

two large stemless crinoid genera from the Cretaceous – *Marsupites* and *Uintacrinus* – although recent interpretations favour a benthic habit. In the Late Silurian to Early Devonian a bizarre group of large camerate crinoids – the Scyphocrinitidae – modified the distal end of the stem into a large chambered ‘bulb,’ which has been interpreted as a flotation structure.

## See Also

**Fossil Invertebrates:** Echinoderms (Other Than Echinoids); Echinoids. **Mesozoic:** Triassic. **Palaeoecology. Palaeozoic:** Devonian; End Permian Extinctions. **Sedimentary Environments:** Carbonate Shorelines and Shelves.

## Further Reading

- Ausich WI (1998) Early phylogeny and subclass division of the Crinoidea (Phylum Echinodermata). *Journal of Paleontology* 72: 499–510.
- Cowen R (1981) Crinoid arms and banana plantations: an economic harvesting analogy. *Paleobiology* 7: 332–343.

- Guensburg TE and Sprinkle J (2003) The oldest known crinoids (Early Ordovician, Utah) and a new crinoid plate homology system. *Bulletins of American Paleontology* 364: 1–43.
- Hess H, Ausich WI, Brett CE, and Simms MJ (1999) *Fossil Crinoids*. Cambridge: Cambridge University Press.
- Meyer DL and Ausich WI (1983) Biotic interactions among Recent and among fossil crinoids. In: Tevesz MJS and McCall PL (eds.) *Biotic Interactions in Recent and Fossil Benthic Communities*, pp. 377–427. New York: Plenum Publishing.
- Moore RC and Teichert C (eds.) (1978) *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2*, vols 1–3. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas.
- Seilacher A, Reif W-E, and Westphal F (1985) Extraordinary fossil biotas: their ecological and evolutionary significance. *Philosophical Transactions of the Royal Society of London B* 311: 5–23.
- Simms MJ (1986) Contrasting lifestyles in Lower Jurassic crinoids: a comparison of benthic and pseudopelagic Isocrinida. *Palaeontology* 29: 475–493.
- Simms MJ (1994) Reinterpretation of thecal plate homology and phylogeny in the Class Crinoidea. *Lethaia* 26: 303–312.

## Echinoids

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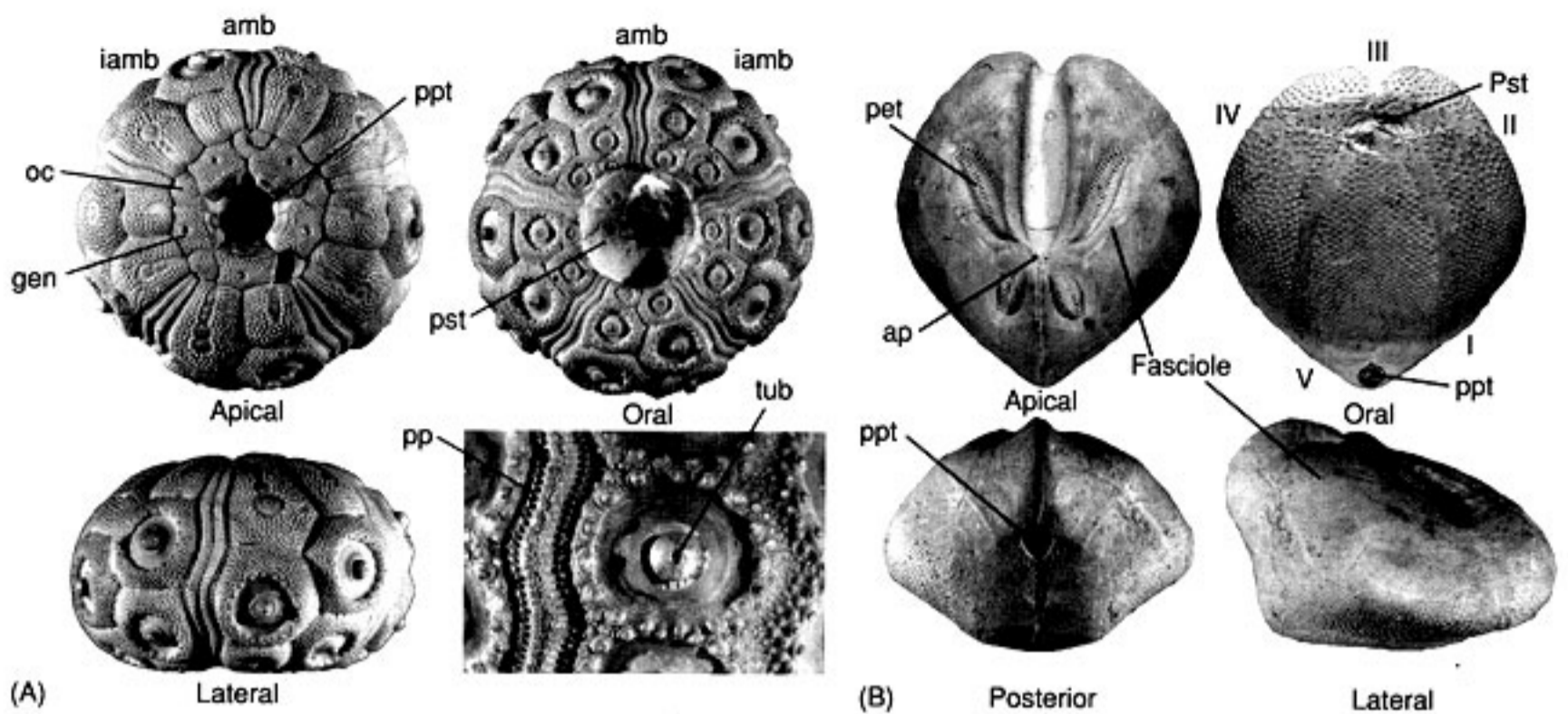
### Introduction

