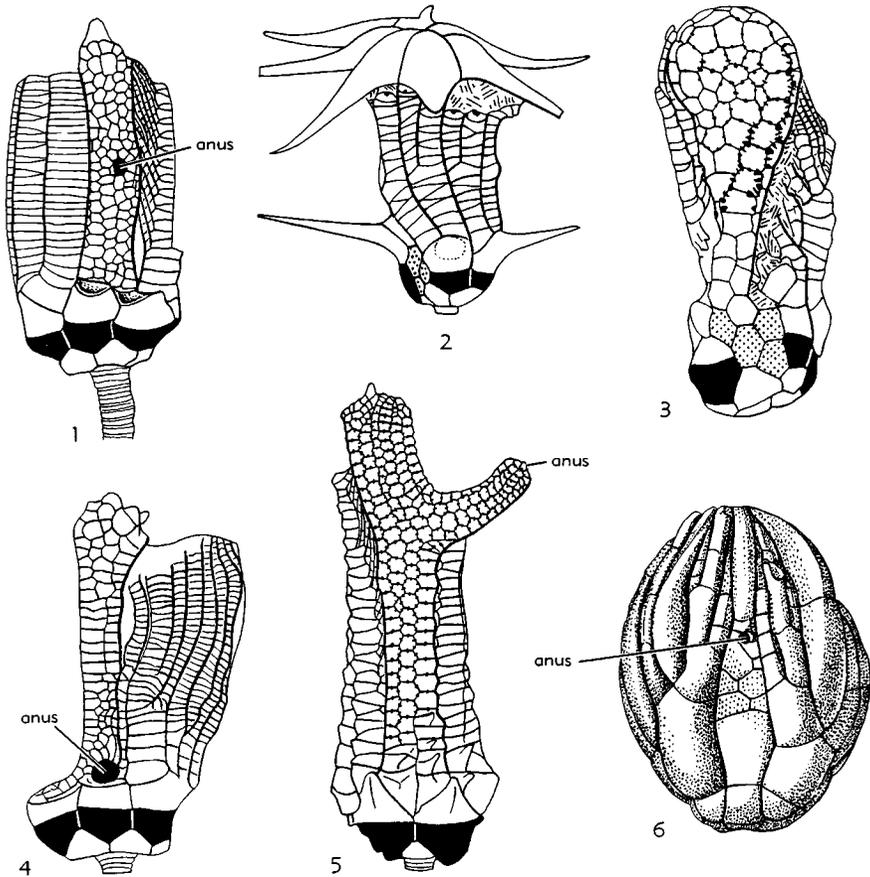


FIG. 159. Morphology of anal sac in cladid (poteriocrinine) inadunates. [Explanation: radials black; anals stippled.]

1. *Scytalocrinus validus* WACHSMUTH & SPRINGER, Miss., USA (Ind.); anterior view; arms of *A* and *E* rays broken off at base,  $\times 1$  (Springer, 1926b).
2. *Tholocrinus wetherbyi* (WACHSMUTH & SPRINGER), Miss., USA (Ky.); *C*-ray view; mushroom-shaped anal sac, except distal spiniferous canopy, concealed by arms,  $\times 1.5$  (Springer, 1926b).
3. *Linocrinus arboreus* (WORTHEN), Miss., USA (Ala.); *CD*-interray view,  $\times 1.5$  (Springer, 1900a).
4. *Eratocrinus commaticus* (MILLER), Miss., USA (Mo.); ant. view; arms of *A* and *B* rays broken off at base,  $\times 1.5$  (Springer, 1926b).
5. *Aulocrinus agassizi* WACHSMUTH & SPRINGER, Miss., USA (Ind.); lat. view; arms in front broken off,  $\times 1$  (Springer, 1926b).
6. *Timorechinus mirabilis* (WANNER), Perm., Timor; *CD*-interray view,  $\times 1.5$  (Wanner, 1916a).

is the sole anal plate that originates as a *C*-ray plate, but it is supported by the interradially located anal  $\bar{X}$ , where the strong median row of plates begins when present (Fig. 94, I-3, p. T123; Fig. 158). Its proximal plates enter into contact with the radial, but only secondarily, after that ele-

ment has been shifted from its original position at the base of the *C* ray toward the posterior (*CD*) interray (Fig. 94, 4, p. T123). These facts suggest that the anal tube of the cladid inadunates was not supported, as in disparid crinoids, by a modified process from the *C* ray, but was merely

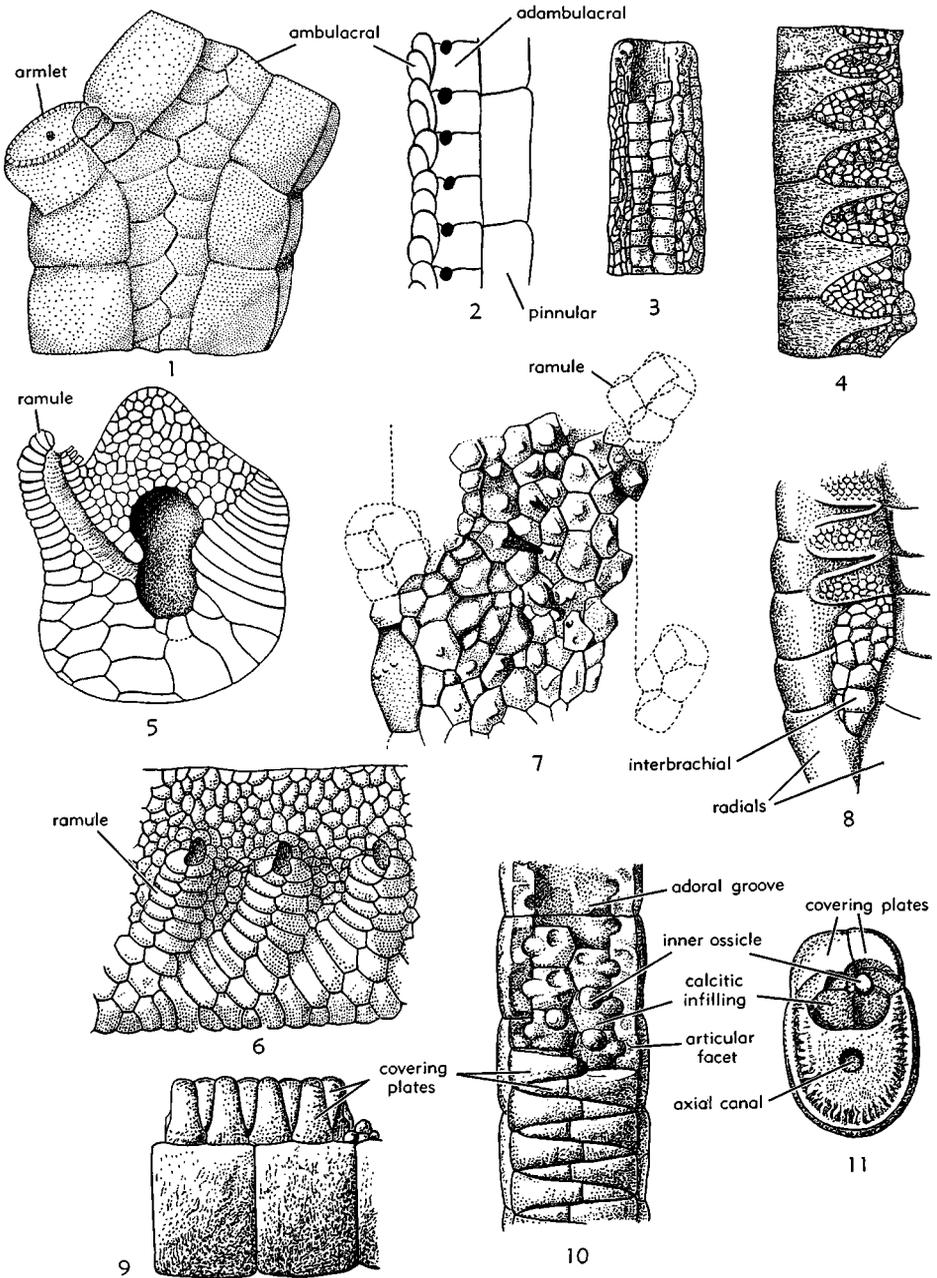


FIG. 160. Perisomic skeleton of the arms.

- 1. *Barycrinus hoveyi* (HALL), Miss., USA (Ind.); note single row of ambulacra over groove of armlet opposed to double row over groove of arm,  $\times 6$  (Van Sant, in Van Sant & Lane, 1964).
- 2. *Neometra spinosissima* (A. H. CLARK), recent, Ind.O.; lat. view of portion of pinnule, enl. (A. H. Clark, 1923).
- 3,4. *Carabocrinus huronensis* FOERSTE, M.Ord., Can.(Ont.); adoral and lat. views of portion

an extension from the posterior interambulacrum, as are the anal tubes of camerate, flexible, and articulate crinoids.

It is among cladid crinoids that this organ reaches its greatest diversity in size and shape (Fig. 159). In size it varies from a small protuberance to a huge inflated structure, the so-called "ventral sac," that may exceed the calyx in size and the arms in height, and may involve almost the entire tegmen. It may be cylindrical, pyramidal, club-shaped, balloon-shaped, or mushroom-shaped; it may taper to a pointed end, or enlarge distally to a more or less rounded, commonly nodose or spiniferous terminal surface (Fig. 159,2); it may be longitudinally ridged, folded, coiled upon itself, and provided with a lateral branch-like process (Fig. 159,5); or it may form niches for the protection of arms, as in the Permian *Timorechinus* (Fig. 159,6). It is generally composed of longitudinal rows of plates, commonly provided with strong folds and deep pits, and ornamented with radial ridges. In some species numerous round or slitlike pores, presumably respiratory, occur on the suture lines between the plates (Fig. 159,3) (see p. T208). The anal opening may be located at the summit (probably the primitive position), but it may also appear at various places along the anterior side: at the base of the sac (Fig. 159,4), midway (Fig. 159,1) toward its summit, or at the end of a lateral spoutlike process (Fig. 159,5). Such anterior position of this opening may be explained by the recurring and more or less complete redoubling of the gut and of its enveloping tube upon themselves, so that the anus may emerge through the wall at any point between the distal end and the base. This deflection and reversal of the gut and tube, the walls of which coalesce where they are brought into contact (as may be observed when ridged

rows of plates occur continuously from one end to the other), accounts for the distal expansion and, at least to some extent, the large size of the saclike tube. But this does not exclude the possibility that the latter contained organs other than the gut itself and performed functions other than to protect this part of the digestive tube. But which organs and which functions are unknown.

### ADORAL SKELETON OF ARMS AND PINNULES

The perisomic tegments of the arms and pinnules are probably never entirely free from any skeletal elements. These vary considerably in size, from tiny spicules almost completely limited to small epidermal folds or lappets bordering the ambulacral grooves on either side, to well-defined plates, the so-called covering-plates or **ambulacrals**. In their simplest form, they are arranged in two alternating rows (rarely in a single row), one on each side of the ambulacral grooves. They are movable, and could be everted or closed down over the grooves. When closed, the two rows meet in the median line by a zigzag suture (Fig. 160,1). Between the ambulacrals and the adoral edges of the brachials and pinnulars may be added small, usually squarish or oblong, side-plates or **adambulacrals**, so that four rows of plates protect the ambulacral grooves (Fig. 160,2).

But the perisomic skeleton of the arms may be much more complex. Thus, in some camerates, especially those that possess powerful brachial trunks, the tegmental pavement extends far up the main arms, which appear to have formed tubular structures (Fig. 160,5-7); in *Trybliocrinus* the adoral covering is even stratified, and it forms a highly arched roof under which the ramules

(Continued from facing page.)

- of arm,  $\times 6$  (Foerste, 1925).
- 5.6. *Trybliocrinus flatheanus* (GEINITZ), L.Dev., Spain; 5, transv. section through proximal part of brachial trunk with stratified ambulacral covering; 6, portion of brachial trunk in lat. view, ramules broken off, ca.  $\times 5$  (Breimer, 1962).
7. *Ctenocrinus* sp., L.Dev., Belg.; portion of brachial trunk in adoral view with tessellated ambulacral covering,  $\times 12$  (Ubaghs, 1945b).
8. *Cupulocrinus jewetti* (BILLINGS), M.Ord., Can. (Ont.); proximal part of E ray in lateral view,  $\times 6$  (Springer, 1911b).
- 9-11. *Cyathocrinites acinotubus* (ANGELIN), Sil., Gotl.; 9,10, lat. and adoral views of brachials and covering plates,  $\times 10$ ; 11, articular face of brachial, with covering plates in position,  $\times 10$  (Bather, 1893a).

penetrate rather deeply (Fig. 160,6). In the diplobathrid *Traskocrinus*, a plated weblike structure between tegmen and arms extends on sides of the ambulacral tracts apparently throughout all arms.

In the cyathocrinine inadunate *Carabocrinus huronensis*, the adoral groove of the arms is protected by two median rows of quadrangular plates, accompanied on each side by a stripe of small irregular plates, which extends laterally as well over depressions developed between the successive brachials (Fig. 160,3,4). A similar arrangement seems to have existed in at least part

of the arms of the dendrocrinine inadunate *Cupulocrinus jewetti* (Fig. 160,8). In some species of the cyathocrinine genera *Cyathocrinites* and *Gissocrinus* heavy plates divided by one or more transverse sutures cover the adoral groove of the arms, to the edges of which they are united by articular facets; they look like small pinnules, and as such have been interpreted by several authors (particularly SIEVERTS-DORECK, 1952); beneath these plates and alternating with them, minute, inner, rounded ossicles may also occur (Fig. 160,9-11).

## VARIOUS SKELETAL STRUCTURES

In this section are described skeletal structures that generally are not located in a single part of the body such as the column, the theca, or the arms, but extend into several body regions, or are related to both the aboral and the adoral skeletons (e.g., the cup and the tegmen). Most of these structures are associated with organic systems (i.e., nervous, digestive, water-vascular, or reproductive systems), or are composed of elements combined for the accomplishment of a particular function, like respiration or digestion.

### STRUCTURES ASSOCIATED WITH NERVOUS SYSTEM

The crinoids have three nervous systems related functionally and morphologically: the ectoneural, hyponeural, and entoneural systems. The first one, being entirely within the soft tissues, leaves no trace on the skeleton and consequently is unknown in fossil crinoids. According to HAUGH (1975), the hyponeural system was represented by ridges and grooves on the inner tegmental surface of many camerates; it has not been detected in fossil representatives of the other subclasses. As to the entoneural or aboral nervous system, which is the main motor system of the crinoids, it lies within the aboral skeleton or near its inner surface, and therefore its former presence is frequently indicated in fossil crinoids by canals within the plates or by grooves or ridges on the interior thecal surfaces, or on internal molds.

The entoneural system is centered in a ganglionic nervous mass surrounding a coelomic cavity divided into five chambers. Typically this **chambered organ**, as it is called, is lodged within the ring of basals in monocyclic and pseudomonocyclic forms, or of infrabasals in dicyclic ones. If the proximal or the two proximal circlets of plates are reduced it may rise up to the next circlet (Fig. 161,1); if they are entirely lacking, or are overgrown by the radials, as in roveacrinid and cyrtocrinid articulates, the whole organ occupies the bottom of the relatively wide cavity enclosed by these plates (Fig. 162). In comatulid articulates it is included in the centrodorsal cavity below the basal plates reduced in size or fused into a rosette (see p. T108).

