

Treatise Editor
Frederick W. Harrison

Microscopic Anatomy of Invertebrates

Volume 14

Echinodermata

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New York • Chichester • Brisbane • Toronto • Singapore

Microscopic
Anatomy of
Invertebrates

Volume 14

Echinodermata

Microscopic Anatomy of Invertebrates

Encyclopedic in scope, contemporary in approach, this comprehensive work constitutes a major and unique contribution to the field—a landmark, multi-volume, fully illustrated reference on the functional anatomy of invertebrates.

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To facilitate timely publication while maintaining the phylogenetic order of the treatise, future volumes may be published out of sequence.

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Frederick W. Harrison

Microscopic Anatomy of Invertebrates

Volume 14

Echinodermata

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Endpapers:

Left: Anchor ossicle of the holothurian *Synaptula hydriformis*. From Clark, H.L. (1898) *Synapta vivipara*: A Contribution to the Morphology of Echinoderms. Memoirs from the Biological Laboratory of the Johns Hopkins University, IV, 2:53-93.

Right: Scanning electron micrograph of an anchor ossicle of *Synaptula hydriformis*. Magnification $\times 920$. Micrograph by Jennifer Frick. Contribution of the Western Carolina University Electron Microscope Facility.

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Dedication

To my wife Sharon and my daughters, Alisa and Maria.

F.-S.C.

With love to Ellen Julia Boyd Harris.

F.W.H.

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Preface to the Treatise

The plan for this treatise, *Microscopic Anatomy of Invertebrates*, had its inception during discussions in the Executive Committee of the American Microscopical Society. While all present agreed that this was a sorely needed project, the consensus was that the treatise would require a lifetime of work to complete. However, the discussion motivated me to pursue development of the idea, an undertaking of which I had dreamed for years. The possibility of joining the magnificent diversity of invertebrate animals with the excitement of modern microscopic anatomy was a thrilling, but challenging, prospect. That same evening I proposed the idea of a series of volumes, a microscopic anatomy encompassing the invertebrate phyla, to representatives of the Wiley-Liss publishing company.

The conceptual framework of the treatise is a straightforward one. The overriding thrust of the treatise is *functional* morphology. Although each chapter might begin with a short treatment of external or gross anatomy, the body of each chapter is devoted to microscopic anatomy, particularly cellular studies at the ultrastructural level.

Each chapter follows a format familiar to students of microscopic anatomy. In certain groups, not all systems are represented and emphases shift as appropriate. Whenever possible, the following outline is adhered to: (1) external anatomy and/or gross anatomy; (2) epithelia and integumentary structures; (3) glands and secretion; (4) connective tissue and supportive structures, including muscle where appropriate; (5) vascular elements and blood; (6) digestive system and associated organs; (7) respiratory structures and gas exchange; (8) excretory structures and fluid exchange; (9) reproductive components; (10) immune system and/or elements; (11) nervous system and sensory elements.

In two volumes, Volume 10 (*Decapod Crustacea*) and Volume 11 (*Insecta*), the format has been altered so that the above sections are written by different authors. The format alteration recognizes the complexity and voluminous nature of the literature dealing with these two arthropod groups.

In Volume 1, we employ the term "protozoa" in the broadest sense, embracing most major protistan assemblages, at least in part. Avoiding the sense of the separated "phylum protozoa," for purposes of this treatise we define protozoa as the primarily motile protists, including those taxa long considered as "true" protozoa.

I am grateful for the enthusiastic support provided to me by Western Carolina University. From the inception of the project, Western Carolina University has generously given financial support and

allowed me time to devote to my duties as treatise editor. I recognize with gratitude Mrs. Nancy King, Mrs. Shirley Weeks, and Mrs. Marcia Jarrell for their pleasant, uncomplaining, and extremely professional secretarial support. My co-workers in this project, the staff of Wiley-Liss, Inc., bring credit to the publishing profession. Finally, and especially, my wife Marion has been, as always, my source of strength.

FREDERICK W. HARRISON
Cullowhee, North Carolina

Chapter 1

Introduction to the Echinodermata

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INTRODUCTION

The most important characteristic shared by all members of the phylum Echinodermata is the water vascular system, which is a complicated set of interconnected tubes that originate from the hydrocoel during development. No animal in any other phylum has such structures. In this system, water enters (or exits) through a sieve plate, the madreporite, and passes into the stone canal, the water ring canal, and then, along the ambulacrae, the radial water canals. A series of lateral canals branch from both sides of each canal; each of these canals is connected with an ampulla and a tube foot (variations exist in some species). The radial water canal terminates as a tentacle. The water vascular system is known to function in locomotion, feeding, sensation, excretion, nutrient transport, and respiration.

Another feature of echinoderms is the endoskeleton, which comprises a series of perforated ossicles produced by mesodermal sclerocytes. The nervous system of echinoderms is diffuse and includes rings, cords, and networks of fibers distributed throughout the body wall and the viscera; however, there

is no concentration of neurons that can be called a brain. Echinoderms generally display a pentamerous radial symmetry, which is secondarily derived; their larvae are usually bilaterally symmetrical. As members of the deuterostome group, echinoderms share such features as radial cleavage, regulative development, enterocoely, and the origin of the anus from the blastopore.

Echinoderms do not have a defined excretory system; metabolic wastes are removed by direct diffusion or transferred via amoebocytes (coelomocytes) through certain parts of the body wall (e.g., tube feet, papulae, gills, tentacles).

There are about 7,000 living species of echinoderms, including sea lilies, feather stars, sea stars, brittle stars, sea urchins, sand dollars, sea cucumbers, and sea daisies; they are all marine. Echinoderms are found from the intertidal zone to the deepest oceanic trenches and occupy a variety of substrates (a few sea cucumbers are pelagic). Although the number of species in this phylum is not as great as the number in some other phyla, the former are often the dominant members of

many benthic communities, in terms of both biomass and ecological importance.

The size of adult echinoderms varies greatly, ranging from less than 1 cm in the largest dimension (some sea cucumbers and brittle stars) to over 1 m in diameter (the largest sea stars) or over 2 m in length (some sea cucumbers). As a whole, echinoderms, especially those in deep and polar seas, are long-lived animals.

Due to their unmistakable body symmetry, relatively large size, and coloration, echinoderms have been the favorite sea creatures of zoologists for many generations. Another reason for their popularity may be that sea urchins have for more than 100 years provided excellent material for experimental embryology. Much of the information on fertilization, ooplasmic segregation, cleavage, mesodermal function, and gene expression is based on sea urchin gametes and zygotes.

With very few exceptions (Chia et al., 1993), echinoderms are gonochoristic and dioecious, but the sexes cannot be easily recognized externally. Their common larval forms include the bipinnariae and brachiolariae of sea stars, the echinoplutei of echinoids, the ophioplutei of ophiuroids, the auriculariae of holothuroids, and the doliolariae (vitellariae) of crinoids. All of these larval forms are bilaterally symmetrical (doliolariae can be considered radially or biradially symmetrical). Metamorphosis often brings about the transformation of a pelagic, bilaterally symmetrical larva into a benthic, radially symmetrical juvenile.

EVOLUTION

During the past century there has been considerable interest in the study of the evolution of echinoderms (Blake, 1987; Gale, 1987) for the following reasons: 1) echinoderms have abundant and good fossil records, 2) brittle stars have a sea star-like body but a sea urchin-like larva, and 3) the existence of radially symmetrical adults begs for the discovery of a radially symmetrical ancestor.

Attempts have been made to search for a group among living organisms that shares a

common ancestor with echinoderms. For various reasons, hemichordates and sipunculids, both of which are bilaterally symmetrical, have been considered (Nichols, 1986).