Echinoids are a diverse and widespread group of marine macroinvertebrates and one of the five classes of echinoderm (see **Fossil Invertebrates: Echinoderms (Other Than Echinoids)**). They are exclusively marine and benthic, living either on or within the sea floor, and with their mouth downward-facing. The group includes such well-known animals as the sand dollar, heart urchin and sea urchin. Like all echinoderms, they have a calcitic skeleton constructed of a mosaic of plates, and these are usually firmly bound together to form a rigid and robust test. This skeleton is architecturally complex and, being mesodermal, is able to provide a wealth of information about the musculature and soft-tissue anatomy. Because echinoids have a rigid skeleton, they have left the best fossil record of any echinoderm class. They are also the best understood echinoderm group from a phylogenetic perspective. This combination of a complex skeleton, good fossil record and extensively studied phylogeny has made echinoids the focus of many important palaeobiological studies in recent years.

There are about 900 extant species equally divided between regular forms (‘regulars’) whose anus opens in the aboral plated surface and that live epifaunally, and irregular forms (‘irregulars’) whose anus is displaced away from the aboral plates into the posterior interambulacral zone and that live predominantly infaunally (Figure 1). All echinoids have a well-developed system of hydraulically operated tube-feet that are important for respiration, feeding and locomotion. Echinoids also have a dense and often highly differentiated covering of calcitic spines used for locomotion and defence.

### Morphology of Post-Palaeozoic Echinoids

Echinoids range in size from just a few millimetres in diameter to over 350 mm and come in a variety of body forms: globular, heart-shaped, cylindrical, hemispherical or even flattened discoidal (Figures 1 and 2). However, irrespective of their overall shape, the skeleton (also known as the ‘test’) in post-Palaeozoic echinoids is always constructed along the same standardized plan. At the apex of the test is a small cluster of up to 10 plates known as the apical disc (Figure 1A). In regular echinoids this series of plates surrounds the



**Figure 1** Morphology of (A) a regular echinoid – *Stereocidaris*, an Upper Cretaceous cidaroid from England, and (B) an irregular echinoid – *Schizaster*, an Eocene spatangoid from Italy. amb – ambulacrum; ap – apical disc; gen – genital plate; iamb – interambulacrum; oc – ocular plate; pet – petal; pp – pore-pair; ppt – periproct; pst – peristome; tub – tubercle. I-V – numbered ambulacral zones.

