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Echinoderms (Other Than Echinoids)

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Introduction

Echinoderms are an important group of marine invertebrates with multiplated calcite skeletons and a long and rich fossil record. Echinoderms first appeared in the Early Cambrian and today are represented by approximately 6000 species distributed throughout all latitudes and from the intertidal zone to the deep ocean trenches. They have one limitation, however: they can tolerate only slightly reduced salinities and are absent from brackish and estuarine habitats. Sessile forms such as crinoids and blastoids are filtration feeders, using their network of arms or tentacles to capture organic particles from the water. Vagile forms are more diverse in their feeding strategies, with scavengers, algivores, carnivores, deposit feeders, and filter feeders all represented. Almost all are benthonic, living on the seafloor or buried just beneath it, although there are rare pseudoplanktonic and true nektonic species.

Key Attributes of Echinoderms

Crown-group echinoderms share several characteristics that mark them apart from other invertebrates and show them to be a monophyletic group.

- They possess multiplated skeletons whose elements are composed of high-magnesium calcite and under magnification have a highly distinctive mesh-like structure termed stereom (**Figure 1**). Because of this, even isolated plates in petrographic thin section are instantly recognizable as being derived from echinoderms. Stereom can have a variety of three-dimensional arrangements, largely depending on the nature of the investing soft tissue.
- Their body plan is basically pentaradiate. This is clearly expressed in all living groups, although there are exceptions, especially amongst some of the more primitive Early Palaeozoic blastozoan groups.
- All crown-group echinoderms possess a water vascular system built to a common plan. The water vascular system is a hydraulically operated system of tube feet and linking canals that is derived from the larval left mesocoel. It is composed of a central

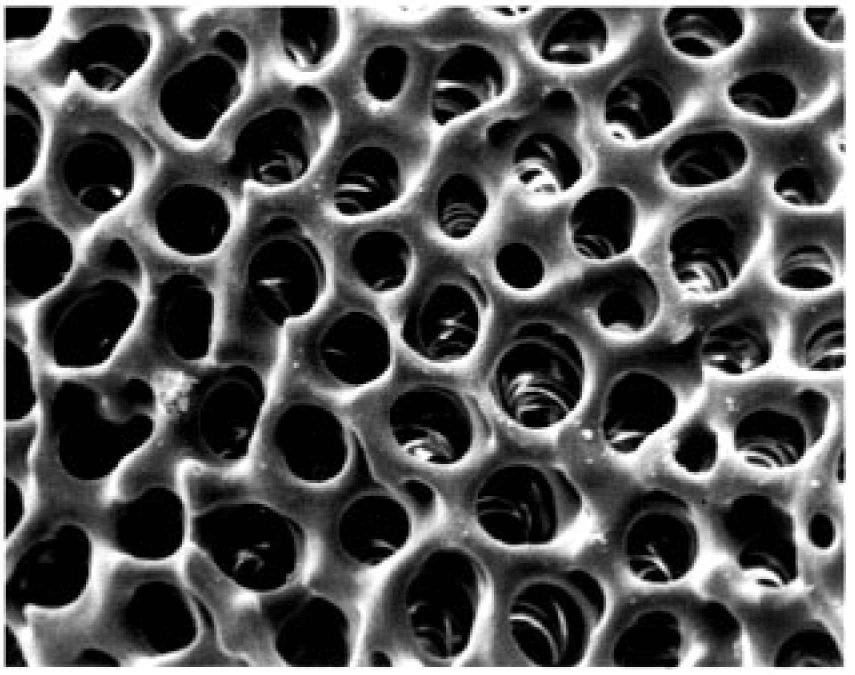

Figure 1 Scanning electron micrograph (magnification ×250) of an echinoid plate showing the three-dimensional mesh (stereom) of which the echinoderm skeleton is composed.

ring canal, which surrounds the start of the digestive system just internal to the mouth. Five primary branches bud off from this ring forming long radial water vessels, which end blindly and which give rise on either side to a series of external tentacles termed tube feet. An additional short branch arising from the circumoral ring leads to the exterior via the hydropore and bears no tentacles. The skeletal elements associated with the radial canals and their tube feet comprise the ambulacral series. Ambulacral-plate series are thus always arranged radially around the mouth.