Generally no trace of the chambered organ is preserved in fossil crinoids. In some camerates, inadunates, and flexibles, however, the proximal or the next to proximal circlet of cup plates carries an inner funnel-shaped structure which probably housed this organ (Fig. 161,1,2). This calcareous structure is trigonal or subpentagonal in outline, and it is divided by short septa into lobed depressions continuous with the stem lumen.

Coelomic vessels, each with a sheath of nervous tissue, proceed from the five lobes of the chambered organ and penetrate directly into the cirri in comatulids, or in stalked crinoids into the axial canal of the column. These coelomic and nervous extensions into the stem may give off branches that go into the cirri, pseudocirri, and

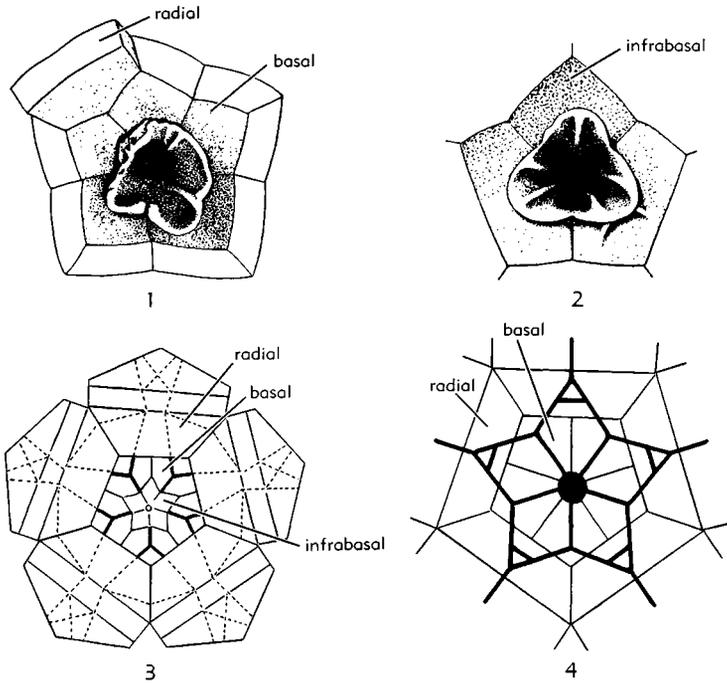


FIG. 161. Morphology of entoneural system.

1. *Ichthyocrinus* sp., Sil.-Dev.; funnel-shaped structure lodging chambered organ; infrabasals too minute to support funnel, which rests upon basals,  $\times 8$  (Springer, 1920).
2. *Forbesiocrinus saffordi* HALL, Miss., USA (Ind.-Tenn.); funnel resting upon infrabasals,  $\times 5$  (Springer, 1920).
3. *Encrinus* sp., Trias., Ger.; course of axial canals within calyx and primibrachs; canals represented by dotted lines when penetrating plates, and by heavy lines when exposed on inner surface of plates (Beyrich, 1858).
4. *Rhizocrinus lofotensis* M. SARS, recent, Atl.; distribution of entoneural canals within the calyx (Carpenter, 1884a).

radicular cirri, which, like the column, are all provided with an axial canal. A description of these longitudinal passageways through the column and its appendages has already been given (p. T79).

Relatively little is known about the entoneural system in the crown of fossil crinoids. Its general pattern, however, is clearly shown in fossil articulates and some dicyclic inadunates, the brachials and pinulars of which are perforated by a single, or rarely a duplicate (as in the Pennsylvanian *Aesiocrinus* or the Triassic *Encrinus*), canal (axial canal) that contained the main brachial nerve (Fig. 161,3). Proximally the axial canal of each ray penetrates into a radial where it divides into two branches, one of which proceeds to the basal on the right, the other to the basal on

the left. If it is duplicate, the two canals simply diverge and, as in the preceding case, extend downward to two separate basals. Within the radials, the axial canals of the five rays are connected by a commissural canal that generally forms a pentagonal ring all around the cup. Proximal to this pentagonal ring interradianal commissures may also occur at the level of the basals. Ultimately, as shown by the recent forms, the cords that are housed in this canal system unite into five primary trunks or pass directly into the nervous sheath of the chambered organ.

Various modifications of this scheme may occur. Thus, in some bathyrcrinid articulates like *Bathyrcrinus* or *Democrinus* the five primary trunks rise through half the height of the radials before they fork (Fig.

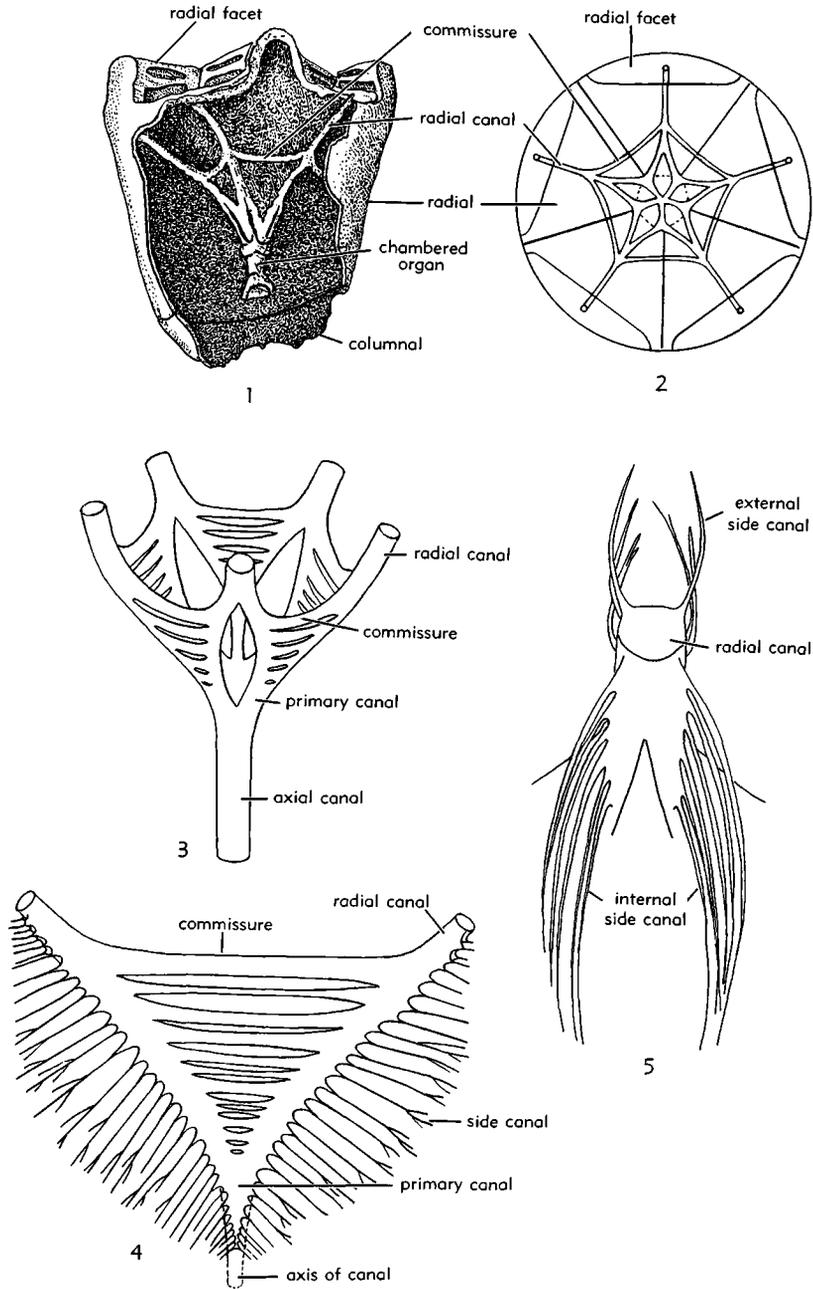


FIG. 162. Course of axial canals within the calyx in cyrtocrinid articulates.—1,2. *Eugeniocrinites caryophyllatus* SCHLOTHEIM, Jur., Eu.; 1, calyx broken open to show silicified axial canals,  $\times 4$ ; 2, distribution of axial canals within calyx (Jaekel, 1891a).—3-5. *Gammarocrinites strambergensis* JAEKEL, Jur., Ger.; 3, reconstruction of entoneural canal system, side canals omitted; 4, detail of canal system between two adjacent radii; 5, detail of radial canal with side canals in ventrolateral view (Zitt, 1973).

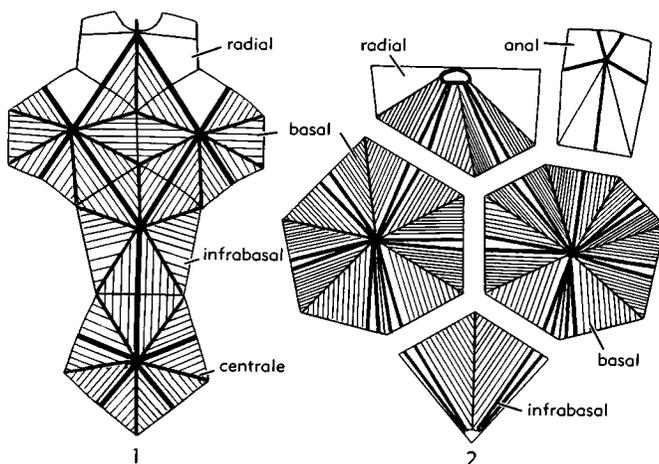


FIG. 163. Diagram of complex entoneural canal system within the calyx. [Explanation: heavy lines indicate primary canals, intermediate lines secondary canals, weak lines tertiary canals.]—1. *Marsupites testudinarius* (SCHLOTHEIM) (diagramm.), Cret., worldwide (Sieverts, 1927).—2. *Calceolispongia* (diagramm.), Perm., Australia, Timor, India (Teichert, 1949).

161,4). In cyrtocrinid articulates that have the cup composed of radials only, the axial canal from the stem, at a short distance above its entrance into the cup, widens and takes a form that suggests that the chambered organ was located there (Fig. 162). Five interradian primary canals proceed from this region, each one dividing into two diverging branches. At various levels of the radials, the neighboring branches meet to form radial canals that pass directly up to the radial facets and the arms. In addition, the branches are connected with each other by a single or, as in *Gammarocrinites strambergensis* (Fig. 162,3-5), multiple commissures. They may also give off side canals toward the periphery of the cup and toward its central cavity (Fig. 162,5).

In the Permian inadunate *Calceolispongia* and in the Cretaceous articulate *Marsupites* a complicated system of canals is present inside the plates near their inner surface (Fig. 163). In the ornamented varieties of *Marsupites* the position of these canals corresponds to the ornament of the calyx. Three sets of canals may be distinguished: 1) main canals, which enter the plates near the middle of the facets and join in the center of the plates, 2) secondary canals that connect the center of the plates with the corners, and 3) tertiary canals that

branch off from the secondary canals and cross the facets at right angles. The secondary and tertiary canals are absent from some plates or sectors of some plates in both *Marsupites* and *Calceolispongia*, and they are entirely lacking in the smooth varieties of *Marsupites*.

An unusual branched (?) canal system has also been observed (PAUL, 1970) in a few calycal plates of a specimen of the Silurian camerate genus *Masupiocrinus*. It consists of a delicate branching and anastomosing structure, which has been [incorrectly according to HAUGH, 1975] interpreted by PAUL (1970) as located within the stereom. Each branch has a median keel and is crenulate with short processes that alternate on either side.

Such complex canal systems as those just mentioned have not been found in any recent crinoids. If they housed branches of the entoneural system, the function of these branches is not clear, for the aboral nervous system serves primarily for innervating muscles, and there are no muscles within the calycal plates.

In flexible, camerate, and most inadunate crinoids the entoneural system was not enclosed within the plates, except very rarely. Nevertheless, in some of these crinoids, particularly camerates, the course of the aboral

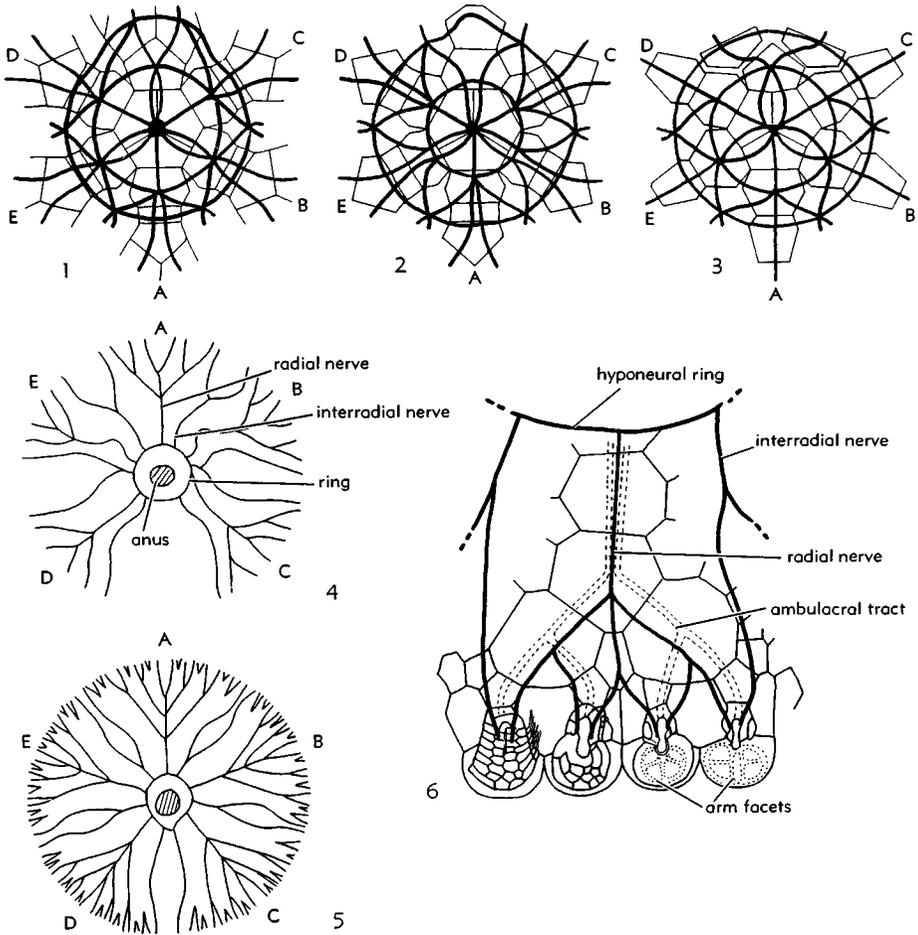


FIG. 164. Diagrammatic plan of the entoneural (1-3) and hyponeural (4-6) systems in some camerate crinoids (all figures from Haugh, 1975b, slightly mod.). [Explanation: A, B, C, D, E, letters designate rays according to CARPENTER.]—1. *Batocrinus icosidactylus* CASSEDAY, Miss., USA.—2. *Dorycrinus quinquelobus* (HALL), Miss., USA.—3. *Steganocrinus pentagonus* (HALL), Miss., USA.—5. *Teleocrinus rudis* (HALL), Miss., USA.—6. View from exterior of a part of a tegmen as if it were transparent in order to show the course of the hyponeural nerves in a single ray and adjacent interrays. (From *Paleobiology*, v. 1, no. 3, Summer, 1975, courtesy of The Paleontological Society and Bruce N. Haugh.)

nerve cords within the calyx appears to be indicated by grooves or ridges on the inside of the calycal plates, or on the surface of internal molds (BROWER, 1973; HAUGH, 1975). It has been frequently supposed also that the external ornamentation of the calyx of fossil crinoids reproduced the plan of the entoneural system, but to what extent is not clear.

