# "ECHINODERMATA"

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## Summary

The Echinodermata (*echino* = spiny; *derm* = skin) is a phylum of deuterostome macroinvertebrates displaying a great diversity of body forms, but most often showing radial symmetry based on five rays. Echinoderms are entirely marine, and extremely intolerant of fresh water. The phylum includes the Crinoidea (sea lilies), Asteroidea (starfish), Ophiuroidea (brittlestars), Holothuroidea (sea cucumbers), and Echinoidea (sea urchins), and a disparate assemblage of less familiar fossil groups. A sixth and still controversial group has been described, the Concentricycloidea (sea daisies), but many now feel that these are specialized asteroids. Echinoderms range in lifestyle from pelagic larvae to infaunal burrowers, and inhabit virtually every conceivable marine environment, from sandy beaches and coral reefs to the greatest depths of the sea. Echinoderms have left a relatively complete and detailed fossil record of more than 13 000 species stretching back 500 million years to the Cambrian (and perhaps even before that in some interpretations). Therefore, the origin and subsequent radiation of the Echinodermata has become a compelling research program, and combined with embryological and molecular studies, the phylum can be used to illuminate evolutionary biology in general.

## 1. Introduction

Even the briefest of surveys of adult echinoderms, fossil and extant, reveals a phylum rich in morphological disparity and unfamiliar structures (Figure 1). Crinoids are characterized by the possession of a central body cup, or calyx, which is surrounded by feathery, usually heavily branched arms. Asteroids typically have five unbranched arms radiating from a central disk which is confluent with the arms themselves. Ophiuroids also typically have five arms, but the central disk is more clearly demarcated from the arms. Holothuroids are soft-bodied and worm-like, with a cluster of tentacles around the mouth at one end, and the anus at the other. Echinoids usually have a rigid body wall of sutured plates upon which are mounted a dense forest of spines. The less familiar fossil forms constitute a variety of both mobile and sessile (stalked and unstalked) animals that show the basic features of echinoderms and forms that reveal their echinoderm affinities only at close inspection (Figure 1).