Of these characteristics, only possession of stereom is ubiquitous to all stem-group echinoderms. Pentameral symmetry is confined to crown-group echinoderms, stem-group members either being completely asymmetrical or showing bilateral or triradiate symmetry. Similarly, only some stem-group echinoderms show evidence of an ambulacral system and ambulacral plating.

Phylogenetic Relationships

Echinoderms are triploblastic Metazoa, which, despite their unique pentaradiate adult body plan, belong to the Bilateria. More specifically, echinoderms are members of the group Deuterostoma, i.e. bilaterians in which the embryonic blastopore develops into the anus rather than the mouth. This aligns echinoderms with chordates and hemichordates, the latter comprising acorn worms, pterobranchs, and the extinct graptolites (*see* **Fossil Invertebrates:** Graptolites). Recent molecular and morphological analyses unambiguously indicate that echinoderms and hemichordates are the more closely related, and together these form the taxon Ambulararia. Both hemichordates and echinoderms have a vascular system of tubes (the water vascular system of echinoderms and the tentacular system of pterobranchs) that originates from the homologous primary body coeloms. In hemichordates the tentacular system is symmetrically paired and forms from both the left and the right mesocoel. In echinoderms only the left mesocoel forms the water vascular system, and hence there is only a single hydropore. As both hemichordates and chordates are bilaterally symmetrical as adults and bear gill slits (pharyngeal openings), the latest common ancestor of echinoderms and hemichordates must also have been bilaterally symmetrical and have possessed gill slits.

Echinodermata are divided into five extant classes, which together form the crown group of the phylum. These are the Crinoidea (feather stars and sea lilies) (*see* **Fossil Invertebrates:** Crinoids), Asteroidea (starfishes), Ophiuroidea (brittle stars), Echinoidea (sea urchins) (*see* **Fossil Invertebrates:** Echinoids) and Holothuroidea (sea cucumbers). Major differences separate the body plan of crinoids from those characterizing the other four classes, and molecular and comparative data all point to crinoids as the most primitive of the extant echinoderm classes. The crinoids and their extinct stalked relatives the blastozoans together form the group Pelmatozoa. Asteroidea, Ophiuroidea, and the Echinozoa form a sister clade, the Eleutherozoa, and are free-living. Molecular evidence suggests that amongst eleutherozoans the Echinoidea and Holothuroidea are the most closely related, and together they form the group Echinozoa. Echinozoa have a globular to cylindrical body form with the aboral surface highly reduced. By contrast, asteroids and ophiuroids have a stellate body plan and their oral and aboral surfaces are equally developed. The extinct edrioasteroids are an important early eleutherozoan group.

There are some numerically small but interesting stem-group echinoderms; most important amongst these are the carpoids (see below). Carpoids all lack pentaradiate symmetry, and most lack an ambulacral system while retaining pharyngeal gill slits.

Geological History

The geological history of echinoderms is summarized in **Figure 2**. The earliest records we have are of isolated plates with the distinctive stereom structure from the Botomian (Early Lower Cambrian) of America. By the end of the Lower Cambrian we have evidence of carpoids, helicoplacoids, blastozoans, and edrioasteroids, suggesting that the crown-group split between pelmatozoans and eleutherozoans had