The evidence at hand suggests that the entoneural network in camerates radiated

from the basal region of the calyx at the point of the stem attachment where the chambered organ was presumably located (Fig. 164, 1-3). From this point, six primary nerve trunks proceeded, one to each ray and one to the anal interray. These trunks were single or double, and they divided or separated at the primaxil of each ray, and at all succeeding higher order axillaries. In addition, branches were present in each of the interrays with, however,

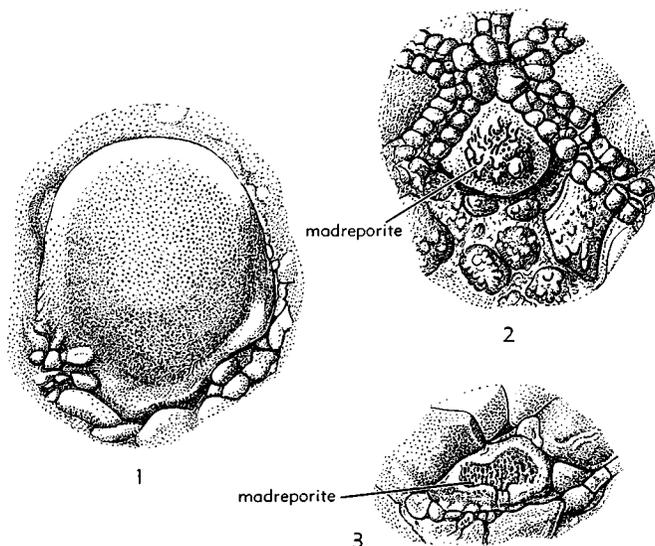


FIG. 165. Morphology of the madreporite.—1. *Aexitrophocrinus jaekeli* MOORE & PLUMMER, L.Carb., Scot., USSR;  $\times 6$  (Springer, 1920).—2. *Gissocrinus incurvatus* (ANGELIN), U.Sil., Gotl.;  $\times 6$  (Bather, 1893a).—3. *Euspirocrinus spiralis* ANGELIN, U.Sil., Gotl.;  $\times 6$  (Bather, 1893a).

in *CD* interray a pattern different from that in the other interrays. Probably two ring commissures interconnected the nerve trunks, but their former presence is commonly vague or even lacking in actual specimens. The resulting general plan of this network closely resembles the plan of the aboral nervous system of the recent crinoids, though the presence of the radial-like *CD* interray trunk produces a dual, trimeral symmetry as opposed to the pentameral symmetry of modern forms (HAUGH, 1975).

Another network of ridges and grooves occurs on the tegminal inner surface of many camerates. According to HAUGH (1975), it would correspond to the hyponeural system of the living crinoids because its plan is very similar to that of this system in the latter. It appears to have consisted of a ring commissure, which was located near the upper part of the tegmen, and from which originated radial and interradial branches. These branches divided so that each free arm received two hyponeural cords, as in modern crinoids (Fig. 164,4-6). If this interpretation is correct, the camerates possessed at least two (and probably three) nervous systems homologous to those of the recent crinoids.

### STRUCTURES ASSOCIATED WITH WATER-VASCULAR SYSTEM

In most fossil crinoids, the water-vascular system has left no trace, or only scanty ones, and one may only suppose it was essentially similar to that of recent forms. A single (more rarely two or three) external pores or a narrow slit or a perforated small tubercle occurs on the posterior (*CD*) oral plate of some disparid, many hybocrinid and cyathocrinine inadunates; this structure has been commonly interpreted as a hydropore (Fig. 148,4). In many flexible genera in which the tegmen is known, an enormously enlarged posterior oral is perforated by numerous pores, and certainly performed the function of a madreporite (Fig. 165,1). Similarly, in various cyathocrinine inadunates, the posterior oral had the structure, and most likely the role, of a typical madreporite (Fig. 165,2,3).

The presence of a madreporite in dendrocrinine and poteriocrinine inadunates has been rarely reported. However, one such plate has been observed in the dendrocrinine *Parisocrinus* by LANE (1975) and in the poteriocrinines *Stellarocrinus* and *Clathro-*

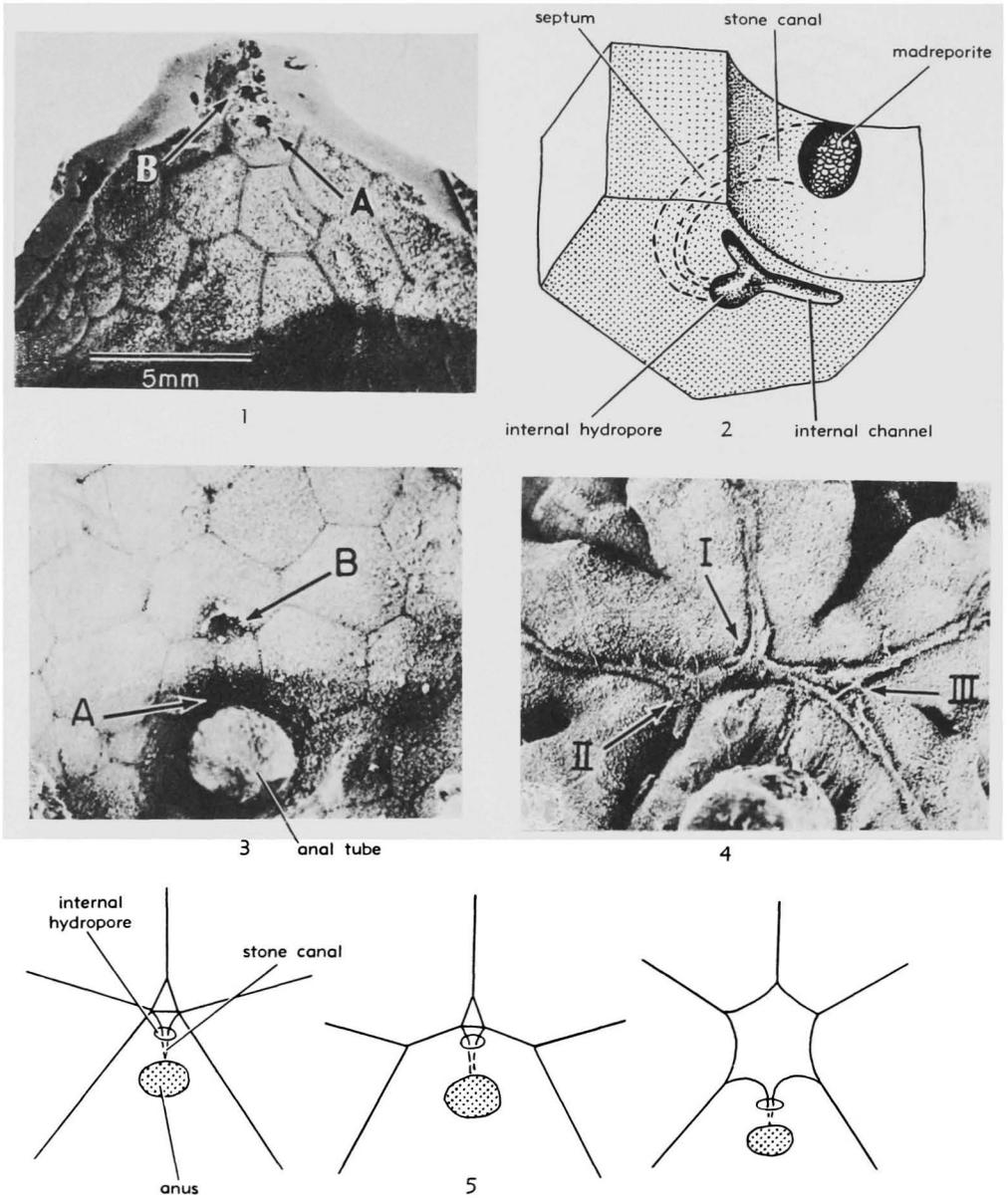


FIG. 166. Structures related to water-vascular system in camerates.

- 1,2. *Batocrinus icosidactylus* CASSEDAY, Miss., USA (Ind.); 1, vertically cut hollow specimen showing location of internal hydropore (A) and madreporite (B) at base of anal tube,  $\times 4.4$ ; 2, posterior oral plate with entrance of water-vascular system, diagram. (Haugh, 1973).
3. *Gilbertocrinus tuberculatus* (HALL), Miss., USA (Iowa); part of inner face of tegmen with

- internal madreporite (A) and hydropore (B),  $\times 3.75$  (Haugh, 1973).
4. *Actinocrinites lowei* (HALL), Miss., USA (Mo.); part of chert mold with three-fold (I, II, III) convergence of radial grooves (here appearing as ridges),  $\times 3.75$  (Haugh, 1973).
5. Various patterns of water-vascular system in camerates according to HAUGH (1973).

*crinus* by STRIMPLE (1973a). According to LANE (1975), a complex tubule system in the anal sac of the Pennsylvanian poterocrinine inadunate *Aesiocrinus magnificus* might possibly represent a hypertrophied madreporitic system that would be an intermediate evolutionary step between the single madreporite plate of more primitive inadunates and the multiple-element ciliated funnel system of articulate.

Unlike flexible and inadunate crinoids, an external hydropore or madreporite has never been recorded for any camerate crinoid. It is true that the function of this structure was previously assigned (BATHER, 1900a) to the so-called respiratory pores, which in some camerates are located near arm bases (see below, p. T207), but this interpretation is made unlikely by the discovery of a structure which probably is an internal hydropore (HAUGH, 1973). This structure has been particularly well observed in *Batocrinus icosidactylus* (Fig. 166), but it has been found also in other camerates and may have existed in many. It is situated in the posterior oral plate at the base of the anal tube. The side of this plate facing the cavity of the tube contains a pore, which may be protected by a calcareous sieve. This pore is followed by an incurved canal within the plate, and this canal, commonly divided by an incomplete longitudinal septum, leads to an internal hydropore with two lateral channels on the inner surface of the same plate. According to HAUGH, this canal would be the stone canal and the two channels, the marks of two branches connecting the stone canal with the water ring or equivalent structure. If so, then the entrance to the water-vascular system in camerates would have been close to the distal part of the gut and completely internal, as in living holothurians.

The other parts of the water-vascular system in fossil crinoids are practically unknown, except possibly in some camerates where radial grooves on the inner surface of the tegmen probably indicate (at least to some extent) the course of the ambulacra and the morphologic plan of the water-vascular system within the theca, but what exactly contained these grooves remains uncertain (Fig. 166; 167,2,3). Their diameter is much larger than that of the water ves-

sels of living echinoderms. In individuals of *Strotocrinus* they penetrate into the plates and are completely within the stereom in some places. If generally each groove is single, it may also be multiple and anastomosing, and may even be provided with many small lateral branches (Fig. 166,4). The grooves may be preserved peripherally and be lacking centrally, as if the structures they were associated with rested against the tegmen near the arm bases and became subtegmental as they approached the center. They may also be entirely lacking, suggesting that the structures in question were largely located below the tegmen. In forms where the grooves meet centrally, their connection may be quite complex, and the grooves may converge to one, three, or five points (Fig. 166,4,5). HAUGH (1973) detected four morphologic patterns in the arrangement of these structures. If this arrangement is a real and reliable expression of the morphologic plan of the water-vascular system, it suggests that the latter differed in organization and symmetry from that of recent crinoids. Thus, according to this view, the radial ambulacral canals in most camerates would have been supplied by a crescent-shaped rather than by a complete ring canal.

## STRUCTURES ASSOCIATED WITH DIGESTIVE SYSTEM

The mouth is situated at the focus of the ambulacral tracts. It is generally exposed on the tegmen in articulate and flexible crinoids, but in inadunates and camerates, it opened typically beneath the tegmen—a condition known as subtegmental. Ordinarily the mouth is located approximately at the center of the body. Secondly it may be displaced along the *A* radius or *AB* interradius; in some cases, as among many recent Comasteridae or in the Cretaceous articulate *Uintacrinus*, it is quite marginal (Fig. 168,1). Such shifting is accompanied by an increase in size of the anal area, which tends to occupy a large surface of the tegmen.

In most articulates the mouth consists of a round, oval, or crescentic opening in the plated or naked integument that forms the tegmen. In some articulates (e.g., *Cyathi-*

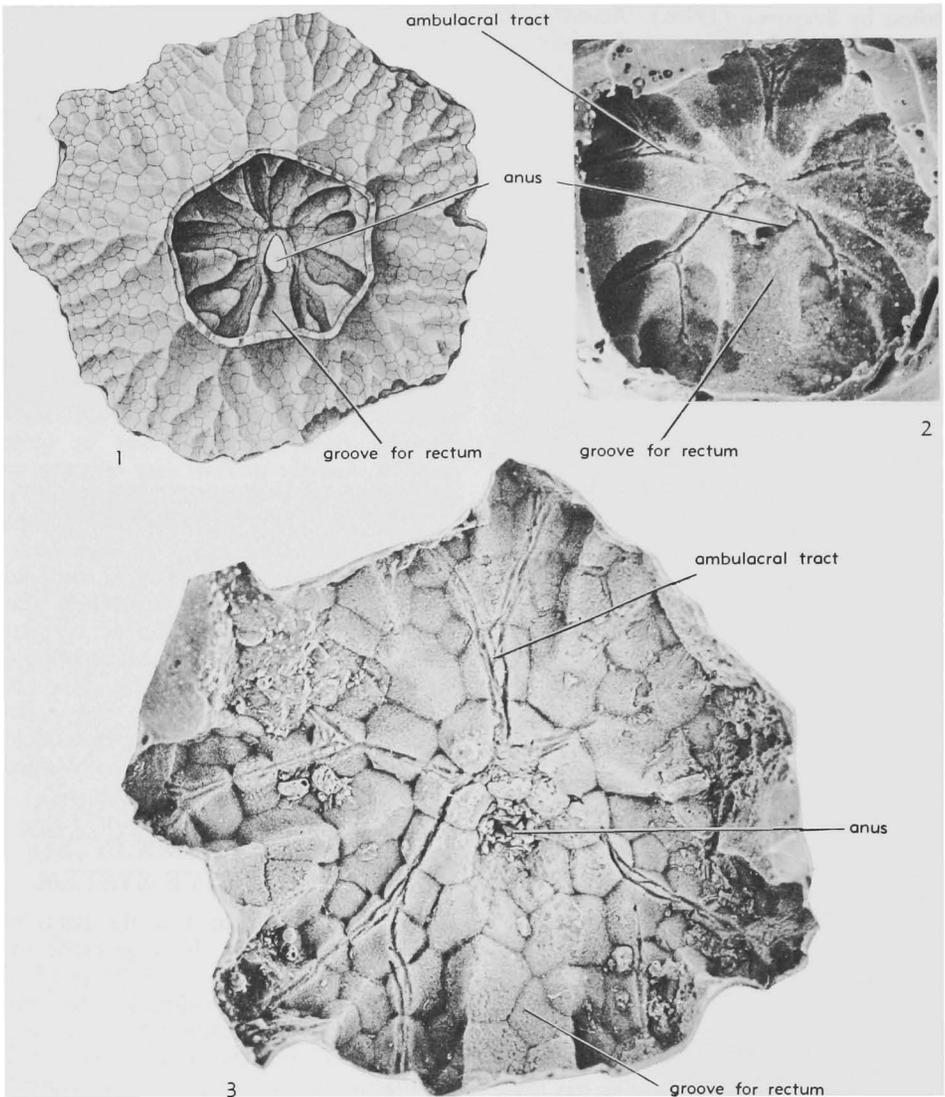


FIG. 167. Inner tegmental structures in camerates.—1. *Strotocrinus regalis* (HALL), Miss., USA (Iowa-Mo.); theca in aboral view, with part of aboral cup broken away, exposing subtegmental galleries and grooves for rectum and ambulacral tracts,  $\times 0.67$  (Wachsmuth & Springer, 1897).—2. *Physetocrinus ornatus* (HALL), Miss., USA (Mo.); inner view of tegmen, latex cast, USNM S 1259,  $\times 2$  (Ubaghs, n).—3. *Strotocrinus regalis* (HALL), Miss., USA (Mo.); inner view of tegmen, latex cast, USNM S 1275,  $\times 3$  (Ubaghs, n).