anus but in irregular echinoids the anus is usually outside and to the posterior (Figure 1B). The larger genital plates are in part derived from larval skeleton and are all that remains of the aboral plated surface that is so well developed in other echinoderms. Genital plates are each perforated by a gonopore, which acts as the outlet for the gonads. One of the five genital plates is also perforated like a pepper pot, which forms the opening to the water vascular system. The smaller plates are also perforate, with their tiny opening marking where the tip of the radial water vessel reaches the exterior: these are the ocular or terminal plates. Plates are added at the distal edge of ocular plates during growth.

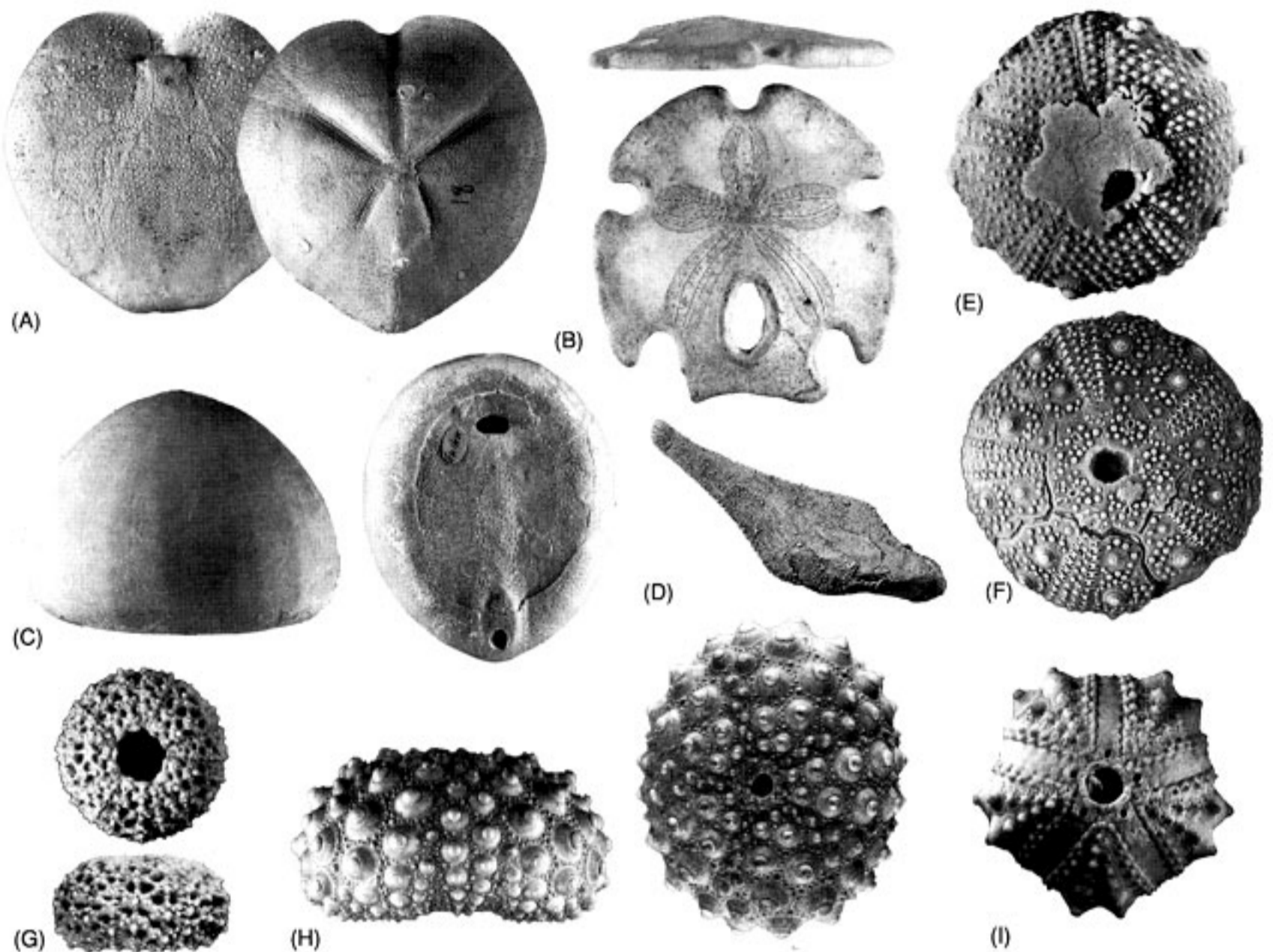
The remainder of the test is composed of 20 columns of plates arranged into alternate pairs of ambulacral and interambulacral elements (Figure 1). Ambulacral plates overlie the radial water vessel and are pierced by single or double pores where tube-feet connect to the interior. Interambulacral plates by contrast are generally larger and are imperforate. They arise on either side of the ocular plate. The external surfaces of both ambulacral and interambulacral plates are covered in tubercles of various sizes and these are the articulation points for spines. Regular echinoids have only a small number of large tubercles whereas irregular echinoids typically have uniform, fine, dense tuberculation (Figure 1A, B). Ambulacral and interambulacral columns of plates converge around the mouth, which lies at the opposite pole from the apical disc.