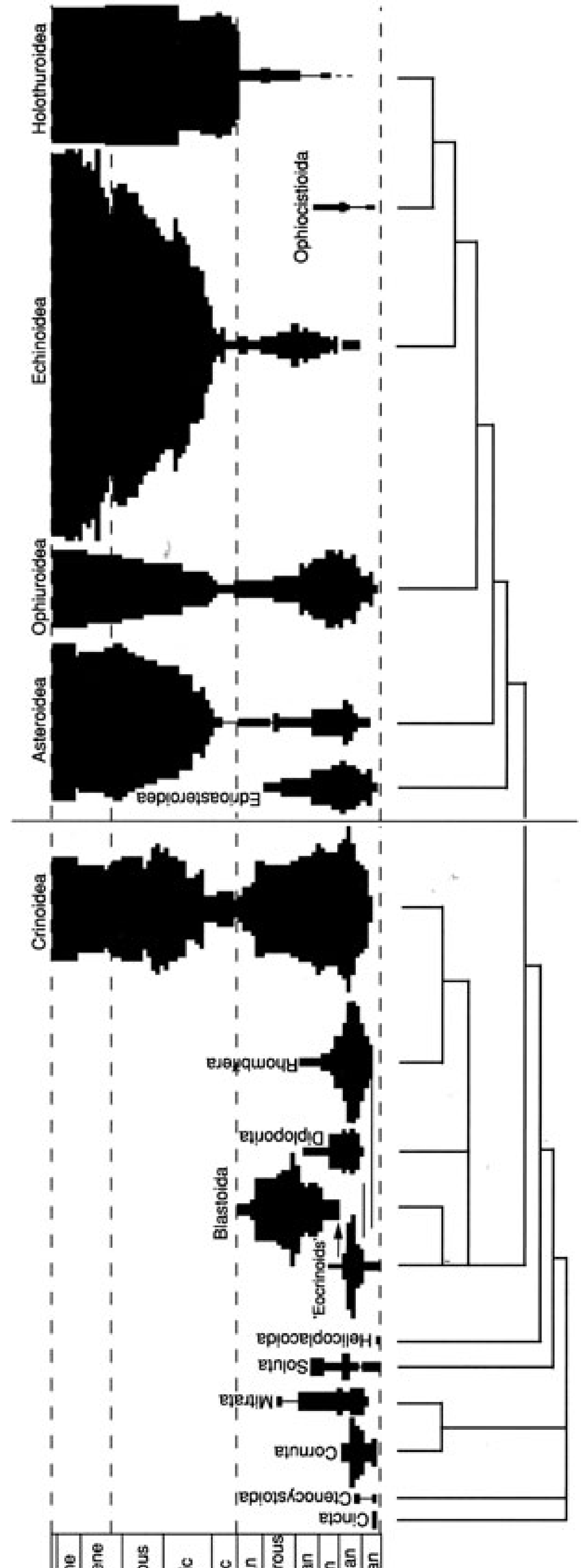

Figure 2 Stratigraphic ranges of the major groups of echinoderm. The widths of the bars are proportional to the taxic (family-level) diversities. The cladogram shows their inferred phylogenetic relationships.

already taken place. However, it is not until the Early Ordovician that definite members of the five extant classes are found. The earliest crinoids, asteroids, and ophiuroids all appear close to the base of the Ordovician, while echinoids appear a little later, in the Middle Ordovician. Holothurians are not definitely known until the Late Silurian. During the Palaeozoic stemmed filtration feeders dominated benthic communities both numerically and taxonomically. Although isolated echinoderm ossicles can be present in such abundance as to be the major bioclastic constituent of some limestones, articulated echinoderm skeletons are for the most part confined to Lagerstätte deposits (*see* **Lagerstätten**) and are relatively rare.

All echinoderm groups went into decline towards the end of the Palaeozoic, and several groups became extinct. Edrioasteroids last occur in the Upper Carboniferous and blastozoans in the Permian. The groups that did survive into the Mesozoic did so only in small numbers, and indeed the modern fauna of echinoids, asteroids, crinoids, and ophiuroids were all initiated at around this time. The evolution in echinoids of a solid and robust test in the Triassic greatly enhanced their preservation potential. The history of echinoderms since the Triassic has been one of unbridled success, and the five classes have continued to diversify and expand their ecological ranges through the Mesozoic and Tertiary. Echinoderms are probably as diverse now as they have ever been.

Major Taxonomic Groups

Carpoids

Carpoids are the most primitive of the stem-group echinoderms. There are four major groups: Soluta, Cincta, Ctenocystoida, and Stylophora; Stylophora is further subdivided into the cornutes and the mitrates.The Stylophora (**Figures 3C** and **3D**) are the most primitive and conform most closely in body plan to a basal deuterostome. Stylophora have a large anterior body with pharyngeal openings and a single posterior appendage (stele), which is muscular and bilaterally symmetrical. Cornutes (**Figure 3D**) are strongly asymmetric in outline, often rather boot-shaped, and have a well-developed marginal frame and a serially repeated set of external atrial openings. Mitrates (**Figure 3C**) on the other hand are more nearly bilaterally symmetrical with no differentiated marginal frame. Paired internal gill bars are present in at least some species. Both have a calcitic skeleton composed of stereom, and neither show evidence of possessing a water vascular system. The presence of gill openings and a motile muscular stele or tail is primitive for deuterostomes as a whole. Stylophora occur from the Middle Cambrian through to the Carboniferous and were recumbent suspension feeders that are thought to resemble tunicates in their feeding strategy (i.e. drawing water into the pharynx where it could be filtered through gill filaments).