*dium*, *Holopus*, *Hyocrinus*) and in those flexibles the tegmen of which is known, it is surrounded or covered by five oral plates, which occupy the apices of the interambulacral areas, the ambulacral tracts running between these plates or beneath their apposed edges.

The mouth of all Paleozoic crinoids except flexibles was covered either by orals, proximal ambulacrals (peristomials) (Fig. 153), or undifferentiated perisomic plates. So far as is known, this plated covering could not be opened in life. Some microcrinoids, however, that lacked arms and in

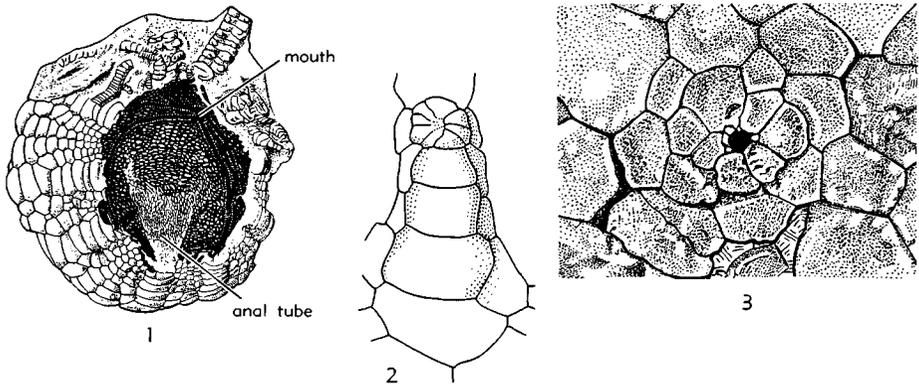


FIG. 168. Skeletal structures associated with digestive tube.—1. *Uintacrinus socialis* GRINNELL, U.Cret., N.Am.; specimen vertically compressed, showing black tegmental integument,  $\times 0.67$  (redrawn from Springer, 1901).—2. *Stelidiocrinus laevis* ANGELIN, U.Sil., Gotl.; Stockholm Museum, no. 11774, series of anal plates with terminal anal pyramid,  $\times 7.5$  (Ubaghs, n).—3. *Eucalyptocrinites tuberculatus* (MILLER & GURLEY), M.Sil., USA (Ind.); anal cover plates, surrounded by accessory plates, enl. (Macurda, n, mod.).

some cases even an external vent were probably able to open their oral plates and expose their soft structures in order to receive food and expel feces.

An external anal opening occurs invariably in crinoids, though, as just said, none has been recorded in some microcrinoids (e.g., *Atremacrinus*, *Pentececrinus*). Typically located in the *CD* interambulacrum, it pierces the tegmen directly or (more generally) is raised on an anal pyramid, tube, or sac. Usually in such cases it is situated at the summit or at the posterior side of this structure, but in cladid inadunates provided with an inflated sac it may occur at the anterior side of the sac, either at the base, or part way up, or at the end of a lateral spoutlike process (Fig. 159,1,4,5). The vent may also occupy various other positions. In extant comasterids, in the Cretaceous *Uintacrinus* (Fig. 168,1), in the Triassic *Encrinus*, and in some camerates with an anal tube it becomes central or subcentral. In the camerate *Siphonocrinus* it may open anteriorly at or even beneath the arm-bases. It has migrated downward into the posterior side of the cup to a position just above the posterior (*CD*) basal in the cyathocrinine inadunate *Gasterocomidae*, and in most *Codiocrinacea*; furthermore, some members of the latter

superfamily have it in perradial position or between a radius and an interradius. It is laterally located also in the hybocrinid genus *Cornucrinus*, probably as the result of hypertrophy of the radial plates.

The anus of crinoids is commonly surrounded by small plates and protected by a valvular pyramid. In many fossil forms it was located in a well-defined thecal orifice, the **periproct**, which in life was covered by a small cone of triangular plates (**periproctals**) or by a plated periproctal membrane. Both these structures are rarely preserved (Fig. 168,2,3).

In most recent and, probably, fossil crinoids the gut makes a single dextral coil, with the mouth in the axis of the coil, a condition known as **endocyclic**. In comasterid articulates it makes several coils, and they do not wind around the axis of the mouth, which becomes marginal, but around the axis of the central anus. Such a gut is said to be **exocyclic**. Some fossil crinoids, like *Uintacrinus*, which had a marginal mouth and a central anus, may possibly have had an exocyclic gut, but this remains to be proved.

The digestive tube of most fossil crinoids has generally left no traces or but scanty ones. In camerates, however, hollow silicified specimens commonly contain highly

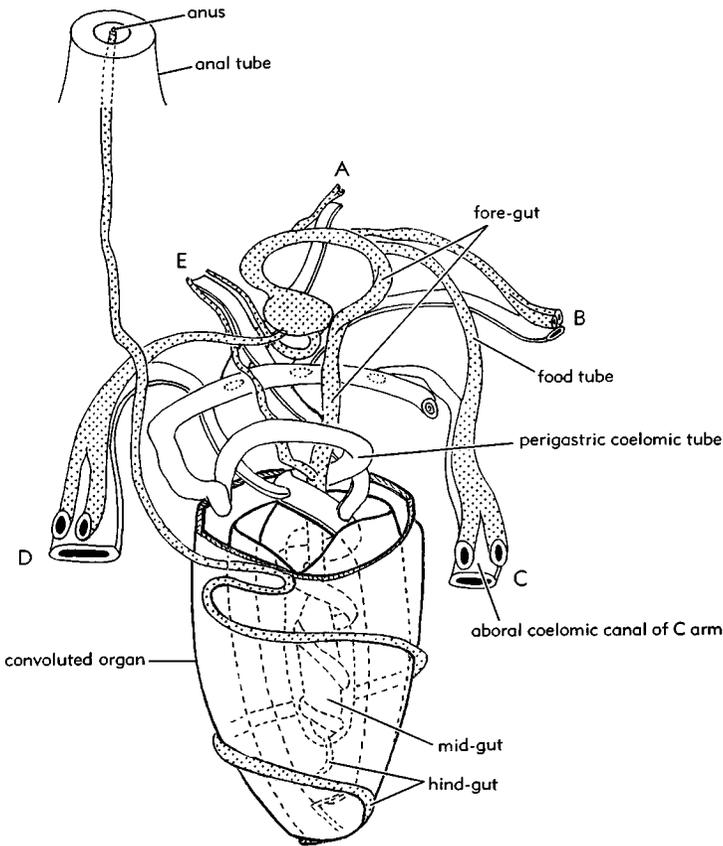


FIG. 169. Diagrammatic reconstruction of the digestive system and part of the coelomic system of camerate crinoids. [Explanation: food tubes and digestive tube stippled. Rays identified by symbol letters of CARPENTER system] (mod. from Haugh, 1975a). (From *Journal of Paleontology*, v. 49, no. 3, May, 1975, courtesy of The Paleontological Society and Bruce N. Haugh.)

distinctive internal structures that have been interpreted as remnants of the digestive and other visceral organs (HAUGH, 1975). It is probable that in life calcitic spicules included in the walls of these organs formed a supportive framework that has been preserved after death by secondary calcification or silicification. We have already noted (p. T133) that the food grooves of the arms were transformed into tubular conduits as they entered the theca. In some cases these conduits appear to comprise an alternating series of floor-plates, probably accompanied by covering plates. They converged into five or six ducts that led, not into an open mouth as do the ambulacral tracts of the flexible and articu-

late crinoids, but directly into the fore-gut, each duct reaching this structure at a separate point (Fig. 169). The lack of an open mouth and its replacement by a bulbous closed terminal chamber were apparently required to prevent the food from penetrating into the visceral cavity.

The fore-gut, after a loop, bent abruptly downward, descended vertically, and then expanded in an elongate mid-gut, from the bottom of which started a constricted tube, the hind-gut. The latter, after one or two turns inside the so-called "convoluted organ" (see below), emerged from the base of this structure, wound around its exterior generally three or four times, and finally entered the anal tube or ended directly in

the vent. Ordinarily near the upper part of the convoluted organ the coiling direction reversed—a change that took place in the *CD* interray.

### STRUCTURE PROBABLY ASSOCIATED WITH COELOMS

The theca of many camerates from the Ordovician to the Mississippian contains a coiled axial body, known as the **convoluted organ** (Fig. 170). This body extends from beneath the origin of the food tubes down to the basal circlet. Open at both ends, it may be fusiform, cylindrical, or trochoid, and appears to have consisted of a helically coiled, vertical wall. This wall in the usual state of preservation is solid and thickly incrustated with inorganic precipitates, probably deposited after burial, but in life it seems to have consisted of a mesentery strengthened by a spicular calcitic meshwork. In many instances, it includes a dark median layer of degraded organic matter from the original tissue.

The convoluted organ, a name introduced by WACHSMUTH & SPRINGER (1879), was first taken by WACHSMUTH (1877) for the alimentary canal itself. Later on WACHSMUTH & SPRINGER (1881, p. 35 [209]) suggested that it could represent “an extensive plexus of blood vessels surrounding the ambulacral canals” and be called the “oesophageal network.” BATHER (1900) considered it as a spicular calcification of the connective tissue around the axial sinus, apparently serving to support the digestive tube. As seen above, it certainly surrounded the fore-gut and the mid-gut passing down its hollow axis and carried the hind-gut coiling around it. There is little doubt that its spicular framework belonged to the visceral skeleton, and that the body cavity was divided by this organ into an inner “perigastric subcoelom” and an outer “peripheral subcoelom.” HAUGH (1957), who proposed these designations, calls this structure the “**perigastric coelomic organ**.”

Within the theca of some camerates one may observe an inner calcareous lining that varies greatly in appearance (Fig. 171). It may consist of simple pillars, or star-shaped protuberances with many rays and deep

depressions between the rays, or stereomic extensions that spread out and join similar extensions at their edges, thus forming a perforated plated structure held away from the thecal plates by pillars. This lining extends under the tegmen and over most of the thecal interior but does not cover the basal plates (Fig. 172). Between it and the thecal wall, a space is left that certainly belonged to the coelom, and, because this structure surrounded most of the viscera, it has been termed **perivisceral coelomic organ** by HAUGH (1975).

At the lower (proximal) edge of the lining, passageways formed openings for the aboral nervous cords, which, coming from the chambered organ and leading to the arms, were located between the lining and the inner thecal plate surfaces (Fig. 131). At the upper (distal) end of the lining, there are six extensions: two in the *CD* interray and one in each of the other four interrays (Fig. 173). Those four latter extensions connect directly with a ring commissure (**perivisceral coelomic ring**) pressed against the upper, inner surface of the tegmen. The two extensions in the *CD* interray are attached to an auxiliary ring, which in its turn is connected with the main ring commissure (HAUGH, 1975).

These complex perivisceral structures in camerates have no certain equivalent in other crinoids. They may possibly correspond to the perihemal coelomic system of the extant forms, though they differ from it by their great expansion in the body cavity, and their apparent lack of tubular branches into the arms. Their discovery under the tegmen of many specimens led some authors (WACHSMUTH, 1877; WACHSMUTH & SPRINGER, 1891; P. H. CARPENTER, 1884a) to consider that in camerates a second integument equivalent to the disk or tegmen of the recent forms occurred below the outer pavement, a subtegminal “disk,” to which the term “vault” or “dome” was applied and which was regarded as a structure peculiar to Paleozoic crinoids, but lacking in their successors. It was supposed that the “vault” represented a part of the aboral system of plates that has grown to cover and protect the originally flexible tegmen. Such distinction between “vault” and “disk” was rejected long ago (NEU-

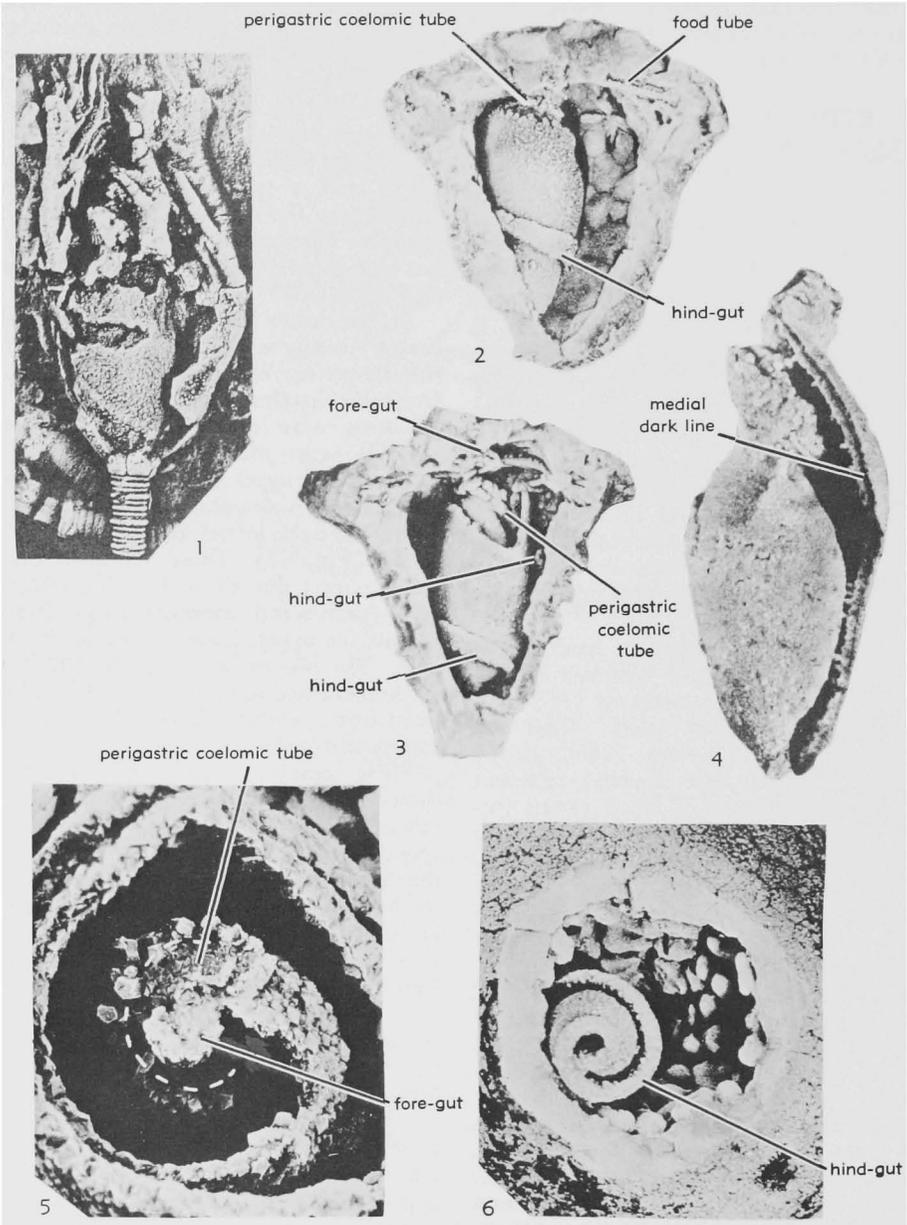


FIG. 170. Convoluted organ of camerate crinoids (2-6, from *Journal of Paleontology*, v. 49, no. 3, May, 1975, courtesy of The Paleontological Society and Bruce N. Haugh).