The mouth is situated in a large opening termed the peristome. This is covered in life by a flexible

membrane with embedded plates that is rarely fossilized. All regular echinoids and many irregular echinoids have an internal jaw apparatus that largely fills the peristome. The lantern is a pentaradially symmetrical and highly complex in structure (Figure 3), being composed of 50 skeletal elements and 60 individual muscles. There are five teeth, each braced in a hemipyramid, and the entire structure can open and close like a grab, as well as moving in and out of the test. Because echinoids have a rigid test of fixed internal volume, having a large and active lantern that moves in and out creates problems. To compensate for changes in internal volume there are 10 expandable soft-tissue sacs around the edge of the peristome that connect directly to the interior and that accommodate any displaced body cavity fluids. Each sac passes to the exterior at a small notch in the peristome (buccal notch). Echinoids that either lack a lantern or have an entirely internal lantern lack buccal notches.

The primary muscles that move the lantern attach to the interior of the test around the rim of the peristome. Enlarged skeletal flanges mark the site of muscle attachment (Figure 3). Flanges developed from the adoral ambulacral plates are termed auricles while those developed from interambulacral plates are termed apophyses. These lantern muscle attachments together form the perignathic girdle.

Appendages that attach to the test include both spines and pedicellariae. Spines vary tremendously in size and shape according to their function (Figure 4). They can be either hollow or solid and either smooth or ornamented externally. There may be a central ligament binding the spine to its articulation ball,