The controversy over the systematic position of ophiuroids (which are either closely related to echinoids on the basis of larval morphology or to asteroids on the basis of adult anatomy) has had a better fate. It is now accepted by most biologists that convergent development indeed brought about the similarities between the echinopluteus and ophiopluteus larvae (Strathmann, 1988). In addition, both fossil records and molecular biological findings have indicated that ophiuroids are more closely related to asteroids than to echinoids.

It is noted that Williamson (1992) believes that "modern echinoderms evolved from forms that were radially symmetrical throughout life and had no planktonic larvae" and that "one of these early radial echinoderms with direct development then acquired a bilaterally symmetrical larval form from another phylum by horizontal genetic transfer. Whereas a minority of modern echinoderms with bilaterally symmetrical larvae are directly descended from this ancestor, the majority acquired their larvae by horizontal genetic transfer within the phylum."

Fossil records (Paul, 1979) indicate that there were periods of great proliferation and mass extinction of both classes and genera in the past (Fig. 1). Figure 1 shows that there were 19 classes of echinoderms at the end of the Ordovician but that the number declined gradually to five or six by the early Carboniferous and has remained steady until today. In contrast, the number of genera has shown different trends, reaching 400 by the end of the Carboniferous, declining to only 40 by the end of the Triassic, then increasing again, reaching an all-time high in recent times.

It is difficult to establish phylogenetic lineages for echinoderms because of the occurrence of parallelism, reversion, and the loss of characters during the group's evolutionary history. Raff et al. (1988) discussed eight evolutionary trees that show possible relation-

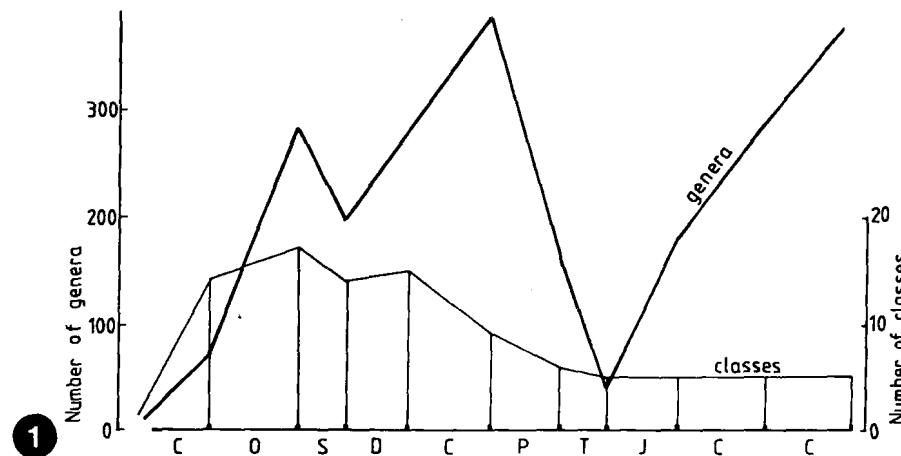


Fig. 1. Diversity of classes and genera of echinoderms, through the Phanerozoic. (From Willmer, 1990, who based it on data from Paul, 1979.)

ships of the five extant classes. Although there is some evidence to support each scheme, the results differ greatly.

The most widely accepted phylogenetic tree (Fig. 2) is that of Paul and Smith (1984), who believe that echinoderms probably originated early in the Cambrian period and very quickly established most of the body forms. The ancestor was a small, bottom-dwelling, bilaterally symmetrical, trimeric, suspension-feeding creature. This ancestor gave rise to carpoids and helicoplacoids, the latter of which were the first echinoderms. Helicoplacoids, which exist only in fossil forms today, were radially symmetrical; however, they had only three ambulacrae and their mouth was located to one side of the body. The common ancestor of the current echinoderm subphyla Pelmatozoa and Eleutherozoa was probably similar to the extinct *Camptostroma*, which showed pentaradial symmetry. Primitive pelmatozoans were, like present-day crinoids, attached suspension feeders with upward-facing mouth and arms that were used for the collection and transportation of food. The Eleutherozoa, which include the other four extant classes (ophiuroids, asteroids, ho-

lothuroids, and echinoids), diverged from the Pelmatozoa through their adaptations to different modes of life (the mouth facing the substrate [except in holothuroids] and, at least originally, the use of the water vascular system primarily for locomotion).

The discovery of a new species, *Xyloplax medusiformis*, from the deep water off the coast of New Zealand in 1986 by Baker et al., caused a good deal of excitement. Baker et al. (1986) and Rowe et al. (1988) proposed a new class, Concentricycloidea, to accommodate this species, although Smith (1988) challenged this scheme by proposing that *Xyloplax* is an asteroid related to the genus *Pteraster*. Smith's idea (1988) was supported by McEdward (1992) on the basis of studies of the details of the embryology and development of *Pteraster tessellatus*.

Brusca and Brusca (1990) have provided a cladogram of the evolutionary history of the echinoderms (Fig. 3). The cladogram depicts a step-by-step analysis of the evolution of all of the major characteristics leading to the present-day classes; it takes seven steps to progress from a trimeric ancestor to the form of crinoids, 13 steps to asteroids, 14 to ophi-

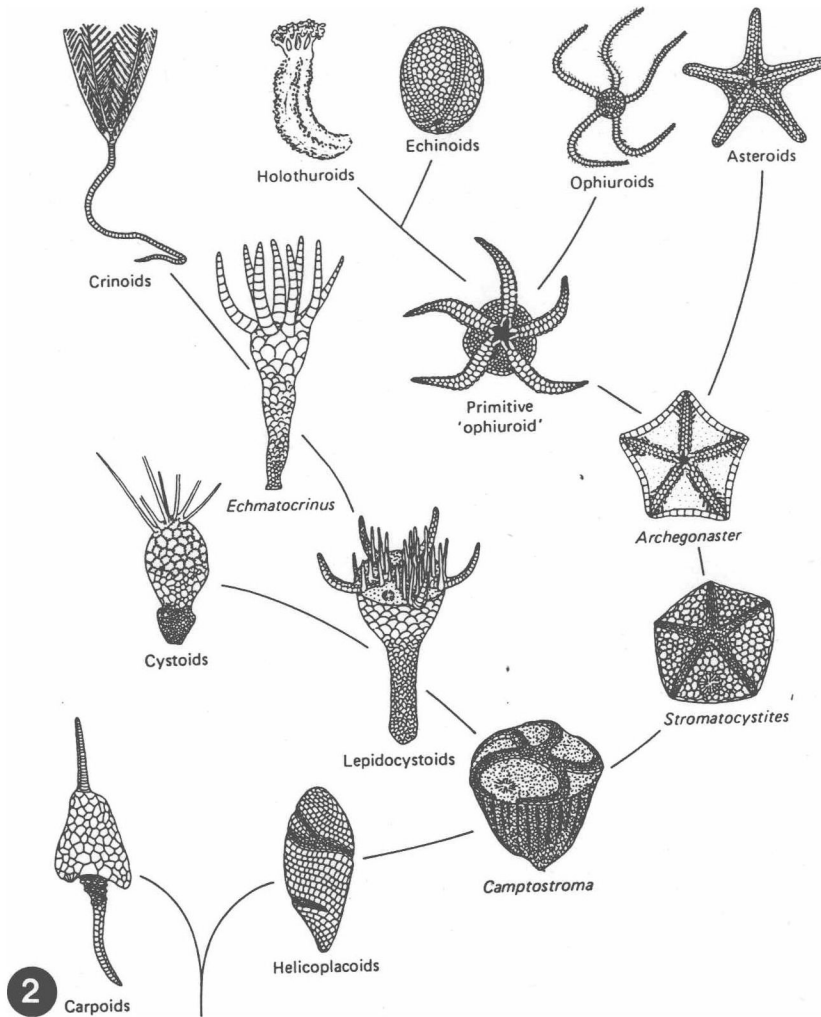


Fig. 2. Suggested evolutionary tree for the early radiation and living classes of echinoderms. (From Paul and Smith, 1984.)

uroids, 16 to echinoids, and 19 to holothuroids. The changes involved in each step are detailed in the legend of Figure 3.