1. *Ptychocrinus fimbriatus* (SHUMARD), M.Ord., USA (Mo.); theca open showing convoluted organ (lat. view),  $\times 4$  (Brower, 1973).
2. *Teleiocrinus umbrosus* (HALL), L.Miss., USA (Iowa); theca open with whole convoluted organ,  $\times 1.1$  (Haugh, 1975a).
3. *Teleiocrinus liratus* (HALL), L.Miss., USA (Iowa); theca open with convoluted organ partly broken,  $\times 0.8$  (Haugh, 1975a).
4. *Actinocrinites verrucosus* (HALL), Miss., USA (Ind.); central part of convoluted organ (Haugh, 1975a).

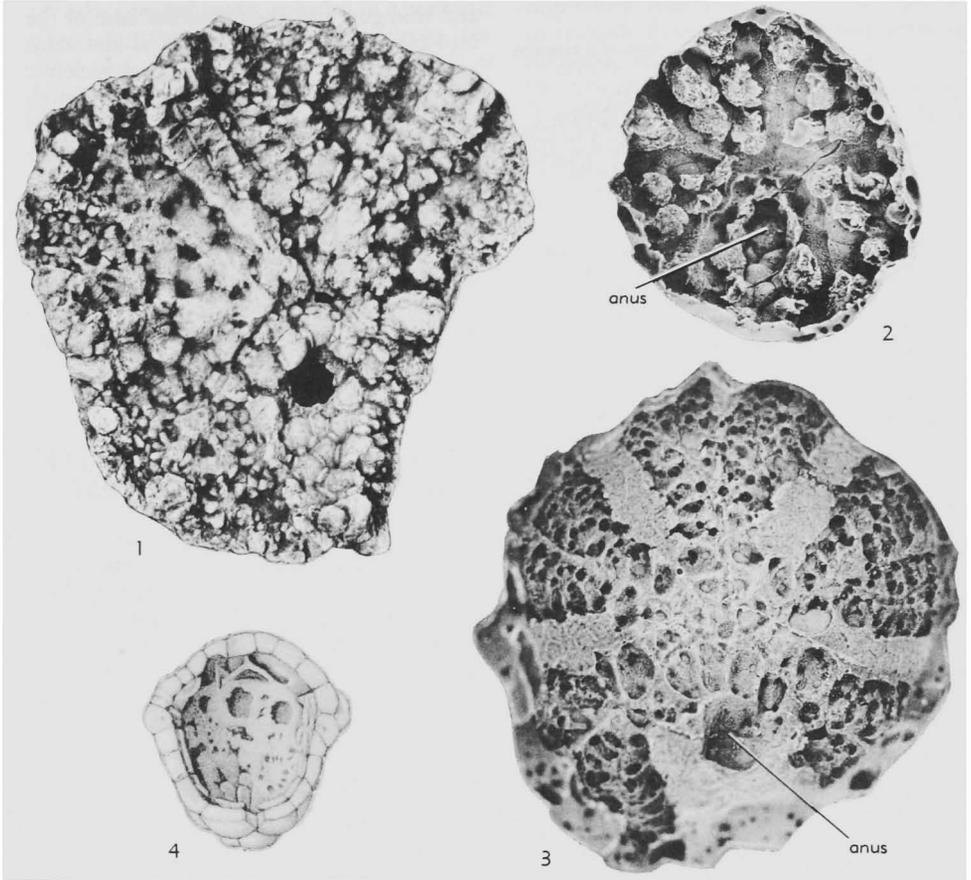


FIG. 171. Perivisceral coelomic lining of camerate crinoids.—1. *Physetocrinus ventricosus* (HALL), Miss., USA (Iowa); inner aspect of portion of tegmen, U.S. Natl. Museum S 1262,  $\times 2$  (T. Phelan, n).—2. *Eutrochocrinus christyi* (SHUMARD), Miss., USA; inner view of tegmen, latex cast, U.S. Natl. Museum S 885,  $\times 2$  (Ubaghs, n).—3. *Teleiocrinus* sp., Miss., Iowa; inner view of tegmen, latex cast, U.S. Natl. Museum SPRINGER Coll.,  $\times 2$  (Ubaghs, n).—4. *Uperocrinus longirostris* (HALL), Miss., USA (Iowa); broken theca showing perivisceral lining within aboral cup and tegmen,  $\times 1$  (Wachsmuth & Springer, 1897).

MAYR, 1889; BATHER, 1890a). It now appears to be groundless.

According to HAUGH (1975), from whom all these proposals have come, tubular coelomic structures were also present in the arms and in the theca of the camerate crinoids in addition to the major body coelom (Fig. 169, p. T200). Best observed at their en-

trance in the thecal cavity, these structures appear as flattened "tubes" that divide the keyhole-shaped arm openings into upper and lower halves. Each free arm has such a tube, and these tubes merge into five (one per ray) primary canals where they enter the body cavity. Just above the convoluted organ, these canals connect with a

(Continued from facing page.)

5. *Strotocrinus glyptus* (HALL), L. Miss., USA (Iowa); convoluted organ with top broken away revealing fore-gut and perigastric coelomic tube,  $\times 4.5$  (Haugh, 1975a).

6. *Eutrochocrinus christyi* (SHUMARD), L. Miss., USA (Iowa); hind-gut emerging from base of convoluted organ,  $\times 2$  (Haugh, 1975a).

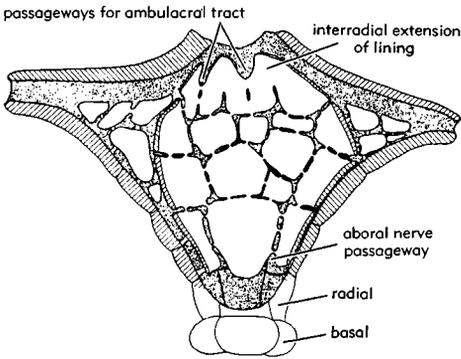


FIG. 172. Diagrammatic reconstruction of the perivisceral coelomic lining of a generalized camerate crinoid (lateral view). The lining is held away from the thecal plates by pillars (Haugh, 1975a). (From *Journal of Paleontology*, v. 49, no. 3, May, 1975, courtesy The Paleontological Society and Bruce N. Haugh.)

loop-shaped portion of a contorted tube (**perigastric coelomic tube**), the two ends of which do not appear to join any other structures. This tube penetrates the convoluted organ, wraps tightly around the fore-gut

and mid-gut, and ends near the base of the mid-gut. The flattened tubes of the arms may be homologous to the aboral coelomic canals of the arms of recent crinoids, though in modern forms these canals do not extend into the thecal cavity but connect directly to the perivisceral compartment of the coelom.

Evidence for the existence of another coelomic system in the arms of camerates corresponding to the subambulacral (subtentacular) canals of the extant crinoids is not conclusive, but this is not proof that such a system was lacking.

### STRUCTURES POSSIBLY ASSOCIATED WITH REPRODUCTIVE SYSTEM

In recent crinoids the gonads are usually located in the genital pinnules, more rarely in the arms, but never in the theca. This peripheral location of the gonads is one of the most distinguishing features of the crinoids, which in this respect stand alone among the stalked echinoderms. Each gonad of a crinoid is connected with a strand

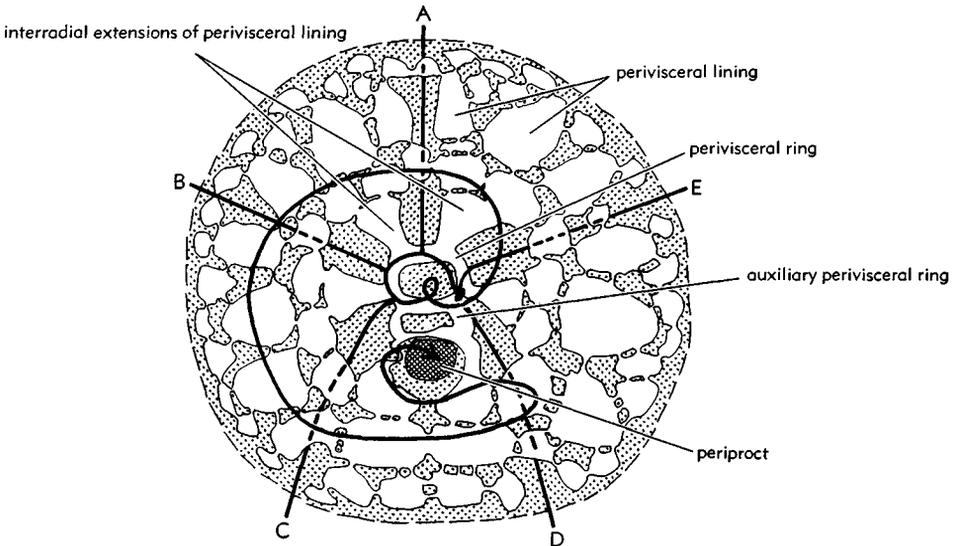


FIG. 173. Diagrammatic reconstruction of the perivisceral coelomic lining of a generalized camerate crinoid (ventral view) (Haugh, 1975a, mod.). [Explanation: rays identified by symbol letters of CARPENTER system. Trace of gut and ambulacral tracts indicated by heavy lines.] (From *Journal of Paleontology*, v. 49, no. 3, May, 1975, courtesy The Paleontological Society and Bruce N. Haugh.)

of cells (genital cord) included in a coelomic canal (genital canal) that transverse the arm and penetrates the theca where it is gradually lost in the meshes of the subtegmental lacunar plexus.

There is no direct evidence of the presence of gonads in the arms or pinnules of fossil crinoids. JAEKEL (1895), it is true, interpreted the distal widening of the pinnules of *Acanthocrinus* and a velum-like extension along the pinnules of *Hapalocrinus elegans* as possibly connected with the former existence of gonads in these two Devonian camerates. But in both cases detailed studies of the structures under question have shown that they were not fit for such a function (W. E. SCHMIDT, 1934; UBAGHS, 1947). Neither is there proof that the gonads were located within the theca and still less within the column as sometimes supposed (YAKOVLEV, 1922). A pore in the posterior (CD) oral plate of several inadunates such as *Hybocystites*, *Hobocrinus*, *Haplocrinites*, *Porocrinus*, or *Lageniocrinus* might well be a hydropore.<sup>1</sup> Pores or slits in the oral plates of *Cupressocrinites* have been regarded as gonopores by SIEVERTS-DORECK (SIEVERTS, 1934), who attributed the same meaning to the pores in the anal sac of many cladid inadunates. A similar supposition was made by GISLÉN (1924), who thought that a part of the gonad, in addition to a part of the intestine, may have been enclosed in the anal sac, and that such intrathecal location of the gonad would explain the extension of the adoral thecal perisome high up between the arms, as seen in many flexibles and inadunates. One or two marginal extensions of the radials of the allagecrinid genus *Trophocrinus* have been conjectured by KIRK (1930) as possibly representing "brood pouches" of a sexually dimorphic type, but this interpretation has been judged not entirely conclusive by PECK (1936) and rejected by STRIMPLE & KOENIG (1956).

## STRUCTURES ASSOCIATED WITH RESPIRATION

Skeletal structures presumed to have had

<sup>1</sup> In *Lageniocrinus* and other microcrinoids without arms, the gonad must have been located within the theca. In such case, genital products may have been emptied outward through a common hydropore-gonopore orifice.

respiratory functions are far less common in crinoids than in other pelmatozoan echinoderms, very likely because the arms of the former offer a much more extensive surface for gaseous exchanges with the sea water than the food-gathering appendages of the latter. Nevertheless, stereomic structures generally regarded as having had a respiratory function occur in some Paleozoic (mainly Lower Paleozoic) species, which for some reason probably needed a supplementary supply of oxygen. In these structures, the gaseous exchanges are supposed to have taken place either at the outer surface of the body wall or to have been effected at the inner surface of the skeletal armor, so that functionally two main types of organs may be distinguished: **exospores**, which were evaginations of the body wall, and **endospores**, which consisted of invaginations of the body wall (HUDSON, 1915).<sup>2</sup>

### EXOSPIRES

Apposed articular faces of thecal plates (rarely of columnals) of some crinoids may enclose simple or branched canals (**interarticular canals**). Each of these canals opens either on the inner or outer surface of the skeleton and so terminates in an internal and an external pore, or it has an internal opening only and no connection with the exterior. These pores are placed either along the sutures, or at the corners of the plates. They may, therefore, be called **sutural pores** and **goniopores**, respectively, though they probably differ in no essential way. In both cases the interarticular canals are supposed to have housed small fleshy projections, similar to the gills or papulae of asteroids, and, like these organs, retractile and provided with a lumen continuous with the general body cavity, so that coelomic fluids could be carried into them and have gaseous exchanges with the sea water.

Several types of these pore-canal structures presumably associated with such branchial vesicles are known. Most of them are remarkably like the sutural pores, or

<sup>2</sup> According to HAUGH (1973), a third type of respiratory organ was perhaps present in camerates. He suggested that the distal section of the hind-gut of these crinoids was possibly associated with a passive respiratory sac or a fluid-filled coelomic cavity acting as a cloacal pump. Evidence for the existence of such structures does not appear to be conclusive.