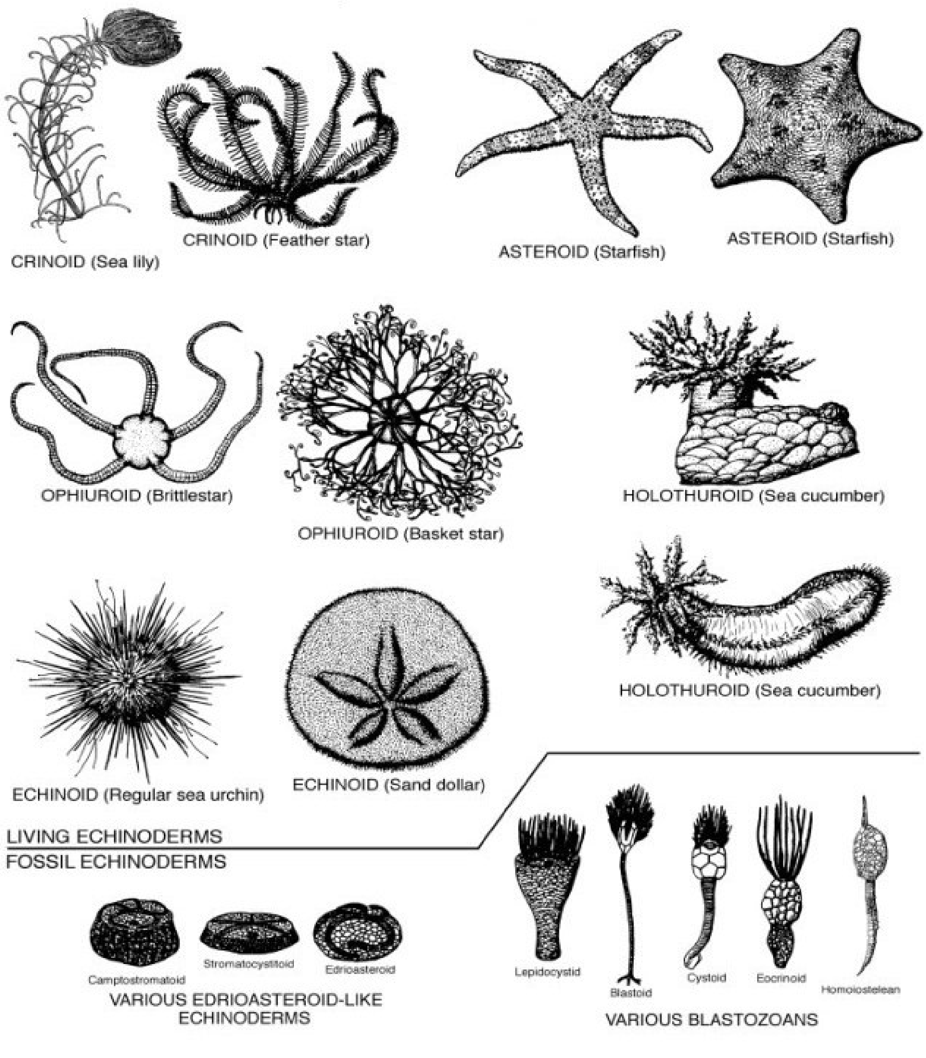


Figure 1. Representative echinoderms

The relationship of echinoderms to other deuterostomes, including the chordates, make them ideal subjects for embryological studies, which shed light on basic developmental patterns even among vertebrates. In addition, their importance to the ecology of both shallow and deep waters and their sensitivity to environmental degradation are indicators of the key role these large and conspicuous invertebrates will continue to have in ecosystem research.

## 2. General Morphology of the Echinodermata

The familiarity of a starfish or a sea urchin and their frequent employment as icons of the marine realm belies their overall strangeness. The Echinodermata is difficult to relate to other phyla. Moreover, the major echinoderm groups also are different from each other. But when echinoderms are viewed in the light of some overarching principles that integrate their unusual characteristics, they form an excellent model for testing ideas about the origins of evolutionary novelty.

### 2.1. Recognizing an Echinoderm

Echinoderms generally possess five unique features, most of which can be seen in or inferred from even the earliest fossils:

1. Calcium carbonate (limestone) skeletal elements in the tissues, especially the body wall. At high magnification, these elements, called stereom, have a spongy appearance due to their porous (trabecular) structure. This makes the skeleton light yet resistant to breakage. Echinoderm hard parts are not external shell, but true internal skeleton inside the body.
2. Mutable collagenous tissue (MCT) made up of ligaments connecting the skeletal elements. MCT can be varied in stiffness by the nervous system. When MCT ligaments are loosened, body parts can be positioned and then locked into position when the MCT stiffens. Echinoderms can then maintain a given posture without expending energy through long-term muscular contraction.
3. A water vascular system (Figure 2). This consists of a circum-esophageal tube, the water ring, which gives rise to five radial canals supplying tube feet in each of the rays. Tube feet are critical parts of an echinoderm's sensory, locomotory, feeding, and respiratory functions. In echinoids and asteroids, a tube foot operates as a hydrostatic skeleton, with muscles in an internal sac, or ampulla, contracting to force water into the tube foot, thereby extending. When longitudinal muscles in the tube foot contract, the tube foot is withdrawn. The madreporite is a perforated plate thought to sieve incoming water to replenish fluid lost through the walls of the tube feet. A stone canal connects the madreporite to the water ring.
4. Metamorphosis from bilateral larvae to pentameral body organization in adults. Larvae are generally bilaterally symmetric and pelagic. After settlement on the sea bottom, metamorphosis involves reorganization of the tissues from bilateral to radial body form. Even in superficially bilateral groups, such as some echinoids, there is an underlying fivefold arrangement dictated by the layout of the water vascular system.
5. A diffuse, subepithelial neural network. Echinoderms lack a head, brain, or any other structure obviously involved in centralized nervous control. There are radial nerves running along the rays, and a nerve ring around the esophagus, but ganglia are rare in echinoderms.