CLASSIFICATION OF ECHINODERMS

For quite some years, echinoderms were considered to comprise two subphyla: the Pel-

matozoa, which are free-living or stalked (attached) forms with the oral surface directed upward (includes the crinoids); and the Eleutherozoa, which are free-living forms with the mouth directed downward or horizontally (includes all of the other extant groups [Hyman, 1955]). This classification

was later modified by some specialists (Moore, 1966–1978), who divided echinoderms into three subphyla: 1) Echinozoa, the armless echinoderms (Echinoidea and Holothuroidea); 2) Crinozoa, all groups of which, except the Crinoidea (sea lillies and feather stars), are extinct; and 3) Asterozoa, which have radiating arms (Asteroidea and Ophiuroidea). This classification was adopted in some textbooks (refer to Dale, 1970; Barnes, 1980). In recent years, zoologists have returned to the former system of classification.

The following classification follows that of Brusca and Brusca (1990).

Phylum Echinodermata

Subphylum Pelmatozoa. Sea lilies, feather stars, and extinct cystoids. Body consists of three parts, stalk, calyx, and arms, facing away from substratum; ambulacra, mouth and anus on upper surface of body; ambulacral grooves open; skeletal ossicles articulate, except fused in calyx; madreporite absent.

Class Crinoidea. Sea lilies and feather stars. About 625 living species (e.g., *Antedon*, *Comantheria*, *Lamprometra*, *Metacrinus*).

Subphylum Eleutherozoa. Body form stellate, discoidal, globular, or cucumber shaped; oriented aboral side up or lying horizontally; no aboral stalk; body may lack arms; brachioles not present; ambulacral grooves open or closed; ossicles separate or fused, forming rigid test; madreporite present.

Class Asteroidea. Sea stars. Radially symmetrical and dorsoventrally flattened; body of central disc with five or more radiating arms; ambulacral grooves open; tube feet ampullae internal; suckers present or absent; madreporite on aboral surface of disc, on CD interambulacrum.

Order Platyasterida. Primitive asteroids. Tube feet without suckers; no anus; two extant genera, *Luidia* and the monotypic *Platyasterias* (*Platyasterias latiradiata*).

Order Paxillosida. Upper surface with umbrella-like patterns of ossicles termed paxillae; tube feet lack suckers; anus may be absent (e.g., *Astropecten*, *Ctenodiscus*).

Order Valvatida. Tube feet possess suckers; anus never absent (e.g., *Archaster*, *Asterodon*, *Linckia*, *Oreaster*).

Order Spinulosida. Tube feet exhibit suckers; 5–18 arms; anus present; usually no pedicellariae (e.g., *Acanthaster*, *Dermasterias*, *Echinaster*, *Henricia*, *Patiria*, *Pteraster*, *Solaster*).

Order Forcipulatida. Tube feet exhibit suckers; 5–50 arms; anus present; pincer-like pedicellariae. Wide distribution; order includes most intertidal forms (e.g., *Asterias*, *Evasterias*, *Heliaster*, *Leptasterias*, *Pisaster*, *Pycnopodia*, *Stylasterias*).

Class Ophiuroidea. Brittle stars and basket stars. Stellate with central, flattened disc, sharply set off from branched or unbranched articulated ambulacral arms; arms of most have jointed appearance; tube feet ampullae internal; suckers lacking; no anus; madreporite oral on CD interambulacral plate; about 2,000 extant species (e.g., *Amphiura*, *Asteronyx*, *Astrocanthem*, *Astrophyton*, *Gorgonocephalus*, *Ophiacantha*, *Ophiocoma*, *Ophioderma*, *Ophiomusium*, *Ophionereis*, *Ophiopholis*, *Ophiothrix*, *Ophiura*).

Class Concentricycloidea. The sea daisies. Deep-water animals; body disc shaped and medusiform; skeletal plates concentrically arranged; water vascular system in double-ring form; interradial connections between two rings; tube feet a uniserial, subperipheral ring; ampullae single, suckers absent; stomach may or may not be present; intestinal tract and anus absent; madreporite on dorsal surface; spermatozoa filiform; two known species (*Xyloplax medusiformis* and *Xyloplax turnerae*). (It should be mentioned again that the status of this class cannot be considered definitive, since information on the development and natural history of these animals is largely wanting.)

Class Echinoidea. Sea urchins and sand dollars. Body spherical, ovoid, or discoid with secondarily bilateral symmetry; skeletal plates usually closely fitted, giving a firm, inflexible body wall, but in some, plates of test overlap producing somewhat flexible

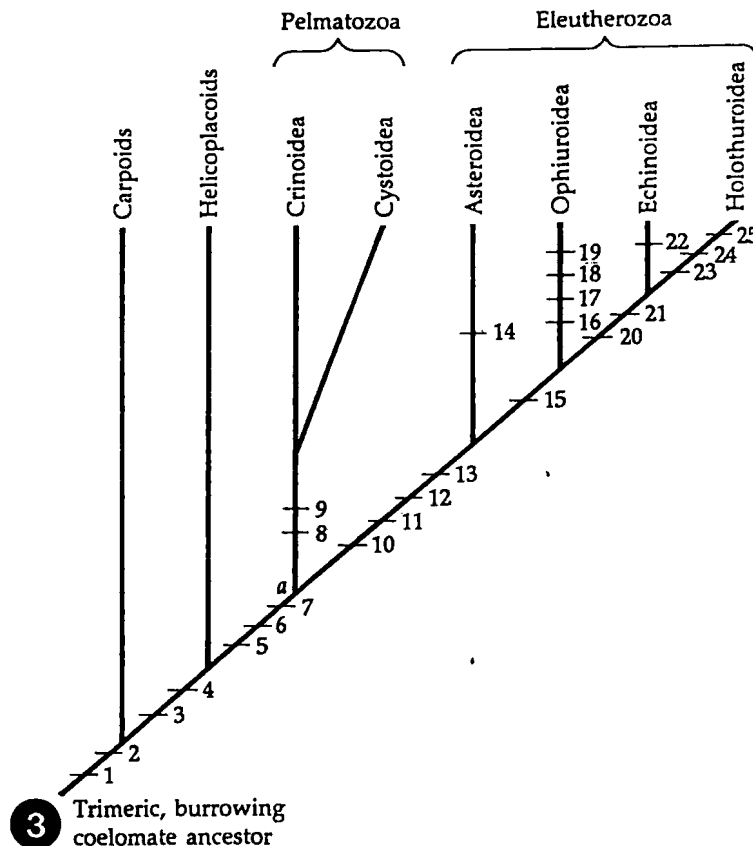


Fig. 3. A cladogram depicting one set of hypotheses about the origins of some important synapomorphies among the major groups of echinoderms. The origin of the echinoderm lineage involved an escape from infaunal life with the evolution of a supportive system of endoskeletal plates with a stereom structure (1) and the use of external ciliary grooves for suspension feeding (2). This "pre-echinoderm" condition is represented in the fossil record by the carpiids. The first true echinoderms may have been the helicoplacoids, whose appearance was marked by the origin of triadial symmetry with three spirally arranged open ambulacral grooves (3) and water vascular system (4), probably with the madreporite opening near the mouth. The immediate common ancestor of the pelmatozoan and eleutherozoan lineages (a) may have been similar to the extinct *Campetostroma*, with pentaradial symmetry (5) evidenced by five open ambulacral grooves, mouth, and anus on the oral surface (6) and attachment to the substratum by the aboral surface (7). From this ancestral form, the pelmatozoans (Crinoidea and Cystoidea) diverged, with the evolution of arms or brachioles bearing open ciliated grooves used for suspension feeding (8) and the loss of the external madreporite (9). The origin of the eleutherozoan clade involved the movement of the anus to the aboral surface (10), a change associated with the orientation of the body, with