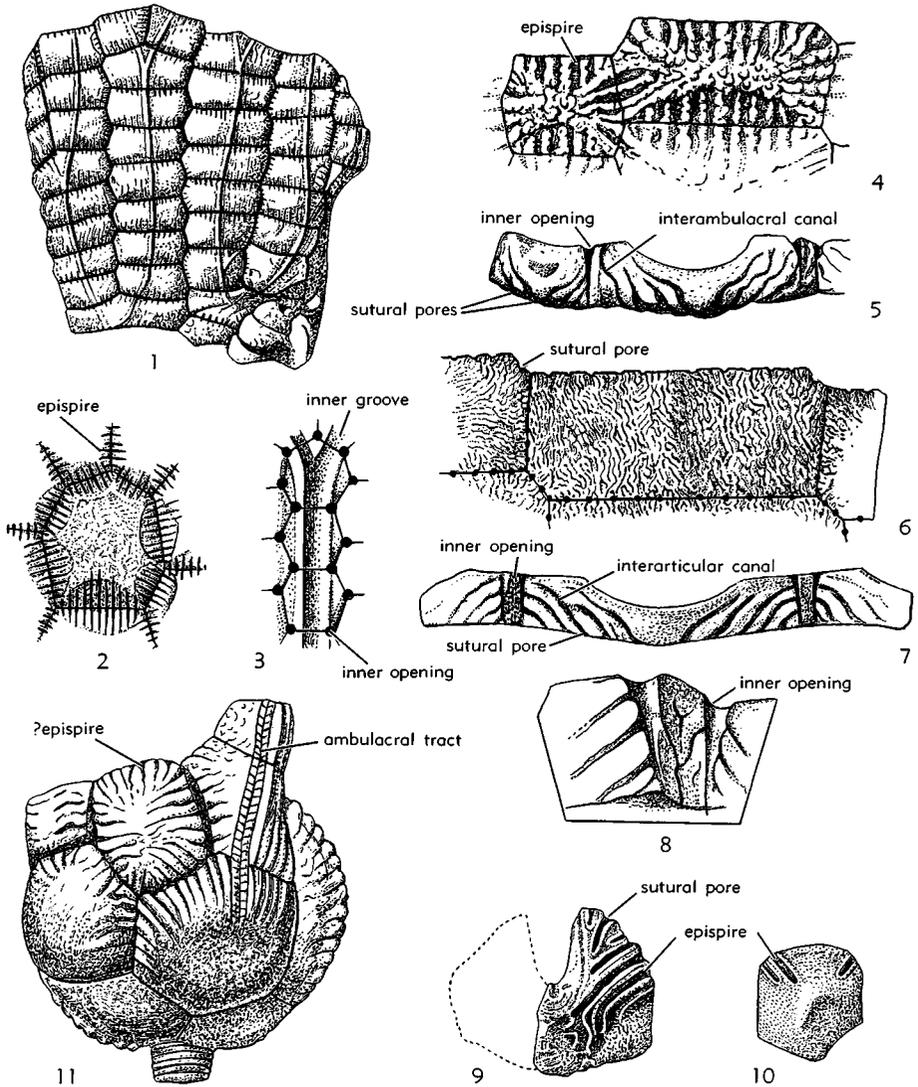


FIG. 174. Morphology of exospires: sutural pores and open epispires.

- 1-3. *Cleiocrinus regius* BILLINGS, M.Ord., Can. (Ont.); 1, fragment of calyx, showing rhombic areas (epispires) with slits crossing sutures,  $\times 3$ ; 2, axillary plate, outer surface,  $\times 4.5$ ; 3, calyx plates, inner surface, with groove and large pores at plate corners,  $\times 6$  (Springer, 1911c).
- 4,5. *Cleiocrinus sculptus* SPRINGER, M.Ord., USA (Ky.); 4, calyx plates, outer surface, with epispires forming rhombic areas across sutures,  $\times 6$ ; 5, distal face of cup plates, showing interarticular canals running from sutural pores on outer surface to funnel-shaped depressions with inner opening at plate corners,  $\times 6$  (Springer, 1911b).
- 6-8. *Cleiocrinus tessellatus* (TROOST), M.Ord., USA (Tenn.); 6, calyx plates with sutural pores, outer surface,  $\times 9$ ; 7, distal face of calyx plates, with interarticular canals discharging into funnel-shaped depressions at plate corners,  $\times 9$ ; 8, funnel-shaped depressions and inter-articular canals,  $\times 12$  (Springer, 1911b).
- 9,10. *Carabocrinus slocomi costatus* FOERSTE, U. Ord., USA (Iowa); radial and anal plates, with bordered epispires,  $\times 3$  (Foerste, 1925).
11. *Hybocystites eldonensis* (PARKS), M.Ord., Can. (Ont.); CD-interray view, with grooves (? epispires) crossing sutures,  $\times 3$  (Springer, 1911b).

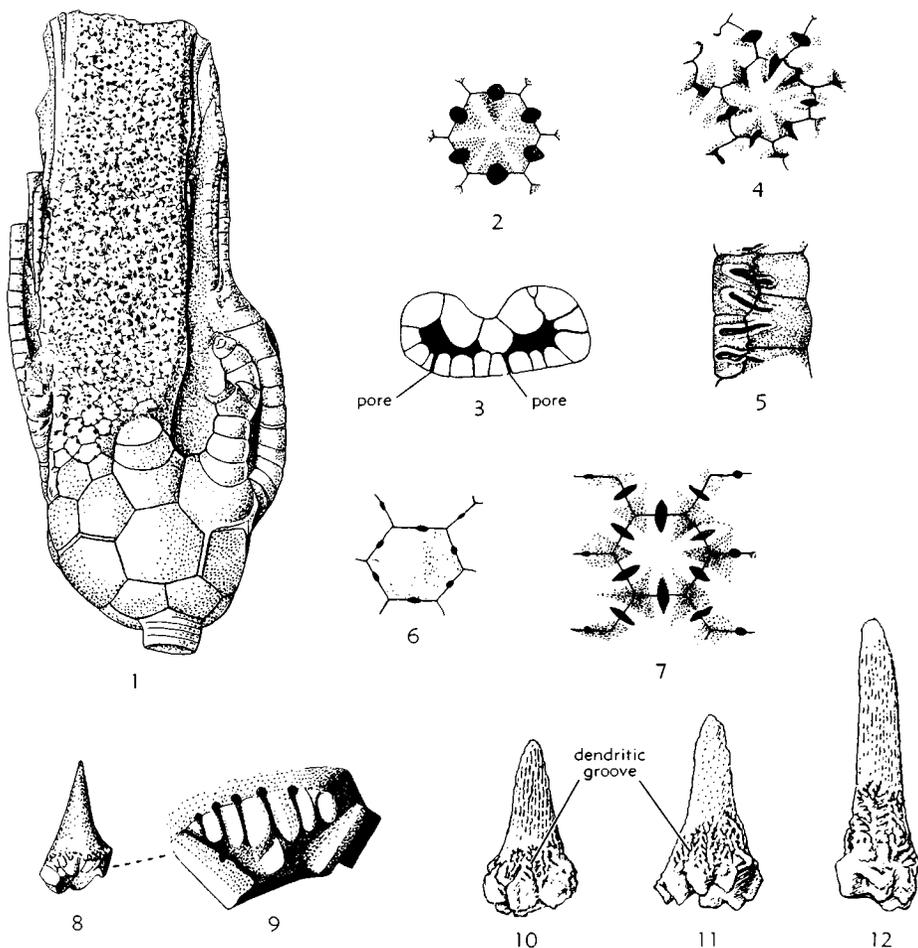


FIG. 175. Pore-canal structures in anal sac of poteriocrinine inadunates.

- 1-3. *Parisocrinus crawfordsvillensis* (MILLER), Miss., USA(Ind.); 1, specimen showing part of perforated anal sac,  $\times 2$ ; 2, plate of sac,  $\times 6$ ; 3, transverse section of sac showing pore-canal structure through sac wall,  $\times 4$  (Springer, 1900a).
4. *Blothrocrinus swallowi* (MEEK & WORTHEN), Miss., USA(Iowa); plates of sac,  $\times 6$  (Springer, 1900a).
5. *Abrotocrinus unicus* (HALL), Miss., USA(Ind.); plates of sac, with slitlike pores,  $\times 6$  (Springer, 1900a).
6. *Auloocrinus agassizi* WACHSMUTH & SPRINGER, Miss., USA(Ind.); plate with tiny pores,  $\times 6$  (Springer, 1900a).
7. *Decadocrinus tumidulus* (MILLER & GURLEY), Miss., USA(Ind.); plates of sac, with pores of various shapes and sizes, lying on ridges across sutures,  $\times 6$  (Springer, 1900a).
- 8,9. *Hydreionocrinus* sp., Perm., Timor; 8, isolated distal plate of anal sac, lat. view,  $\times 1$ ; 9, articular facet of same, with pore-canal structures,  $\times 4$  (Wanner, 1916a).
- 10-12. *Hydreionocrinus* sp., L.Carb., Scot.; isolated spiniferous distal plates of anal sac, lat. view,  $\times 2$  (Bather, 1912).

epispire, of eocrinoids, and may be so termed. They consist of interarticular canals and sutural pores or gonipores only, or of those structures coupled with epithecal

extensions (grooves or canals) that lay on the outer surface of the thecal plates. Thus, in the camerate genus *Cleioocrinus* (Fig. 174,1-8), external pores are present along

the sutures and at the angles of the calycal plates. They are extremely numerous; probably several thousands of them are present in a mature individual. They may remain simple or be accompanied by narrow grooves that extend across the adjacent plates and form rhombic striated areas bisected by the sutures. The interarticular canals corresponding to the pores do not generally pass directly through the test, but lead to large, funnel-shaped depressions that open into the thecal cavity at the corners of the plates (HUDSON, 1911; SPRINGER, 1911b). At the junction of the orals, radials, and anal *X* in some species of the cyathocrinine inadunate *Carabocrinus* (e.g., *C. esthonus*, *C. radiatus*, *C. slocomi*, *C. treadwelli*), there is a series of narrow grooves that cross the common junctures of these plates and extend for some length on their outer surface (Fig. 174,9,10); these grooves may be bordered by slightly raised rims. They vary greatly in number and size even within a single species, and are connected with sutural pores and vertical canals penetrating to the interior; thus, they form complex structures very much like the epispires of the eocrinoid genus *Lichenoides*. According to SPRINGER (1911b), similar structures are present on the anal and adjacent plates of the hybocrinid *Hybocystites eldonensis* (Fig. 174,11), and possibly on the anal plate of *Hybocrinus tumidus*.

In some inadunates (e.g., *Culmicrinus regularis*, *Hallocrinus* ? *inagilis*, *Lophocrinus minutus*, *Poteriocrinites* ? *broadheadi*) small perforations occur at most angles of cup plates. The exact function of these so-called goniopores is unknown, but it may have been similar to that of the just-described sutural pores.

Sutural pores may also occur in the adoral skeleton. This is particularly true of many poteriocrinine inadunates, the anal sacs of which have countless perforations (Fig. 175). These small, round or slitlike openings are typically located at the middle of the sutures, generally in depressions between axial folds (Fig. 175,2,4), more rarely on folds that cross the sutures at right angles (Fig. 175,7). In some cases, these pore-canal structures become very complex; branching repeatedly as they approach the outer edges of the plates, they form a

dendritic system of shallow grooves that may extend on the outer plate surface and the base of spines (Fig. 175,11,12).

In all of the preceding examples, the interarticular canals are thought to have been open to the exterior, but those of some crinoids were not so. Thus, in the anal sac of the poteriocrinine inadunate *Aesioocrinus magnificus* grooves forming a complex tubule system on lateral articular faces of plates terminate on the outer surface in rounded, commonly expanded tips that are sealed off from the exterior (LANE, 1975). The cup plates of the cyathocrinine genus *Palaeocrinus* are ornamented with parallel, hollow ridges that cross the sutures at right angles and have no opening to the exterior (Fig. 176). In *P. striatus* the lumen of each ridge communicates directly with a large sutural canal, which opens into the interior of the calyx through a vertical canal (HUDSON, 1911). In *P. planobasalis*, the ridges are grouped into raised bundles, and their canals open into a rhomb-shaped central chamber, which in turn opens into the calyx interior (Fig. 176,4). Series of transsutural hollow ridges occur also on the outer surface of the cup of the monocyclic inadunate genus *Tiaracrinus* (Fig. 176,5-7). But here each ridge contains a canal, which arises from a pore on the inner surface of one radial, crosses the adjacent interradial suture, and ends in a pore located on the internal surface of another radial. Such a set of pore-canal structures is quite similar to a simple humatirhomb as found in some rhombiferan cystoids. Function of these structures in crinoids has been discussed by HUDSON (1911), BROWER & VEINUS (1974), and LANE (1975), and in cystoids by PAUL (1972). It is supposed that body fluids flowed through these interarticular and tangential canals in life, and that gaseous exchanges took place through their thin stereom outer covering. Possibly the hollow ridges of the peritocrinid *Tetracionocrinus* and of some other early crinoids provided with very thin plicated cup plates served the same role, for they represent extension of the thecal cavity close to the outer body surface, and increase the surface area.

Probably similar in function, though structurally different, are the interarticular pits called **gonioporoids** by W. E. SCHMIDT

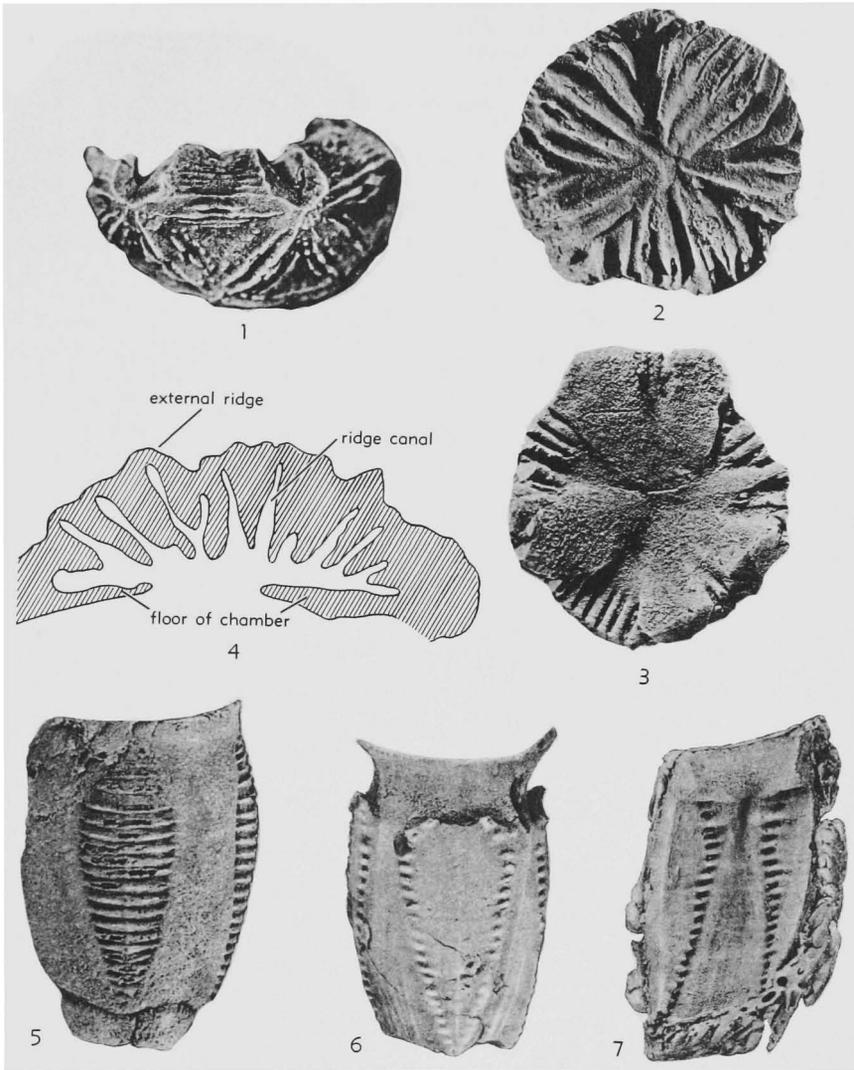


FIG. 176. Morphology of covered epispires.