Solutes are the most echinoderm-like of the carpoid groups. They have a sac-like body and two appendages asymmetrically arranged at opposite poles (**Figure 3A**). One of these appendages is an ambulacrum in the form of a single arm, so clearly this group had a tentacular water vascular system. Furthermore, the presence of a single rather than paired hydropore indicates that it was built on the echinoderm plan. The other appendage is a stalk, which is muscular near the theca and more rigid distally with a basal attachment pad. Solutes appear in the Lower Cambrian and survived until the Early Devonian. They were suspension feeders, using their ambulacrum to capture particles.

Cinctans have an ovate body with a well-developed marginal frame and a single rather rigid bilaterally symmetric appendage (**Figure 3E**). There is a small mouth opening through the marginal frame and to either side there is a groove that is roofed by a flexible sheet of cover plates. The right-hand groove is always the less well developed and may be lacking in some species. It seems likely therefore that cinctans possessed a pair of hydrocoel tentacles, with the left being better developed than the right. Whether these are both from the left hydrocoel or represent a hemichordate-like paired system is unknown, since hydropores have not as yet been definitely identified. At the anterior there is a large opening covered by an opercular plate, which acted as an outlet valve. This is best interpreted as an atrial opening and suggests that cinctans, like stylophorans, were active suspension feeders with some form of pharyngeal filtration basket. Like stylophorans they lived recumbent on the seafloor. Cinctans are restricted to the Cambrian.

Finally, the ctenocystoids are a small group of carpoids without a stem or tail, external gill slits, or ambulacra (**Figure 3B**). Their precise phylogenetic position remains uncertain, but they were free-living and possibly pharyngeal basket feeders like the Stylophora. They are found from the Middle Cambrian to the Upper Ordovician.

Helicoplacoids

The stratigraphically oldest fossil echinoderm assemblages known are dominated by helicoplacoids. Helicoplacoids are cigar-shaped echinoderms with a basal attachment at one end and a terminal anus at the other (**Figure 3F**). They have a lateral mouth, about two-thirds of the way up from which three ambulacra