the oral surface against the substratum (11). In this "new" position, eleutherozoans adopted alternative feeding modes and an errant lifestyle; the podia became suckered (12) and used for locomotion rather than feeding. The madreporite migrated along the CD interambulacrum to the aboral surface (13). Given this scenario, the asteroids arose with the evolution of five rays (arms) broadly connected to a central disc (14). The remaining three groups have closed ambulacral grooves (15) in common. The ophiuroids invaded soft substrata and lost the podial suckers (16). In addition, they evolved five highly articulated rays, with internal vertebral plates in each arm "segment" (17) and secondarily lost the anus (18). The madreporite migrated back to the oral surface along the CD interambulacrum (19). The echinoid-holothurian clade arose with the extension of the ambulacral grooves along the sides of the body from the oral to the aboral pole (20), thereby reducing the aboral surface to a small region around the anus (21). The echinoids evolved with the fusion of the skeletal plates, which formed a rigid globular or discoidal test (22). The origin of the holothurians involved a reduction of the skeletal plates to isolated ossicles (23), movement of the madreporite internally (24), and elongation of the fleshy body on the oral-aboral axis (25). (From Brusca and Brusca, 1990.)

body wall; moveable spines; ambulacral grooves closed; tube feet emerge from openings within ambulacral plates; two extant subclasses.

Subclass Perischoechinodea. Test globular; one tube foot per ambulacral plate; pencil-like spines; anus at aboral pole; no dermal gills; most are extinct; often viewed as most primitive echinoids; pencil urchins; about 140 species (e.g., *Cidaris*, *Eucidaris*, *Psychocidarid*).

Subclass Euechinodea. Globular or discoidal test; variable numbers of tube feet and spines per plate; anus variably positioned, aboral to "posterior." "True" urchins; about 800 species in 4 superorders.

SUPERORDER DIADEMATA (e.g., *Aspidodidema*, *Caenopedina*, *Diadema*, *Plesioididema*).

SUPERORDER ECHINACEA. Most of the common "regular" urchins (e.g., *Arbacia*, *Echinometra*, *Echinus*, *Heterocentrotus*, *Paracentrotus*, *Salenia*, *Strongylocentrotus*, *Toxopneustes*, *Tripneustes*).

SUPERORDER GNATHOSTOMATA.

Order Holoctypoida. Most are extinct; often considered intermediate between "regular" and "irregular" urchins; three extant species in two genera: *Echinoneus* and *Micropetalon*.

Order Clypeasteroidea. True sand dollars (e.g., *Clypeaster*, *Dendraster*, *Echinarachnius*, *Echinocardium*, *Echinodiscus*, *Encope*, *Fibularia*, *Mellita*).

SUPERORDER ATELOSTOMATA. The spatangoid heart urchins and other "irregular" urchins (e.g., *Cassidulus*, *Echinolampas*, *Lovenia*, *Maretia*, *Metalia*, *Urechinus*).

Class Holothuroidea. Sea cucumbers. Body orally-aborally elongated; cucumber-shaped and fleshy; single internal gonad; skeleton typically reduced to ossicles; pentamerous symmetry may be secondarily modified through loss of "dorsal" tube feet along C and D ambulacra; sometimes lacking tube feet; madreporite internal; closed ambulacral grooves; about 1,150 extant species in three subclasses.

Subclass Dendrochiroata. The 8–30 oral tentacles are finger-like to highly branched;

retractor muscles present in tentacles and oral region; tube feet present (e.g., *Cucumaria*, *Eupentacta*, *Psolus*, *Thyone*).

Subclass Aspidochiroata. The 10–30 oral tentacles are shield-like or leaf-like; no retractor muscles in oral region; tube feet present (e.g., *Enypniastes*, *Holothuria*, *Isostichopus*, *Parastichopus*, *Pelagothuria*, *Scotoplanes*, *Stichopus*).

Subclass Apodacea. Up to 25 tentacles, varying from digitate to pinnate; tube feet highly reduced or missing (e.g., *Claudina*, *Euapta*, *Leptosynapta*, *Molpadia*, *Synapta*, *Trochoderma*).

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Chapter 2

Crinoidea

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INTRODUCTION

Crinoids (sea lilies and feather stars; Figs. 1, 2) represent an ancient group of echinoderms whose fossil record dates back into the Lower Cambrian (Paul and Smith, 1984). Like other echinoderms, adult crinoids are pentamerous and exclusively marine organisms. Their body can be divided into three parts (Fig. 2): 1) the stalk, which in many extant forms is present only in the stage of the stemmed larva and by which the animals are attached to the substratum (Oji, 1989); 2) the usually small simple bowl-shaped or conical calyx ("disc," "theca," "body"; for glossary see Moore et al., 1978), which harbors the intestinal tract, an elaborate system of coelomic spaces, the axial organ, and the main part of the nervous system; and 3) the arms, which extend from the calyx and which are the principal feeding structures.

The arms and their lateral branches, the pinnulae, contain the gonads (see Figs. 6C, 7, below) and are further characterized by the ambulacra (feeding grooves; see Fig. 11, below). Ambulacra, mouth, and anus are located on the upper surface of the body, facing away from the substratum. Frequently the arms branch (see Fig. 4, below), the branch-

ing points being characteristically in a proximal location. Structures located in the plane of the mouth or directed toward this plane are termed oral or orally directed structures. Structures located at the opposite side of the animal are said to be in an aboral location. Arms, body, and stalk (if present) are heavily calcified; thus the animals are rendered quite rigid and exhibit limited locomotory capabilities. This is correlated with suspension feeding, an ancient mode of feeding that characterizes all crinoids. Crinoids show less diversification of feeding habits than other echinoderms. The enormous accumulations of calcareous deposits (calcium carbonate in the form of calcite) imply that construction of the massive mesodermal skeleton is of major physiological importance for the animals. Skeletogenesis presumably occupies a major proportion of their metabolic activities, although nothing is known about the possible endocrine or nervous control of calcium metabolism in crinoids.

The basic structure of crinoid skeletal elements is closely comparable to that in other echinoderms. The skeleton is composed of numerous variously shaped individual ossicles, all of which are characterized by the