1-4. *Palaeocrinus planobasalis* BROWER & VEINUS, M.Ord., USA (Tenn.-Va.); 1, cup in BC-interray view,  $\times 1.7$ ; 2, isolated basal, external face, with canals of internal ridges exposed by weathering at some places,  $\times 2.7$ ; 3, same, internal face,  $\times 2.7$ ; 4, cross section of isolated plate,  $\times 10$  (Brower & Veinus, 1974).

5-7. *Tiaracrinus moravicus* UBAGHS & BOUČEK, L. Dev., Czech.; 5, cup in lat. view,  $\times 3$ ; 6, internal mold of thecal cavity, with infilling of inner pores partially preserved,  $\times 3$ ; 7, internal surface of isolated radial plate,  $\times 3$  (Ubaghs & Bouček, 1962).

(1931) (Fig. 177). These pits or depressions open into the thecal cavity, but do not reach the outer surface of the skeleton. They are located at the corner of the plates in the calyx and also in the tegmen (including the anal sac) and possibly (though

somewhat modified) in the column. They may be simple and cylindrical, or be provided with lateral ampulla-like cavities, which extend on the adjacent articular facets (Fig. 177, 1-3, 5). All these cavities form a complex system in open connection

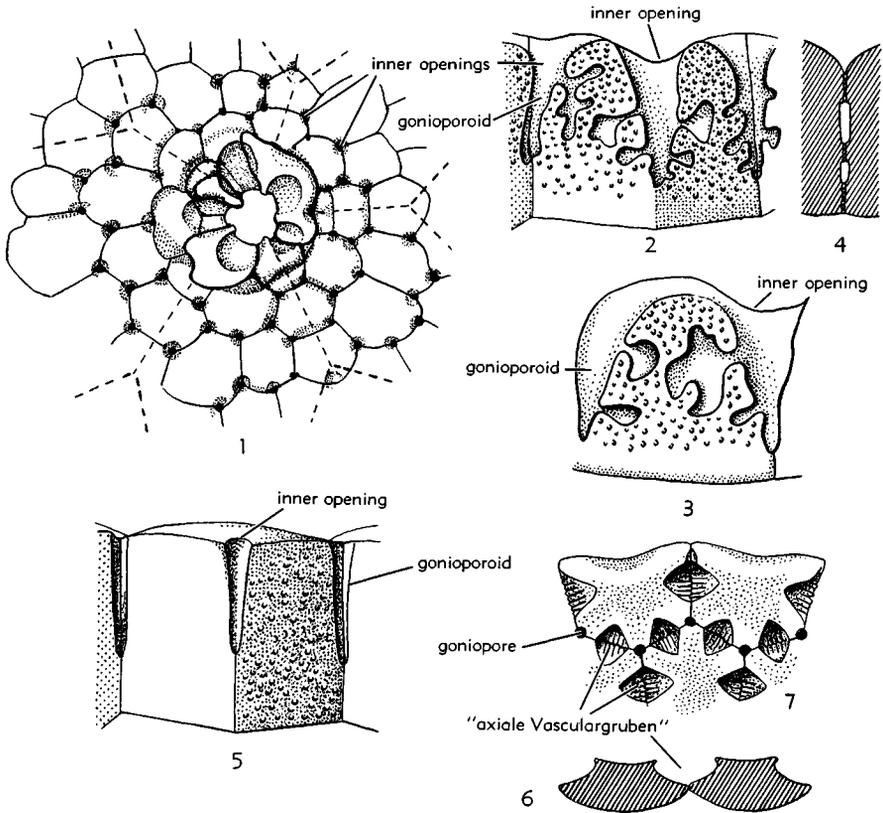


FIG. 177. Morphology of gonioporoids and gonioporoid-like structures.

1-5. *Trybliocrinus flatheanus* (GEINITZ), L.Dev., Spain; 1, proximal part of cup, internal side; rays indicated by interrupted lines,  $\times 1.5$  (W. E. Schmidt, 1932); 2,3, articular faces of cup plates with branched gonioporoids,  $\times 4$  (W. E. Schmidt, 1932); 4, diagram. section through juncture of two cup plates with two gonioporoids (W. E. Schmidt, 1932); 5, ar-

ticular faces of cup plate with simple gonioporoids, diagram.,  $\times 4$  (Ubaghs, n).

6,7. *Culmicrinus regularis* (VON MEYER), L.Carb., Ger.; 6, transverse section of two radials, inner side above,  $\times 6$ ; 7, inner side of two radials and parts of three basals,  $\times 6$  (redrawn from W. E. Schmidt, 1930).

with the thecal cavity, and thus probably represent an extension of the coelom into the skeletal armor. The occurrence of gonioporoids has been recorded mainly from camerate species, but similar structures seem to have developed also in some inadunates. For instance, deep sutural pits that do not open to the exterior mark the inner surface of the anal sac of the poteriocrinine species *Synphocrinus magnus* (Fig. 178). Other inadunates (i.e., *Culmicrinus regularis*, *Hallocrinus* ? *inagilis*, *Lophocrinus minutus*) show diamond-shaped depressions bisected

by the plate sutures at the inner side of the cup; the very thin and fragile outer wall of these depressions may be both reinforced and divided into narrow compartments by small ridges running transversely across the plate junctions (Fig. 177,6,7); though they are placed on plate sides rather than at plate corners, these "axiale Vasculargruben" as W. E. SCHMIDT (1930) called them, are best regarded as only one particular type of gonioporoids.

Another type of gonioporoid is exemplified by the irregular spaces between the

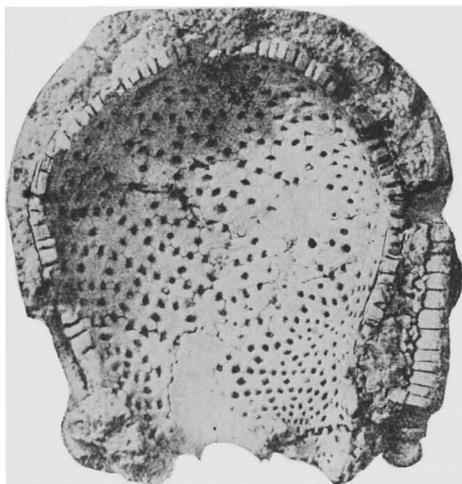


FIG. 178. *Synphocrinus magnus* YAKOVLEV & IVANOV, M.Carb., USSR; distal part of anal sac, broken open to show gonioporoids on inner face and section,  $\times 1$  (Yakovlev & Ivanov, 1956).

tegmenal plates of the camerate species *Trybliocrinus flatheanus*; in open connection with the coelomic cavity, these spaces could have provided circulation of coelomic

fluids among the plates of the tegmen (Fig. 179,2). Also, in the stem of this crinoid, on the articular face of the columnals, radiating grooves open into the axial canal through vertical slits but terminate near the periphery without communicating with the exterior. They may have had a role similar to that of the gonioporoids of the theca (Fig. 54,11, p. T75).

Somewhat different in nature but possibly not in function was the system of narrow canals that in some crinoids are found within (not between) the plates. Thus, the tegmenal plates of the just-mentioned *Trybliocrinus flatheanus* (Fig. 179, 1,3), and the undivided basis of the strange species *Lodanella mira* encloses a complicated network of branching canals that open into the thecal cavity but end without reaching the exterior; even if in life those canals were filled with uncalcified tissues, they must have facilitated the circulation of the body fluids in the skeleton armor, and thus helped respiration.

### ENDOSPIRES

The endospires are respiratory organs in which the gaseous exchanges take place below or near the inner surface of the thecal

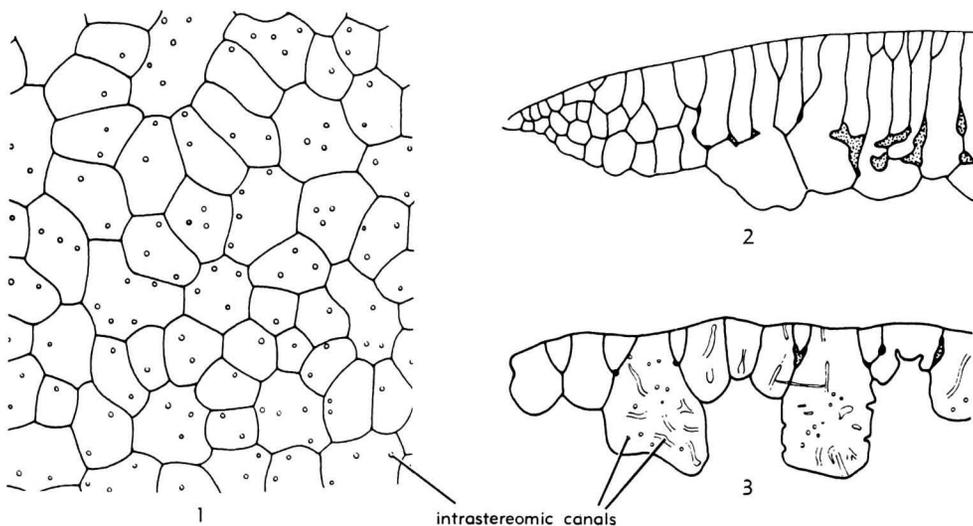


FIG. 179. *Trybliocrinus flatheanus* (GEINITZ), L.Dev., Spain; morphology of tegmen, ca.  $\times 3$  (Breimer, 1962).—1. External view of slightly weathered surface, showing canal system within plates.—2. Section through tegmen, with stratified margin at left, and lacunae between plates at right (stippled).—3. Section through tegmen, with inner expansions and canal system within plates.

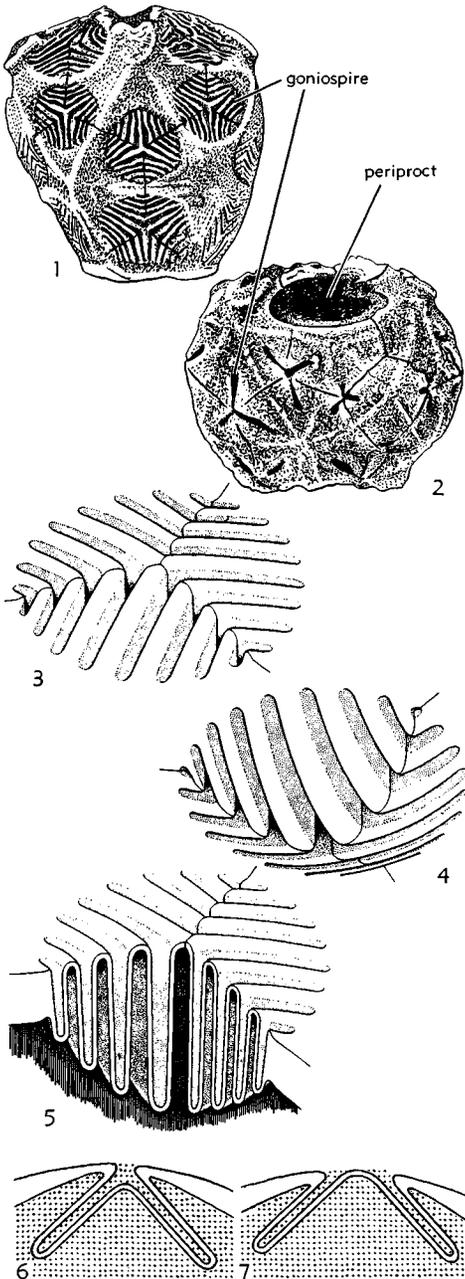


FIG. 180. Morphology of goniospires.—1. *Porocrinus shawi* SCHUCHERT, M.Ord., Can.; A-ray view,  $\times 4$  (Kesling & Paul, 1968).—2. *Triboloporus cryptoplicatus* KESLING & PAUL, M.Ord., USA (Va.); CD-interray view,  $\times 5$  (Kesling & Paul, 1968).—3-5. Diagram. representation of gonio-

armor. The calyx of some fossil crinoids is provided with folds, or deep depressions, into which a fresh supply of sea water is presumed to have been introduced continuously by ciliary action to replace that from which the oxygen had been extracted. Neither the folds nor the depressions open into the calyx cavity. It is only through extremely thin sheets of stereom or possibly sac walls that respiration could be effected.

A primary type of endospire structure is represented by the goniospires (HUDSON, 1915) found in the calyx of the cyathocrinine inadunate *Porocrinus* (Fig. 180, 1, 3-5). Each goniospire consists of three sets of parallel folds that meet the plate sutures at an angle. Folds of two half-sets on any one plate correspond to those of the adjacent half-sets on the adjacent plates; at the plate juncture they bend at an angle of about  $120^\circ$ . The longest fold was the first formed; it lies nearest the plate corners. The others were added in succession; their length decreases toward the middle of the plate sides. The folds had extremely thin walls, so that respiratory exchanges could be effected through them. In some species the goniospires are relatively small, in others, large; some were protected by being depressed into the plates, others by being adjacent to highly developed ridges. Those of the related genus *Triboloporus* are very simple; they appear externally as three clefts located at meeting points of plate corners, each cleft being the confluent of two lateral folds (Fig. 180, 2, 6, 7). The function of goniospires has been discussed in detail by KESLING & PAUL (1968).

A second type of endospire is exemplified by the perittocrinid inadunate *Perittocrinus*. It differs from the first type by the fact that the folds, instead of being located at plate corners, are placed on small triangular accessory plates that are inserted between the large calyx plates (Fig. 181). Each accessory plate has three groups of folds, one

spire in *Porocrinus* as viewed obliquely from (3) ext., (4) int., and (5) with one plate removed to expose folds (Kesling & Paul, 1968).—6, 7. Diagrammatic sections through plate corners to show structure of goniospires; 6, *Triboloporus cryptoplicatus* KESLING & PAUL, M.Ord., USA (Va.); 7, *T. xystratus* KESLING & PAUL, M.Ord., USA (Pa.) (Kesling & Paul, 1968).