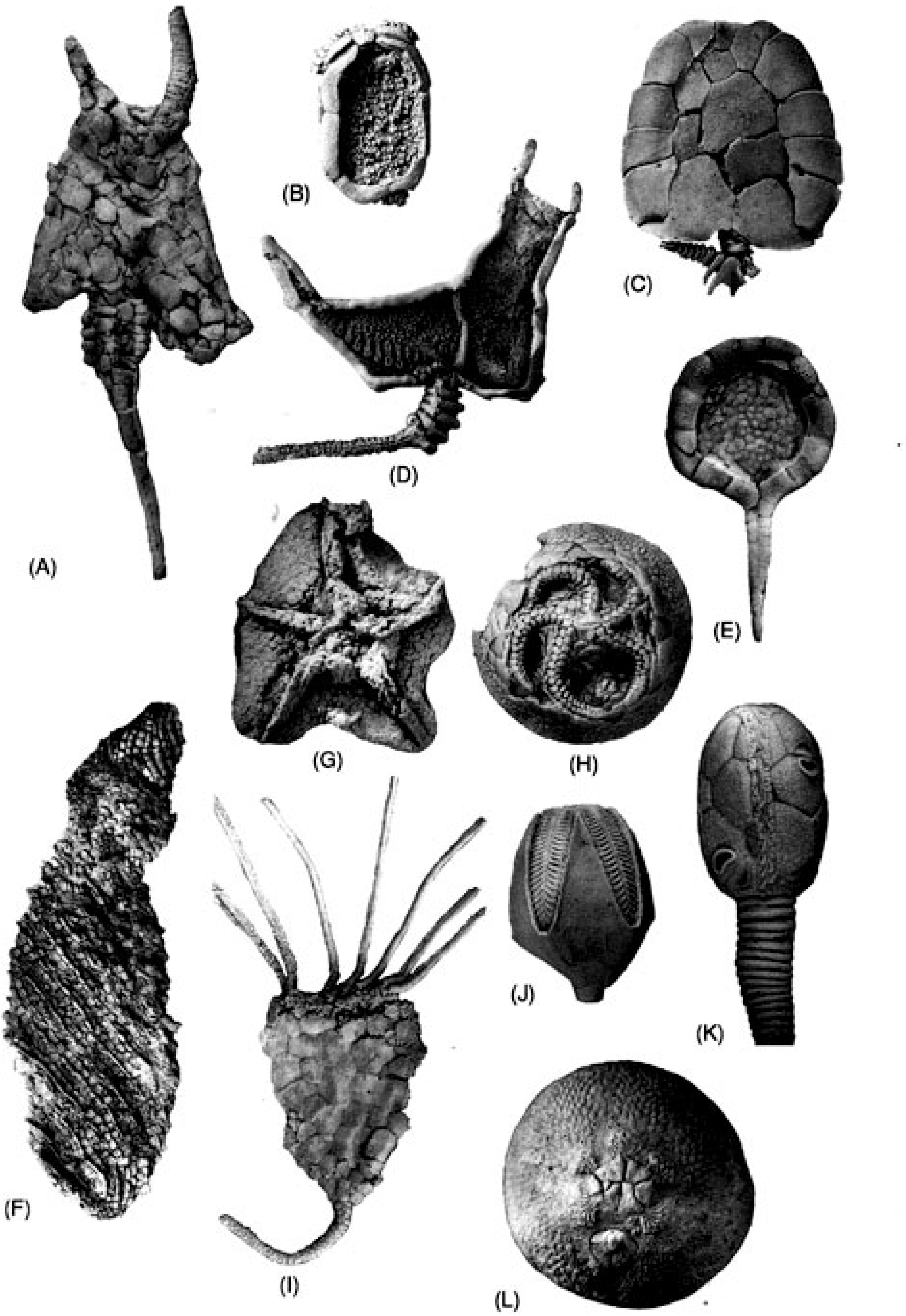

Figure 3 Representative fossil echinoderms. (A) The solute *Dendrocystoides* from the Upper Ordovician (magnification ×0.5). (B) The ctenocystoid *Ctenocystoides* from the Middle Cambrian (magnification ×3). (C) The mitrate stylophoran *Mitrocystites* from the Middle Ordovician (magnification ×1.4). (D) The cornute stylophoran *Cothurnocystis* from the Upper Ordovician (magnification ×1.4). (E) The cinctan *Trochocystites* from the Middle Cambrian (magnification ×1.4). (F) The helicoplacoid *Helicoplacus* from the Lower Cambrian (magnification ×1.4). (G) The stromatocystitid edrioasteroid *Stromatocystites* from the Middle Cambrian (magnification ×1). (H) The isorophid edrioasteroid *Carneyella* from the Middle Ordovician (magnification ×1.7). (I) The eocrinoid *Gogia* from the Middle Cambrian (magnification ×1.4). (J) The blastoid *Pentremites* from the Carboniferous (magnification ×1.4). (K) The rhombiferan *Apiocystis* from the Middle Silurian (magnification ×1.4). (L) The diploporite *Haplosphaeronis* from the Upper Ordovician (magnification ×1.4).

radiate, two spiralling upwards and one spiralling downwards. Each ambulacral series is composed of a double column of flooring plates and two flaps of cover plates. Pores indicate the positions of tube feet. The remainder of the body is covered in spirally arranged columns of rectangular elements. There is some evidence that helicoplacoids could extend and contract their body by changing the angle of spiralling. Helicoplacoids are confined to the Lower Cambrian and were suspension feeders living on algal-bound sediments. They used their tube feet to capture particles in the water column.

Blastozoans

Blastozoans are a large and morphologically diverse group of primitive stemmed echinoderms that mostly resemble crinoids in appearance and lifestyle. The plated body or theca bears a mouth, anus, and usually some form of specialized respiratory structure. The stem takes the form of a polyplated holdfast, a more regular stem comprising five series of vertically aligned ossicles, or a holomeric stem composed of disc-shaped columnals. A few blastozoans are secondarily stemless and either cemented directly to the seafloor or were free-lying. The mouth faces upwards, away from the seafloor. All blastozoans have some form of filtration fan composed of unbranched brachioles, which presumably bore tube feet and a water vascular system. However, in contrast to crinoid arms, which are formed as direct outgrowths of the body wall and carry extensions of the primary body coelom, blastozoan brachioles are side branches of the ambulacra and are not directly connected to the body coelom. Although many blastozoans show an obvious pentaradiality, diverse body forms, symmetries, and ambulacral architectures are to be found in this group. As currently constituted they are probably a polyphyletic group.