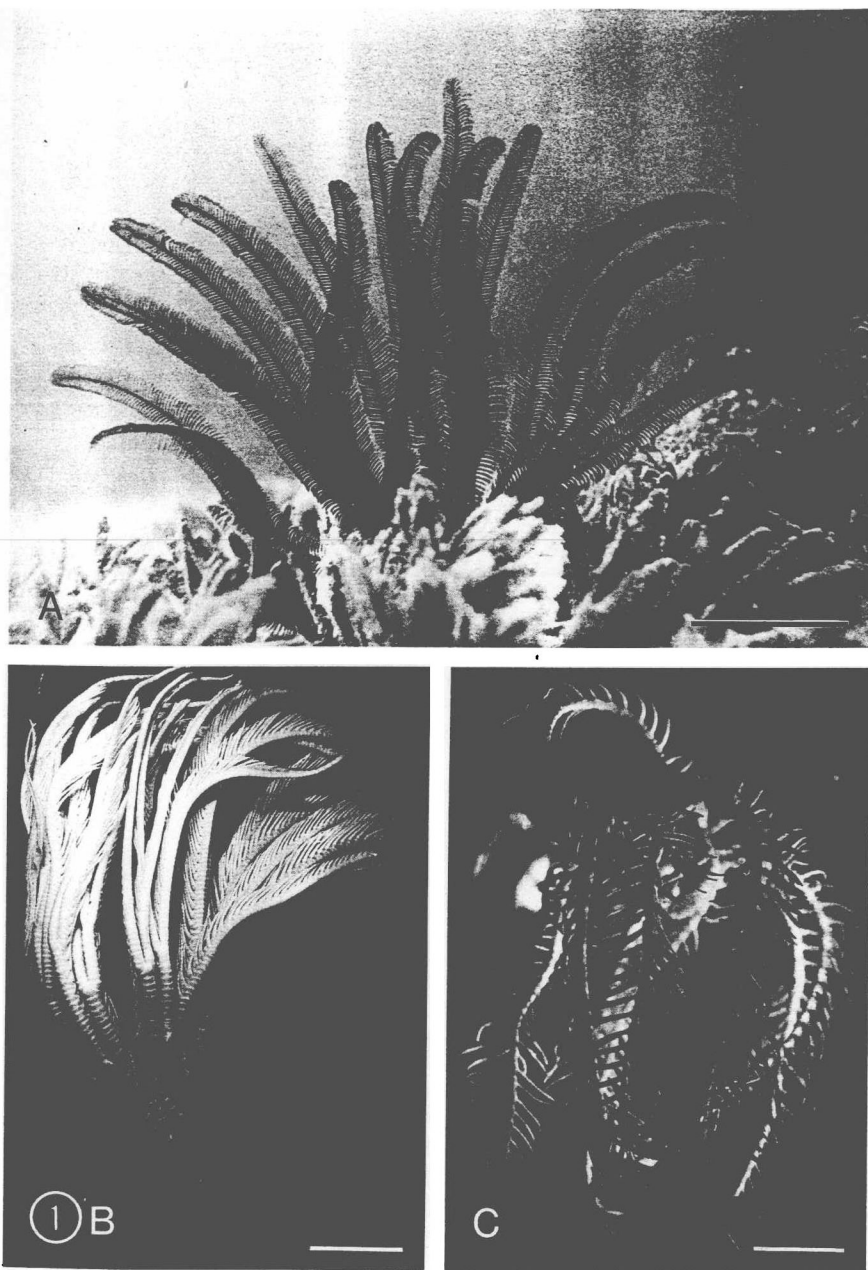


Fig. 1. External aspects of crinoids. A: Live specimen of the feather star *Heterometra savignyi* in its natural habitat (Red Sea), displaying nocturnal fan-like catch position. Bar = 5 cm. Courtesy of Prof. D. Magnus, Darmstadt. B: The crown (calyx and arms) of the sea lily *Metacrinus interruptus*, fixed specimen. Bar = 2 cm. C: The feather star *Lamprometra palmata* with the arms bent far aborally. Fixed specimen. Bar = 0.5 cm.

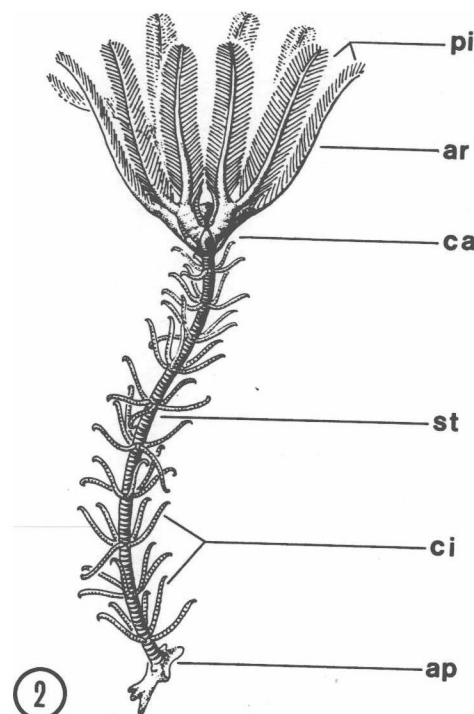


Fig. 2. Diagrammatic view of crinoid body parts. ap, attachment plate; ar, arms; ca, calyx; ci, cirri; st, stalk; pi, pinnules.

stereom structure (Macurda et al., 1978; Fig. 3). The connective tissue of crinoids includes "mutable" collagenous ligaments, which occur in other echinoderms as well.

Within crinoids major evolutionary trends concern: 1) the reduction of the stalk (which in a few fossil species exceeded 20 m), leading to abandonment of the sessile mode of life; 2) an increase in the number of arms (primitive number, 5; highest number, 200; single palaeozoic species have odd arm numbers such as 1, 3, or 6; cf. Table 1); and 3) a reduction in the size of the body, which in primitive forms is usually higher than wide but in more modern types is flattened. The small body usually is correlated with relatively simple intestinal structure.

TABLE 1. Number and Length of Arms and Total Length of Food Grooves in Some Selected Crinoid Species

Species	No. of arms	Length of arms (mm)	Total length of food groove (m)
<i>Comatula pectinata</i>	10	90	4.37
<i>Comanthus parvicirrus</i>	20	50	7.16
<i>Lamprometra protectus</i>	43	50	23.44
<i>Tropometra afra</i>	10	255	47.69
<i>macrodiscus</i>			
<i>Antedon petasus</i>	10	110	16.28
<i>Stephanometra spicata</i>	26	130	38.48
<i>Himerometra magnipinna</i>	49	90	61.23
<i>Metacrinus rotundus</i>	56	210	71.68

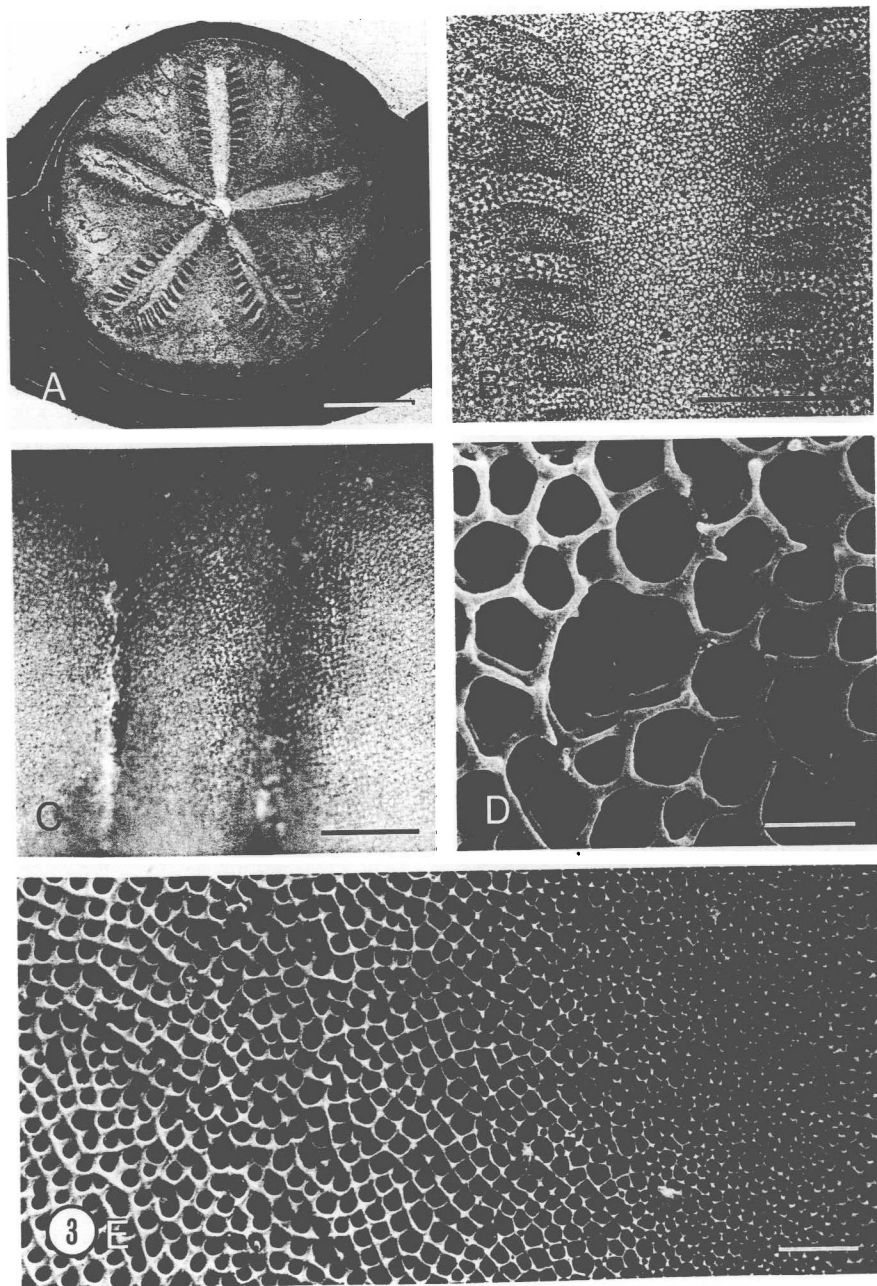
Modified from Lawrence, 1987, according to Gislén, 1924.