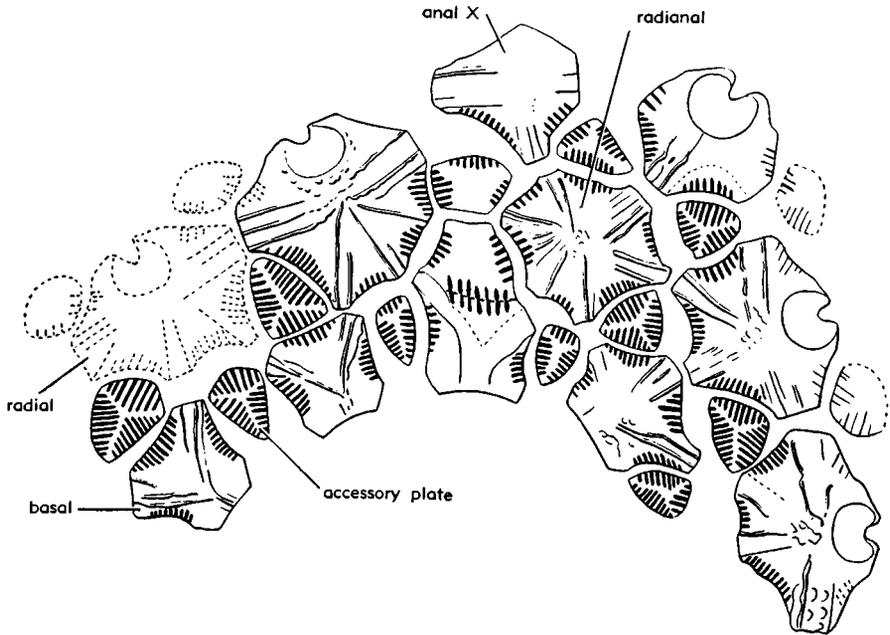


FIG. 181. *Perittocrinus radiatus* (BEYRICH), ?L.Ord., Baltic regions; diagr. of cup, showing location of goniospire structures on accessory plates (Ubaghs, 1971a).

group on each of its curved margins. The folds cross the sutures without bending, and extend into the adjacent large plates. The longest (oldest) folds are at the middle of the accessory plate sides, the shortest (youngest) ones near the accessory plate corners. Technically these structures should be called **craspedospire**s (according to HUDSON's nomenclature, 1915), because the folds are at plate margins. In fact, they do not differ essentially from the goniospires of *Porocrinus*, for the accessory plates with which they are associated could only develop by truncating the corners of three large plates.

Although these structures and the pectinirhombs of the rhombiferan cystoids were structurally similar and probably had similar functions, they differed in position and ontogeny (HUDSON, 1915; KESLING & PAUL, 1968; UBAGHS, 1971a). The pectinirhombs are confined to the margins of the plates, their folds are perpendicular to these margins, the last-formed folds lie nearest the plate corners, and during plate growth the folds elongated by simple addition of cal-

careous material on each side of the suture (Fig. 182,3). The goniospires are situated at plate corners (or on accessory plates developed at the expense of the corners of three large plates), the folds meet the sutures at an acute angle, the last-formed folds lie near the margin centers, and during growth adjustment was constantly needed to keep the direction of the folds unchanged, since the growth lines of the plates are angled or arcuate (Fig. 182,1,2). These differences suggest that the goniospires and the pectinirhombs evolved independently.

A third type of endospire characterizes the calyx of the Permian poteriocrinine inadunates *Indocrinus* and related genera (Fig. 183). They consist of rounded or subtriangular depressions occurring at every junction of three plate corners. The bottom of these depressions is so thin as to be translucent, but it may be strengthened by small ridges running from edge to edge across the sutures (Fig. 183,2,3). In *Indocrinus rimosus* and the genus *Metaindocrinus* the depressions at plate corners are re-

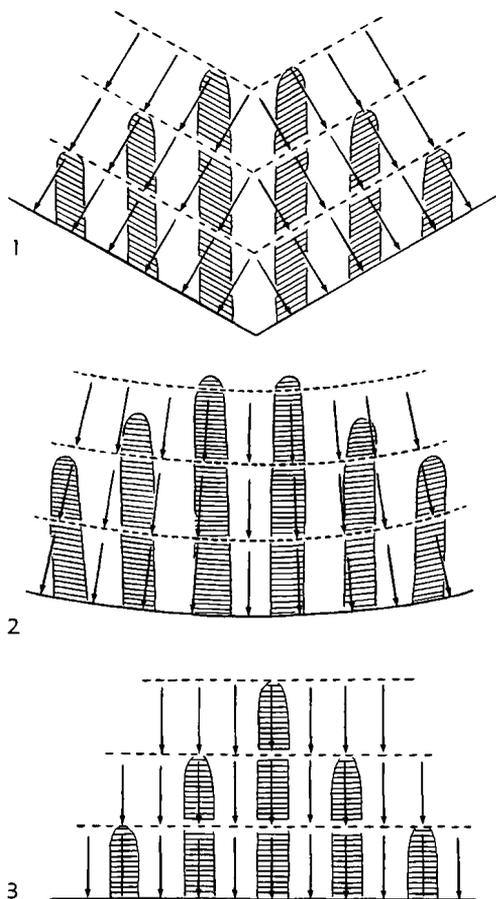


FIG. 182. Differences in mode of growth and development between goniospire of *Porocrinus* (1), goniospire-like structure of *Perittocrinus* (2), and pectinirhomb of cystoid (3) (Kesling & Paul, 1968; Ubaghs, 1971a). [Explanation: heavy lines, plate edges; dotted lines, growth lines; arrows, direction of growth.]

placed by slitlike troughs that cross the sutures at right angles; the longest (oldest) troughs are at the middle of the plate sides, the shortest (youngest), near the corners (Fig. 183,5). YAKOVLEV (1950) is the first to have recognized the probable respiratory function of these structures, for which the term **bothrospires** is proposed herein. They differ from goniospires by the fact that they are not composed of folds but of mere pitlike or slitlike depressions on the calyx surface.

A fourth type of endospire is found in the disparid *Acolocrinus* (Fig. 183,6,7). According to description and interpretation by KESLING & PAUL (1971), the respiratory system of this genus is divided into five unconnected parts, which are alike (except for the area around the anal plate). Each part develops along an interradius, with extensions along the inferradial-superradial joint faces and along the basal-inferradial joint faces. Serrate portions of sutures located around each point of meeting of two inferradials with two superradials and around each point of junction of one basal with two inferradials may have acted as incurrent slits. Parts of these slits that are farthest from these points of junction lead to canals within plates (each canal being shared by two plates), whereas the parts adjacent to junctions lead to channels (possibly provided with membranous sacs) inside of cup plates. These channels extend most of the length of the sutures between adjacent inferradials; those from above and those from below lead through short excurrent canals to a common pore at the middle of the suture. It is supposed that water entered through the serrate sutures and was expelled through the pores, and that gas exchange took place through membranous sacs inside the channels. A somewhat similar apparatus may have existed in another disparid genus, *Agostocrinus*, but it has not been worked out in sufficient detail.

### PINNULE OPENINGS IN THECA AND ARM TRUNKS

In many camerates belonging to various families, such as the Batocrinidae, Actinocrinitidae, Dolatocrinidae, or Platycrinitidae, pores occur at the limit of the cup and the tegmen, between arm bases. They have been called "respiratory pores," "ovarian apertures," or "thecal pinnular openings," according to their presumed function or morphological significance. They also have been designated as "interbrachial pores" and "thecal pores."

These pores do not penetrate the plates, but lie at their corners or within sutures. They may stand in close relation with the arm openings (Fig. 184,3), or be located at some distance from them (Fig. 184,1).

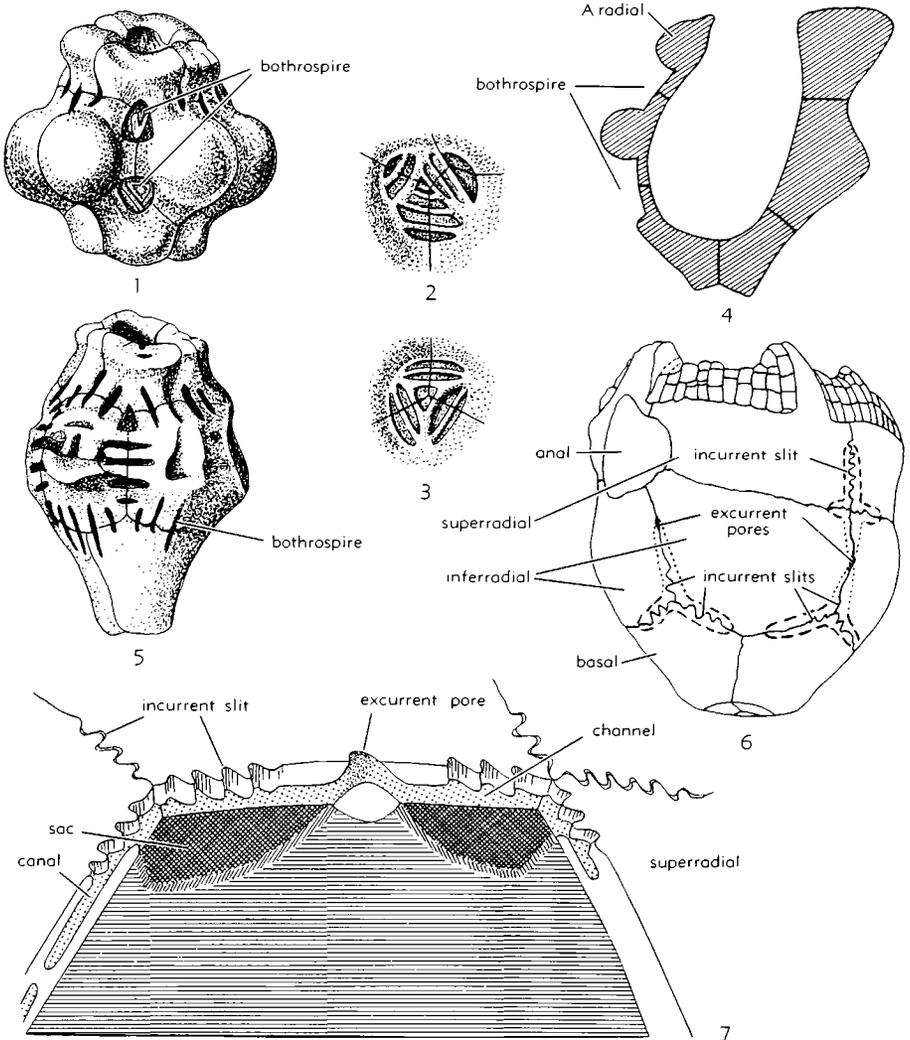


FIG. 183. Morphology of some endospire structures.

- 1-4. *Indocrinus elegans* WANNER, Perm., Timor; 1, cup in A-ray view,  $\times 2$  (Wanner, 1924); 2,3, detail of bothrospires,  $\times 4$  (Wanner, 1923); 4, vert. sec. through cup passing through A ray and CD interray,  $\times 3$  (Wanner, 1916a).  
 5. *Indocrinus rimosus* WANNER, Perm., Timor; cup in A-ray view,  $\times 3$  (Wanner, 1916a).  
 6,7. *Acolocrinus hydraulicus* KESLING & PAUL, M.

Ord., USA (Tenn.-Va.); 6, C-ray view of cup and arms [Explanation: interrupted lines, outlines of inner canals; dotted lines, outlines of inner channels],  $\times 5$  (Kesling & Paul, 1971, mod.); 7, diagram. view of part of cup with one inferradial plate removed to expose respiratory system; hypothetical respiratory sac indicated (Kesling & Paul, 1971, mod.).

In many cases they are obviously the outer apertures of passageways leading to the main ambulacral tracts. In other cases, such connections are not evident. Their number

varies from one to eight per interray. They generally are round and small, but they may have the shape of narrow vertical slits (Fig. 184,4). They may be present in im-

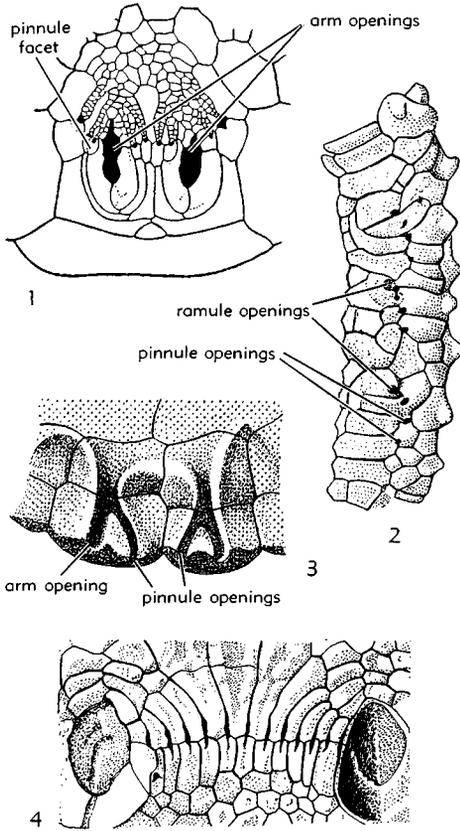


FIG. 184. Pinnule openings in camerates.—  
 1. *Marsupiocrinus inflatus* (TROOST), Sil., USA; part of ray showing pinnule openings and ambulacral tracts leading to them,  $\times 1.5$  (Springer, 1917).—2. *Eucladocrinus millebrachiatus* WACHSMUTH & SPRINGER, Miss., USA (Iowa-Ill.); part of arm trunk, lat. view,  $\times 1.5$  (Wachsmuth & Springer, 1897).—3. *Abatocrinus clypeatus* (HALL), Miss., USA; transv. sec. of theca at arm-opening level, plates separated at sutures,  $\times 4$  (Springer, 1917).—4. *Dolatocrinus grandis* MILLER & GURLEY, M.Dev., USA (Ky.); part of interray with 12 slitlike pinnule openings,  $\times 2$  (Springer, 1921a).

mature individuals and permanently closed in adults. Similar pores occur on both sides of arm trunks of *Eucladocrinus* (Fig. 184,2) and *Steganocrinus* at the limit of brachials and covering plates.

The internal passageways that correspond to these pores may be complex. Thus, in *Batocrinus icosidactylus* the lower part of the passageways is divided into a blind chamber and a canal that connects with the ambulacral tract of the adjacent arm. The external pore was protected in life by a covering, apparently movable, flap that is composed of the two proximal plates of the proximal pinnule, the hinge socket of which may be observed on the theca below the pore; adjacent to this flap is the first normal, free pinnule (HAUGH, 1973) (Fig. 129,3, p. T158).

As suggested by WACHSMUTH & SPRINGER as early as 1881 and conclusively demonstrated by SPRINGER in 1917, these pores are the outer openings of pinnules. This interpretation is supported by the following evidence: 1) in very well-preserved specimens pinnules are still attached at the emplacement of these openings; 2) hinge sockets of pinnules may be present below them (Fig. 184,1); 3) pores contiguous to arm openings are connected directly with the main arm groove by a narrow diagonal canal (Fig. 184,3); 4) if located farther from the arm openings, their connection with the main ambulacral tracts may be marked by the tracing of covering plates on the tegmen (Fig. 184,1). These pores therefore belong to the proximal pinnules, which generally became partially incorporated in the calyx during growth. These pinnules might have been somewhat different from the others, as just seen in *Batocrinus icosidactylus*, and like those of recent comatulids might have served special functions. Possibly also in some species the free parts of these pinnules were lost in life, while the pores remained open. But the role of the pores in such a case is unknown. One thing seems almost certain: they were not replacements for the hydropore or madreporite of some inadunates and flexibles, as supposed by BATHER (1900a), for they coexist in some camerates with a structure that has all the appearance of an internal hydropore or madreporite (see p. T197) (HAUGH, 1973).