Eocrinoids are a paraphyletic assemblage of basal pelmatozoans that have an irregularly plated theca (**Figure 3I**). Simple sutural gaps termed epispires that notch the thecal plates are the only respiratory structures ever developed. Eocrinoids include the ancestors of all other blastozoan groups and probably of the crinoids also. Diploporites (**Figure 3L**) have larger and more regular plating and lack any form of ambulacral flooring plates; the brachioles arise directly from the thecal plates. Thecal plates are pierced by numerous pairs of pores (diplopores) that have a respiratory role. Rhombiferans (**Figure 3K**) have stout arms arising directly from around the mouth. Respiratory structures are always present and take the form of thin folded rhomboidal structures or tubes that run close to the inner or outer surfaces of the plates. Blastoids (**Figure 3J**) have the most regular thecal plating of any blastozoan, always constructed of three basals, five radials and five lancet plates. Pentameral symmetry is extremely well expressed. Ambulacra are well developed and form an integral part of the theca, giving rise to a dense fan of brachioles. Small openings along the margins of the ambulacra lead into an internal hydrospire system – a highly convoluted and thin-walled respiratory organ. The oldest blastozoans are eocrinoids of Lower Cambrian age. Diploporites and rhombiferans appear at the start of the Ordovician, while blastoids do not appear until the Silurian. The group finally went extinct at the end of the Permian.

Edrioasteroids

Edrioasteroids are an extinct group of sessile stem-group eleutherozoans that were discoidal, clavate, or subglobular in form (**Figure 3G** and **3H**). They have a central mouth from which five ambulacra radiate. The ambulacra can be straight, but are commonly spiralled to provide a larger surface area, and extend to a marginal ring of plates marking the edge of the oral area. A single hydropore and gonopore open close to the mouth. Edrioasteroids lived with the mouth facing upwards and used their five ambulacra to capture organic material suspended in the water.

The earliest edrioasteroids (stromatocystitids: **Figure 3G**) were fully plated and appear not to have been attached to the substrate. These may represent basal eleutherozoans, ancestral to all later forms. The great majority of edrioasteroids, however, fall into a derived clade, the Isorophida (**Figure 3H**), that specialized as hard-ground colonizers. Isorophids lived attached to hard substrates, such as the shells of brachiopods, by their lower uncalcified surface. They were not permanently fixed but were able to realign themselves during life. Some isorophids developed the outer part of the disc as an extendible stalk, which allowed them to lower or raise the oral zone with the ambulacra, presumably in response to water flow conditions.

Stromatocystitids first appear in the Lower Cambrian, while isorophids appear a little later, in the Upper Cambrian, and survived through to the Upper Carboniferous.

Asteroids

Asteroids are stellate echinoderms with arms that merge without a break into a central body (**Figure 4A**). The mouth is central and faces down towards the substrate, and an ambulacral groove runs from the mouth along the lower surface of each arm. In asteroids the arms are hollow and extensions of the digestive system and gonads extend along each. Asteroids lack a jaw apparatus but are active predators, ingesting small prey whole. Some burrow after infaunal animals, while others are epifaunal hunters. One group has evolved an ingenious method of preying on bivalves. They clasp the bivalve using their tube feet and prise the two valves apart. They need to create only a small slit-like opening because they then evert their stomach into the bivalve and digest the animal. The asteroid skeleton is rarely robust and consists of a series of small elements embedded in a collagenous membrane. Consequently, they disarticulate rapidly after death and have left a rather poor fossil record. Asteroids first appear in the Early Ordovician and are never common or abundant.