These trends are to be seen in relation to the development of a free mode of living, allowing selection of spatial and temporal feeding activities and avoidance of predators (Meyer and Macurda, 1977). An interesting question is whether such an active life is possibly correlated with an increase in nervous tissue and a more complex differentiation of the nervous system.

The morphological study of crinoids is hampered by the enormous amounts of calcified structures in the mesodermal connective tissue. This usually necessitates a decalcification process, which may have detrimental effects on the preservation of structural details. Another hindrance in the study of crinoids is the limited availability of well-preserved material from the stalked species, which generally are confined to deep sections of the oceans. Therefore, our knowledge of the stalked forms is still scanty, while more is known on the stalkless forms, which usually inhabit shallow parts of the sea.

Nearly all crinoids are marked by a strange elegance and plant-like beauty (sea "lilies"), which often is enhanced by brilliant coloration. Only representatives of the cyrtocrinid group are of a somewhat stout shape (Fechter, 1973; Bourseau et al., 1987; Grimmer and Holland, 1990).

Early important studies on crinoid histology were conducted in the last decades of the nineteenth century (W.B. Carpenter, 1866; P.H. Carpenter, 1884; Ludwig, 1877; Ha-



mann, 1889) and in the early parts of the twentieth century (Reichensperger, 1905, 1912; Chadwick, 1907). Cuénot's contribution on crinoids in Grassé's *Traité de Zoologie* (1948) defines the level of knowledge in the middle of the twentieth century, which in many respects did not progress significantly beyond that presented by the early authors around 1900. A new interest in crinoids becomes obvious with the advent of new techniques and new understanding of ecological questions in the 1960s and 1970s, a process that continues to a moderate extent until now. Principal authors who increased our knowledge on anatomy, ultrastructure, development, and ecology of crinoids during the last two to three decades are Holland, Grimmer, Macurda, Meyer, Magnus, Breimer, LaHaye, and Jangoux. Special merit goes undoubtedly to N. Holland. Biochemical and genuinely physiological studies are very few in number.

GENERAL MORPHOLOGY

Body Plan

The body plan of crinoids is initially based on the principles of deuterostomial bilateral morphology. However, during metamorphosis this primary body plan becomes overlain, as in other echinoderms, by a secondary pentameric radial symmetry. However, at second glance this secondary symmetry is quite incomplete, externally as well as internally.

The most conspicuous external feature upsetting the radial geometry is either an anal tube arising excentrically from the tegmen (the plane around the mouth opening) or an

eccentrically placed mouth (see Figs. 11, 12, below). In the first case, the site of the eccentric anal tube serves to define something like a body pole, e.g., the CD interray (interradius), opposite the ray (radius) A, the rays and interrays being named in clockwise order when looking at the tegmen (P.H. Carpenter, 1884). In the second case, the eccentric mouth is situated in the AB interray. Internally, the radial symmetry of some organ systems, e.g., skeletal or neural, interferes with asymmetrical arrangement of others, e.g., parts of the hemal or of the coelomic systems.

The position of a structure can be given unequivocally by the letter of its ray or interray and, additionally, by indicating whether it is found orally or aborally, respectively. These coordinates replace the—in crinoids often conjectural or even misleading—indications of anterior and posterior (in stalked crinoids and in the *Pentacrinus* larva of stalkless forms the stalk points in an anterior direction), of ventral and dorsal (at least the CD interray might be accepted as ventral side), and of left and right.

The skeleton is by far the dominating compartment of a crinoid body. This preponderance of differentiated mesenchyme should not hamper the recognition of the remarkable organogenetic potency of epithelia, derived either from ecto- or endodermal germinal layers or from mesoderm (coelomic epithelia). For this reason basement membranes¹ deserve special attention in crinoid microscopic anatomy. However, the association of certain organs (or at least parts) with a certain germinal layer is not incontestable in all cases; this holds true, for instance, for the nervous system, which is certainly partly of ectodermal origin, the main part of which, however, has

Fig. 3. Stereom as the basic structure of crinoid skeleton. A,B: Polished cross section (25 μ m thick) of the petrified stalk of the Jurassic *Sericrinus subangularis*. A: Embedded in shale, a stalk columnar presents densified areas in a pentameric order that are related to the typical crenulated surface of columnals. Bar = 2 mm. B: magnified sector of A, showing the stereom structure in the manner of a dark lined meshwork. Bar = 0.5 mm. C: Stereom structure of ossicles (the example presented here shows brachials of *Gymnocrinus richeri*) often can be observed shining through the epidermis. Bar = 0.5 cm. D: SEM. A macerated brachial of *Tropiometra afra* showing the filigree of stereom trabeculae. Bar = 10 μ m. E: SEM aspects of an interbrachial articular face of *Tropiometra afra* showing regions of coarse (left) and fine (right) stereom structure. Bar = 50 μ m.

¹The term basement membrane, as used in vertebrate histology (e.g., Botstein Griep and Robbins, 1988), comprises three components: lamina lucida, lamina densa = basal lamina, and lamina fibroreticularis. In crinoid material fixed for electron microscopy with glutaraldehyde, generally a distinct basal lamina is observed while at most places a distinct lamina fibroreticularis is hardly to be detected. In such cases the term basal lamina is used *pars pro toto*.

been proposed to be of mesodermal origin (Hamann, 1889; Cobb, 1987).

Supportive Structures

The crinoid skeleton is an endoskeleton and is of mesodermal origin. The structures responsible for the animal's shape and locomotory capacity are ossicles interconnected in the manner of a synostosis (calyx) or of different kinds of articulations: either nonmuscular and exclusively by ligaments, as are symplexes between stalk ossicles (see Fig. 9 below), syzygies between arm ossicles (the latter being preformed sites for autotomy; Fig. 5), and synarthries (Figs. 4C, 6F); or muscular articulations (Figs. 4C,D, 6E) with ligaments of mutable connective tissue (see Common Connective Tissue; and Ligaments, below) and bundles of myocytes (see Obliquely Striated Brachial Muscles, below).

According to Breimer (1978), the largest part of the crinoid skeleton consists of a group of aboral ossicles that belong to what ontogenetically is termed the primary skeleton. Only this main skeletal part will be outlined briefly. The primary skeleton consists of 1) columnals in the stalk (see Fig. 9A–D below), 2) cirrals in the cirri (see Fig. 9E–H, below), 3) brachials (Figs. 4, 5) and pinnulars (Figs. 5B, 6) in the arms, and 4) ossicles that contribute (from the aboral to the oral side) to the calyx: the uppermost columnal (in sea lilies) or the centrodorsale (in comatulids), infrabasalia (if present), basalia (often fused and removed into the interior of the calyx: rosette), and radialis (Figs. 8, 10C).