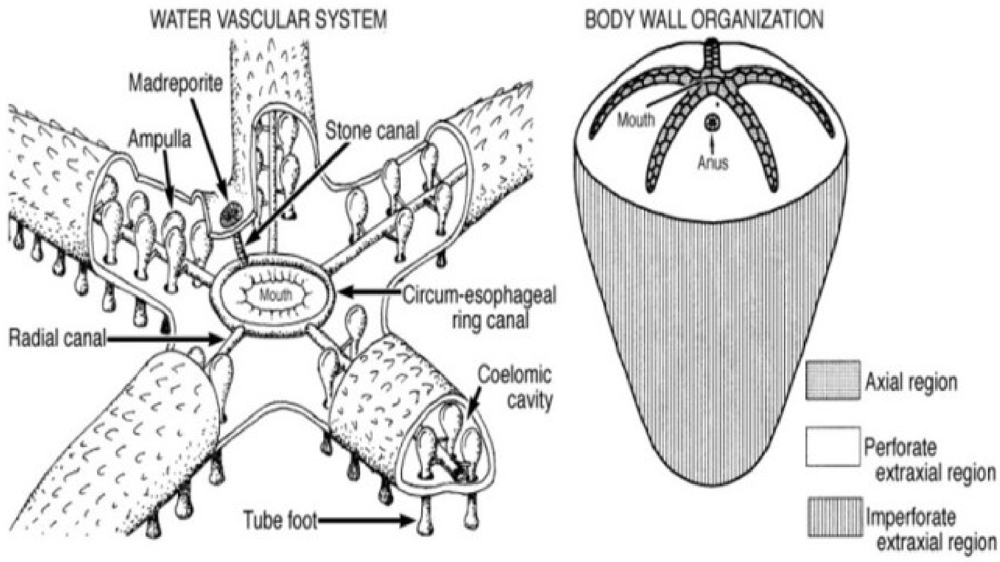


Figure 2. Water vascular system of an asteroid and body organization of a generalized early echinoderm



## 2.2. Organization of the Echinoderm Body

The disparity among sometimes bizarre body organizations makes the major echinoderm groups difficult to relate to each other. For vertebrates, we have a system of evolutionarily related parts (homologies) that allows one to see clearly how structures such as a bird's wing and a human arm originated. Such a system has been slow to develop for the Echinodermata. However, using morphological data from extant forms, fossils, and embryological development, a model for echinoderm organization is emerging, and making it easier to relate even the most bizarre of the earliest echinoderms to the modern forms.

### 2.2.1. Morphological Pattern

The model recognizes two main body regions: extraxial and axial (Figure 2). The idea has been dubbed the "EAT," for extraxial-axial theory. In the extraxial region, new skeletal elements can be added anywhere. In primitive echinoderms, extraxial skeleton can be divided into perforate (which is pierced by the anus, the reproductive openings, and several other orifices peculiar to echinoderms), and imperforate (which contains no orifices).

The axial region is always associated with the water vascular system. Axial elements are added according to a specific pattern called the "ocular plate rule." According to this rule, the oldest elements are near the mouth, and the youngest are out at the tip of the ray. In almost all echinoderms, new elements form in a double, zigzag series, and each element is associated with a tube foot.

### 2.2.2. Embryological Pattern

During early development, three pairs of body cavities (coeloms) appear along the longitudinal axis of the larva. The left cavity of the middle pair is also known as the "hydrocoel," and this compartment develops into the water vascular system. The hydrocoel encircles the esophagus, and five lobes appear along the perimeter of the resulting ring, each elongating to form the five radial canals of the adult. The left cavity of the posterior pair of cavities moves under the hydrocoel, interacting with the latter to produce the first manifestations of the adult pentameral form. This region is known as the rudiment.

The axial region is strictly associated with the rudiment, particularly with the hydrocoel. During metamorphosis, much of the non-rudiment portion of the body is lost or remodeled. However, significant portions of nonrudiment coelomic and skeletal components are retained into adulthood in some groups, particularly crinoids and many early fossil forms, and this represents the extraxial region. Therefore, the two major divisions of echinoderm body wall, axial and extraxial, are derived from the rudiment and the non-rudiment parts of the larva, respectively.

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**Biographical Sketch**

**Rich Mooi** is Curator and Chairman of the Department of Invertebrate Zoology and Geology at the California Academy of Sciences in San Francisco, California. He is also the Scientific Coordinator of SFBay:2K, an initiative to survey and document the benthic animals of San Francisco Bay, and Research Professor at San Francisco State University. His major research interest is the origin of evolutionary novelty, which he studies by analyzing the phylogenetic systematics, paleontology, skeletal homologies, and development of echinoderms. His first and abiding love is for sea urchins and their allies, particularly sand dollars.