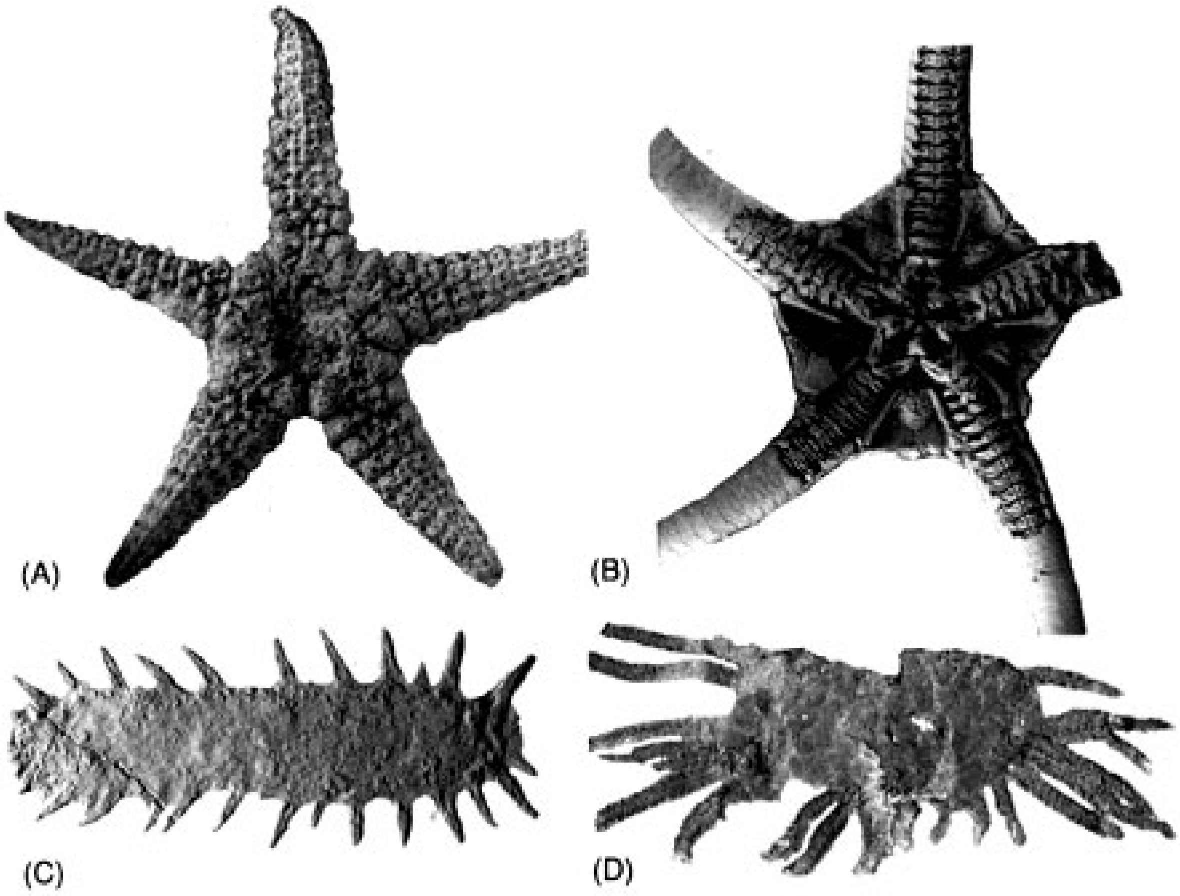

Figure 4 Representative fossil echinoderms. (A) The asteroid *Siluraster* from the Upper Ordovician (magnification ×2). (B) The ophiuroid *Palaeocoma* from the Lower Jurassic (the upper surface of the disc and the proximal parts of the arms have been lost, revealing the solid vertebrae filling the core of the arms and the central jaw) (magnification ×1). (C) The holothurian *Oneirophantites* from the Middle Triassic (magnification ×0.3). (D) The ophiocistiod *Sollasina* from the Upper Silurian (magnification ×0.7).

Ophiuroids

Ophiuroids resemble asteroids in having a stellate body plan, with five or more arms radiating from a small circular disc (**Figure 4B**). Unlike asteroids, however, their arms are solid, being supported by a series of internal disc-like ossicles termed vertebrae. Consequently, there are no extensions of the gonads or digestive system into the arms. The mouth is central and faces downwards. The digestive system is a simple blind sac (there is no anus), and the lower surfaces of the arms carry the water vascular system and the tube feet. All ophiuroids are carnivorous and possess a formidable jaw apparatus with strong musculature and batteries of tooth-like spines.

There are two major post-Palaeozoic groups, the euryalids and the Ophiuroida. In euryalids the arms are typically branched many times to form a filtration fan and bear short spike-like spines. Euryalids are suspension feeders that use their network of arms to ensnare small nektonic prey such as arrow worms, which are then passed to the mouth. The great majority of Ophiuroida are active predators and are able to move rapidly over the seafloor by using their highly motile arms. A few are also able to suspension feed by extending one or more arms into the water column and using their tube feet to secrete ribbons of sticky mucous to ensnare small prey.

The ophiuroid skeleton is rather fragile and readily disintegrates upon death. Consequently, like asteroids they have left a relatively sparse fossil record, starting in the Lower Ordovician.