The comatulid centrodorsale (Fig. 8) possibly combines a series of nodals (columnals bearing cirri; Fig. 9A,B; Rasmussen and Sieverts-Doreck, 1978). The centrodorsale is often discoidal in shape and may lack cirri completely (e.g., *Comanthus parvicirrus*) or bear laterally a few rows of cirrus sockets (e.g., *Tropiometra afra*). In other species, e.g., in many antedonaceans, the centrodorsale is conical and gives rise to numerous cirri. At its oral rim the centrodorsale (or in sea lilies the topmost columnale, respec-

tively) is followed by one circlet of basalia: monocyclic forms according to Wachsmuth and Springer (1897; extant Millericrinida, Bourgetticrinida, Cyrtocrinida) or by two circlets of basalia and infrabasalia: dicyclic forms (most recent crinoids). The infrabasalia, however, are to be observed only in juvenile growth stages of comatulids, e.g., in the genera *Antedon* and *Promachocrinus*, and are rudimentary or absent in adult animals (Breimer, 1978), which therefore are termed cryptodicyclic. The basalia form a circlet of interradian plates that in stalked forms, despite certain modifications, may form large parts of the calyx (Fig. 4A), while in most comatulids the basalia fuse and form a "rosette" that covers the cavity of the centrodorsale at the oral side.

In most adult crinoids only five radial ossicles form the wall of the calyx in synostosis with the centrodorsale (majority of comatulids) or with basalia (stalked forms). In rare cases, e.g., in the genus *Promachocrinus*, the number of radials is secondarily doubled (Fig. 8D). Radialia are the ossicles from which the arms arise. Together with the first brachial ossicle, the primibrachiale, a radiale forms an articulation that is typical for most interbrachial articulations. In this articulation the relief is quite similar at both articular facets, which, aborally to a horizontal or oblique ridge = fulcrum, are interconnected by an aboral collagenous ligament, while orally a pair of interarticular collagenous ligaments and a pair of thick muscles keep the ossicles in position (Figs. 4C,D, 5B, 6E).

Coelomic Cavities and Hemal Lacunae

Classic investigations of crinoid development (Barrois, 1888; Seeliger, 1892) produced detailed descriptions of ontogenetic processes including the complicated transformations of the coelomic anlagen. In the latter, crinoids generally follow the developmental patterns seen in other echinoderm classes but in some important respects exhibit distinct differences. To some extent these differences remain a matter of debate. Briefly summa-

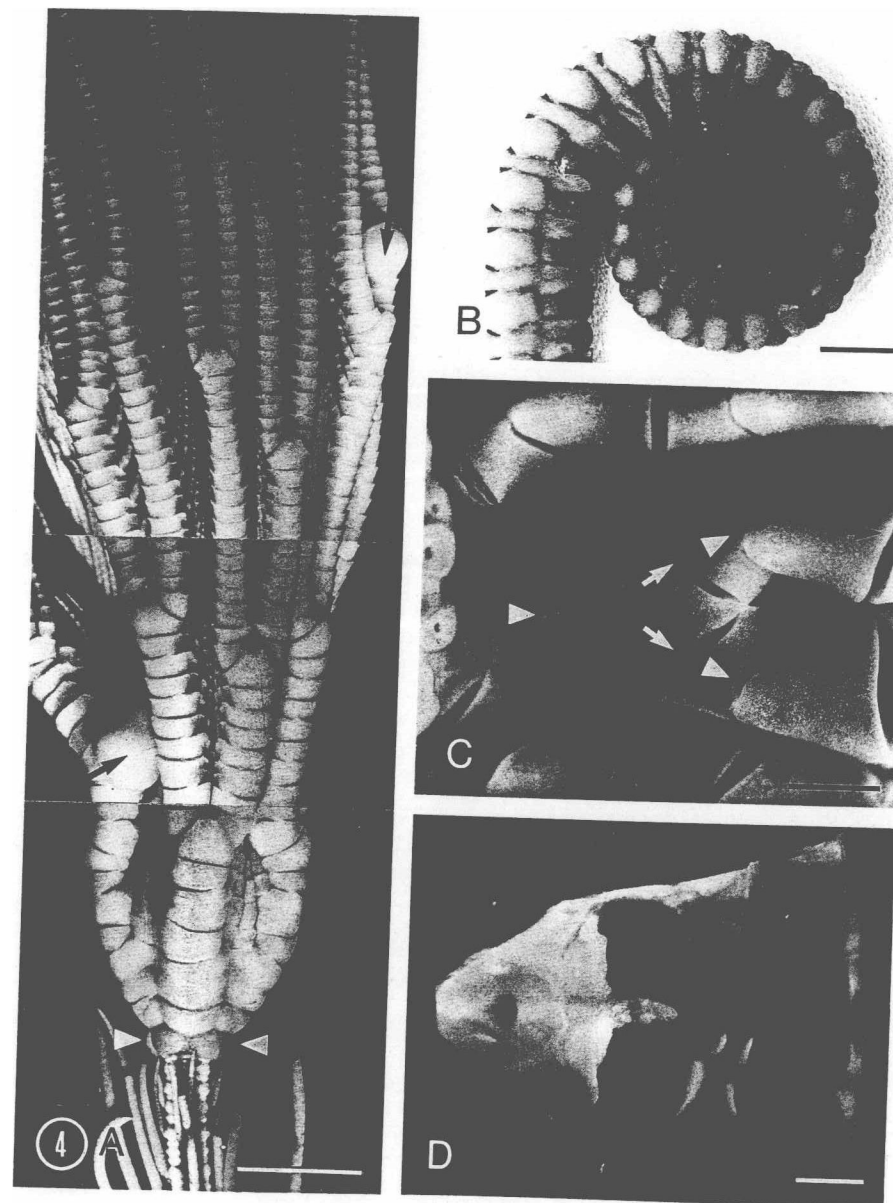


Fig. 4. Skeletal aspects of crinoid arms. A: Arm branching pattern of *Metacrinus rotundus*. Note the quite different levels of axillary ossicles where arms dichotomize. Arrows point to globular thickenings, caused by parasitic myxozostomids; arrowheads point to the basalia of the calyx. Bar = 1 cm. B: Curled arm of *Gymnocrinus richeri*. Bar = 0.5 cm. C: Proximal branching of *Promachocrinus kerguelensis* as seen from the

aboral side with alternating types of articulation, synarthries (arrowheads) and muscular-ligamentary articulation (arrows). Bar = 5 mm. D: Partly macerated preparation of an arm of *Promachocrinus kerguelensis* seen from the oral side showing the flexor muscles (stars) belonging to the articulations that are indicated in C by arrows. Bar = 2.5 mm.

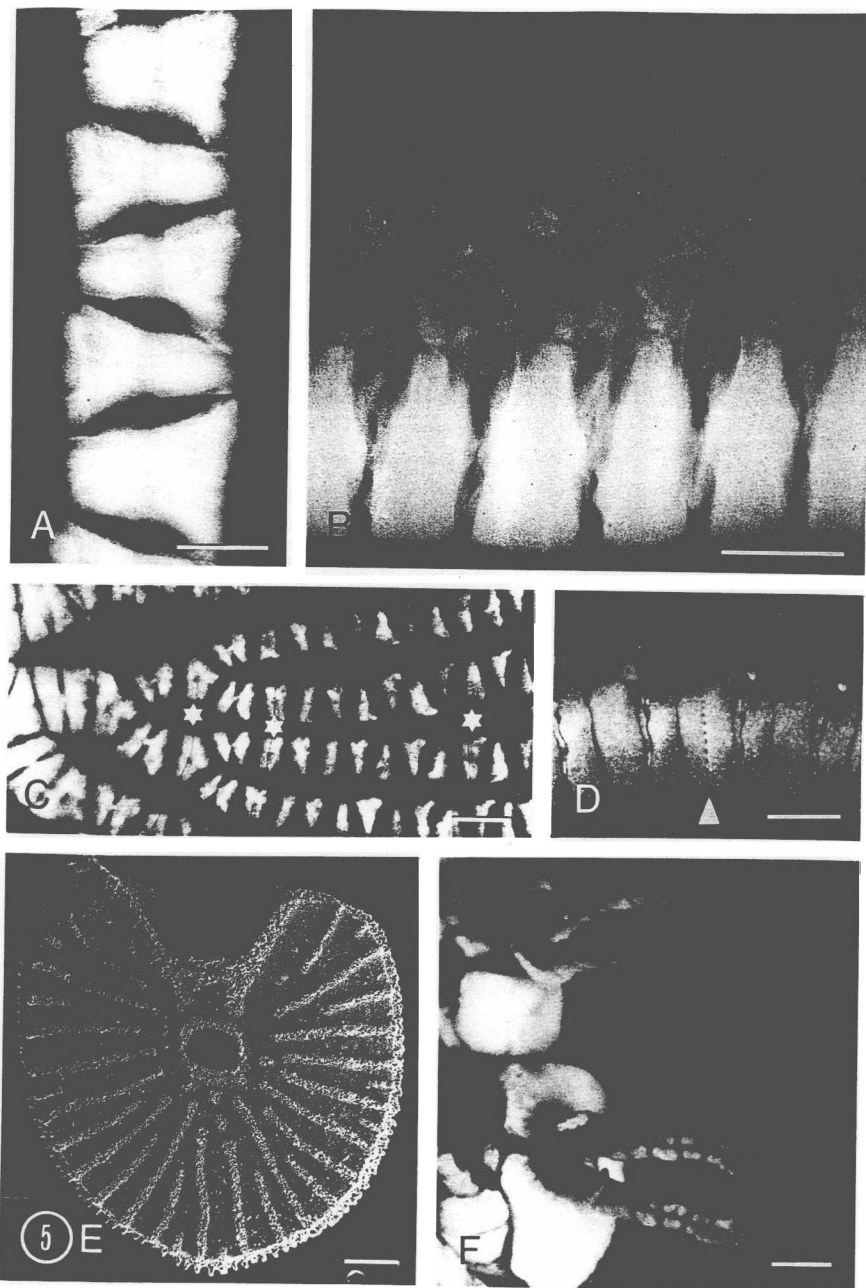


Fig. 5. A: X-ray photograph of an arm of *Clarkcomanthus littoralis* in oral-aboral projection. Note the wedge-like shape of the brachials. Bar = 1 mm. B: X-ray photograph of an arm of the sea lily *Endoxocrinus parvae* from the side, with the oblique ridges of the interbrachial articulations in alternating directions. Bar = 1 mm. In A and B the brachial nerve canal is faintly seen. C-F: Syzygial articulation. C: X-ray photograph. Position of

syzygies (stars) in an arm of *Comanthus suavia*. Bar = 2.5 mm. D: External site of a syzygy (arrowhead) in *Himerometra robustipinnia*, recognizable by the dotted line. Bar = 1 mm. E: REM picture of a syzygial face of *Tropiometra afra* showing the typical crests. Bar = 300 μ m. F: Arms of *Clarkcomanthus littoralis* broken at syzygies with outgrowing regenerates. Bar = 1 mm.

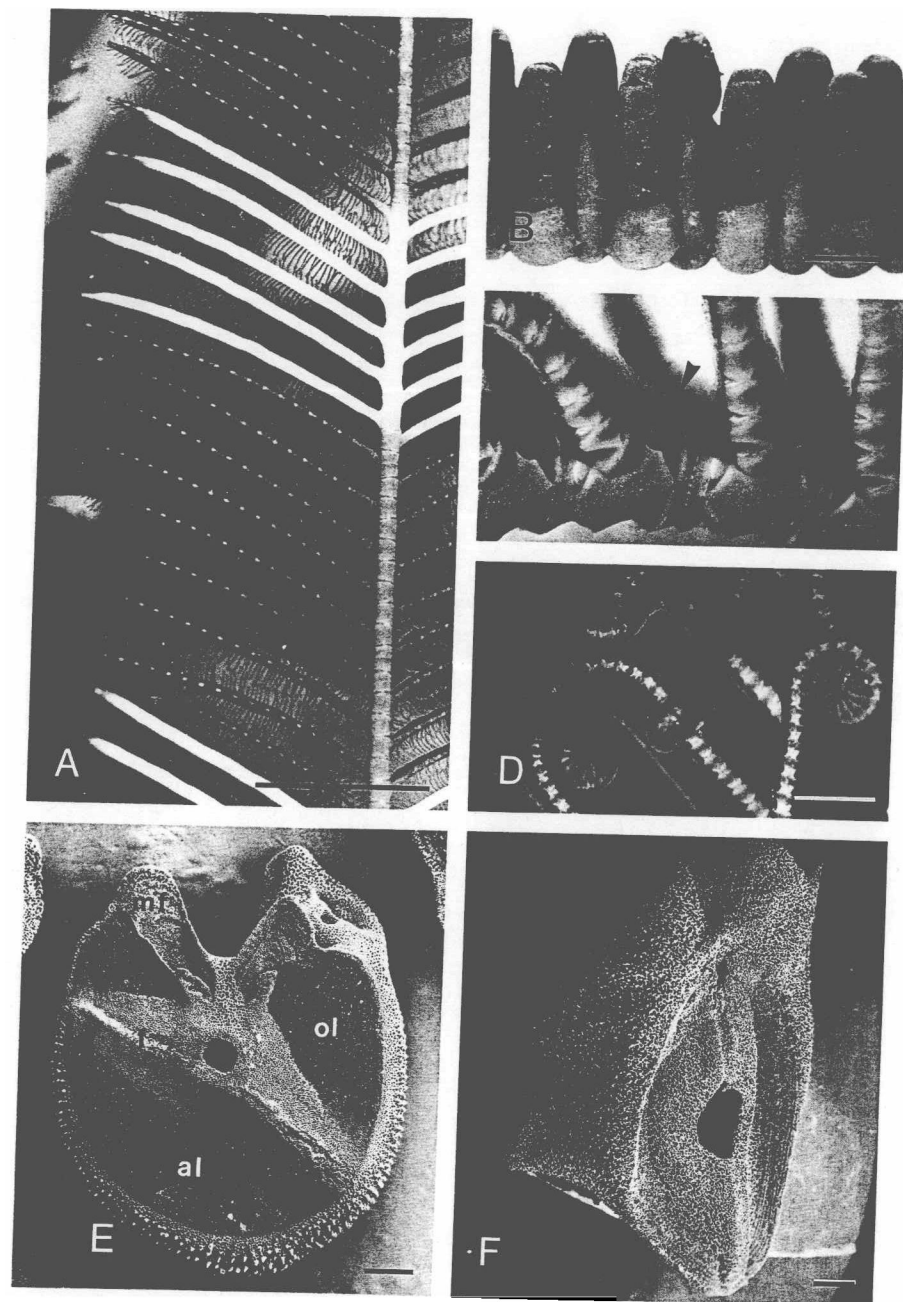


Fig. 6. Morphology of pinnules. A: Detail of the catch fan of a living specimen of *Heterometra savignyi*. The pinnules rise obliquely from the arm and bear unusually long tentacles that control the space between the pinnules. Bar = 5 mm. Courtesy of Prof. Magnus, Darmstadt. B: Lateral view of a stretched arm of *Gymnocrinus richeri* showing the curled pinnules rising at right angles from the arm. Bar = 2 mm. C: Pinnules of *Clarkcomanthus albinotus* with ripe gonads (arrowheads; cf. Fig. 7b).

Bar = 2 mm. D: Oral pinnules of *Comatula solaris*. Bar = 2 mm. E: REM. Brachial ossicle of *Tropiometra afra*, showing a muscular-ligamentary articulation face with oblique fulcrum and, forming on its shoulder, a synarthral joint (arrow) with the first pinnular ossicle. Bar = 0.5 mm. al, aboral ligament; f, fulcrum; mf, muscular facet; ol, oral ligament. F: REM. Interbrachial synarthry. *Promachocrinus kerguelensis*. Bar = 0.5 mm.