Ophiocistioids

Ophiocistioids are a small but interesting extinct group of globular eleutherozoans with large plated tube feet (**Figure 4D**) that are related to both echinoids and holothurians. The mouth in ophiocistioids is central and downward facing, and there is a complex jaw apparatus identical in all important respects to the Aristotle's lantern of echinoids. They were therefore presumably active predators, like early echinoids, using their jaws to capture small benthic prey. The large plated tube feet were locomotory in function, and their water vascular system lay beneath the ambulacral plates, as in echinoids and holothurians, rather than externally, as in asteroids and crinoids. In early members the body is covered in a series of small plates. In at least one taxon, however, the body wall is reduced to microscopic spicules, which are wheel-shaped and identical to those seen in apodid holothurians. Ophiocistioids first appear in the Middle Ordovician and continue to the Early Carboniferous. They are always rare.

Holothurians

Holothurians have a cylindrical body plan with the mouth at one pole and the anus at the other (**Figure 4C**). The mouth is surrounded by a ring of

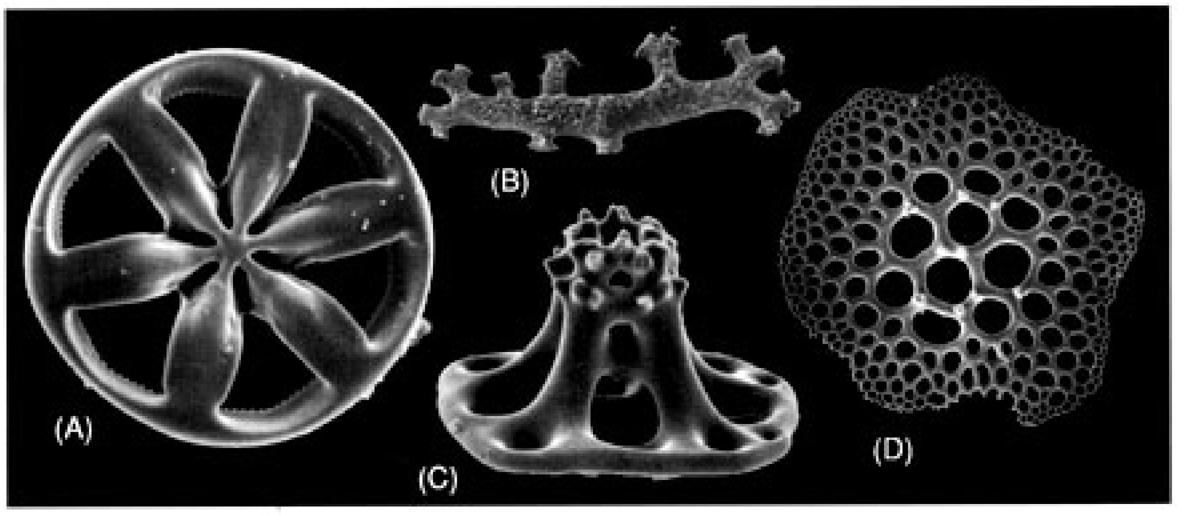

Figure 5 Characteristic spicules from the body walls of holothurians. (A) Wheel (magnification ×600). (B) Rod (magnification ×700). (C) Button (magnification ×800). (D) Plate (magnification ×50).

tentacles, which are often highly branched and are used in feeding. There is no jaw apparatus. Some holothurians have long highly branched tentacles that are extended into the water column and used for suspension feeding. Others have short finger-like tentacles that are used in deposit feeding. Today holothurians are the major deposit feeders in back-reef habitats. They live either on the surface or in shallow burrows.

Holothurians are the most diverse of the five extant classes of echinoderm, with over 2000 extant species, but they have the poorest of fossil records. This is because their skeleton is reduced to microscopic spicules. The only elements of any size are 10 ossicles that surround the mouth and provide an anchorage for the oral tentacles; these form the circumoral ring. Each holothurian has many thousands of microscopic spicules in its body wall. Many are distinctive, such as the anchor-like elements of apodians and the wheel-like elements of molpadiids (**Figure 5**). A few body fossils are known from Lagerstätte (**Figure 4C**) but almost all of our information on the history of holothurians comes from the study of their isolated spicules distributed in the sedimentary record. The first holothurian body fossil comes from the Late Silurian, but spicules probably attributable to holothurians are known from the Ordovician onwards.

See Also

Fossil Invertebrates: Crinoids; Echinoids; Graptolites. **Lagerstätten. Palaeoecology**.

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