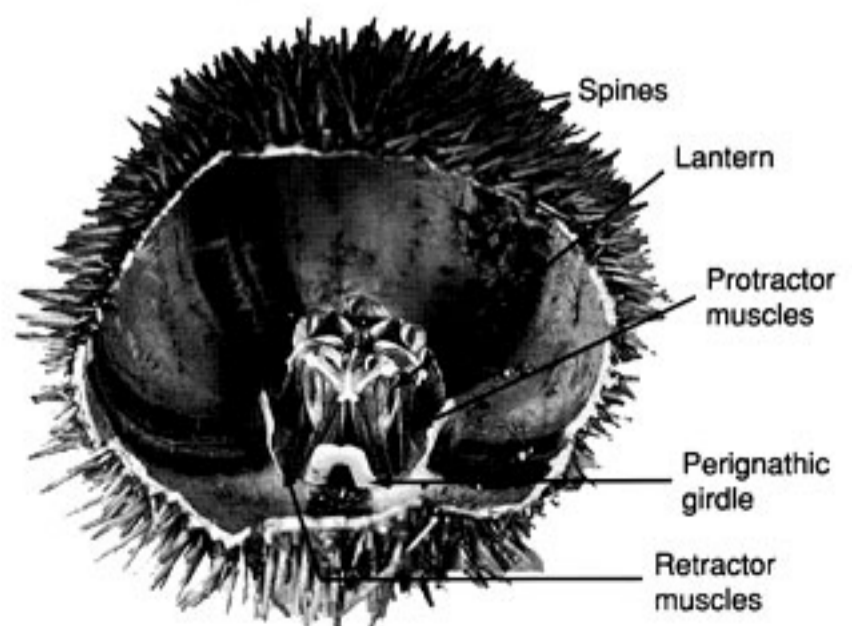


**Figure 2** Representative fossil post-Palaeozoic echinoids. (A) the spatangoid *Micraster* in oral and apical views, from the Upper Cretaceous of England ( $\times 0.7$ ). (B) the clypeasteroid *Encope* in lateral and apical views, from the Pliocene of the U.S.A. ( $\times 0.4$ ). (C) the holasteroid *Echinocorys* in lateral and oral views, from the Upper Cretaceous of England ( $\times 0.4$ ). (D) the holasteroid *Hagenowia* in lateral view from the Upper Cretaceous of England ( $\times 2$ ). (E) the salenioid *Novosalenia* in apical view, from the Cretaceous of the Czech Republic ( $\times 2$ ). (F) the pedinoid *Hemipedina* in apical view, from the Lower Jurassic of England ( $\times 3$ ). (G) the temnopleuroid *Viaudechinus* in apical and lateral views, from the Miocene of France ( $\times 2$ ). (H) the echinoid *Heterocentrotus* in lateral and apical views from the Recent of the Indo-West Pacific ( $\times 0.7$ ). (I) the arbacioid *Murravechinus* in apical view from the Miocene of Australia ( $\times 1.5$ ).

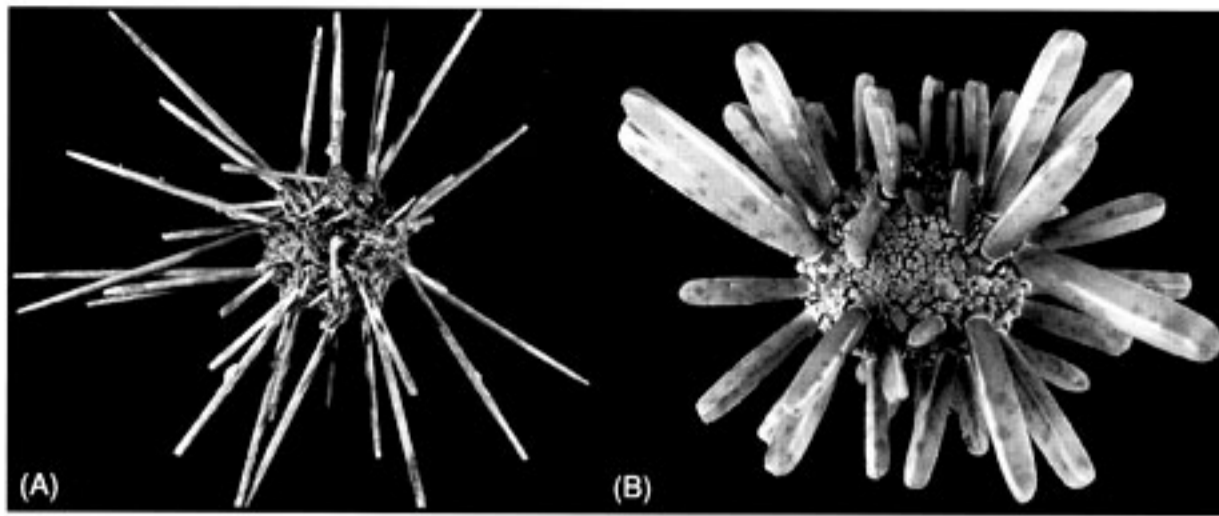
in which case the associated tubercle is perforate (Figure 1A) and the surrounding platform may be smooth or crenulated. Greatest functional differentiation is found in irregular echinoids where spines perform a variety of different roles. Pedicellariae are microscopic stalked, jawed appendages that resemble tulips in shape and that are used to deter small ectoparasites. They evolved from clusters of spines and are present in all echinoids from the Silurian onwards. There are many different forms of pedicellaria making them very useful species-level indicators but, unfortunately, they are rarely preserved in fossils.

### Morphology of Palaeozoic Echinoids

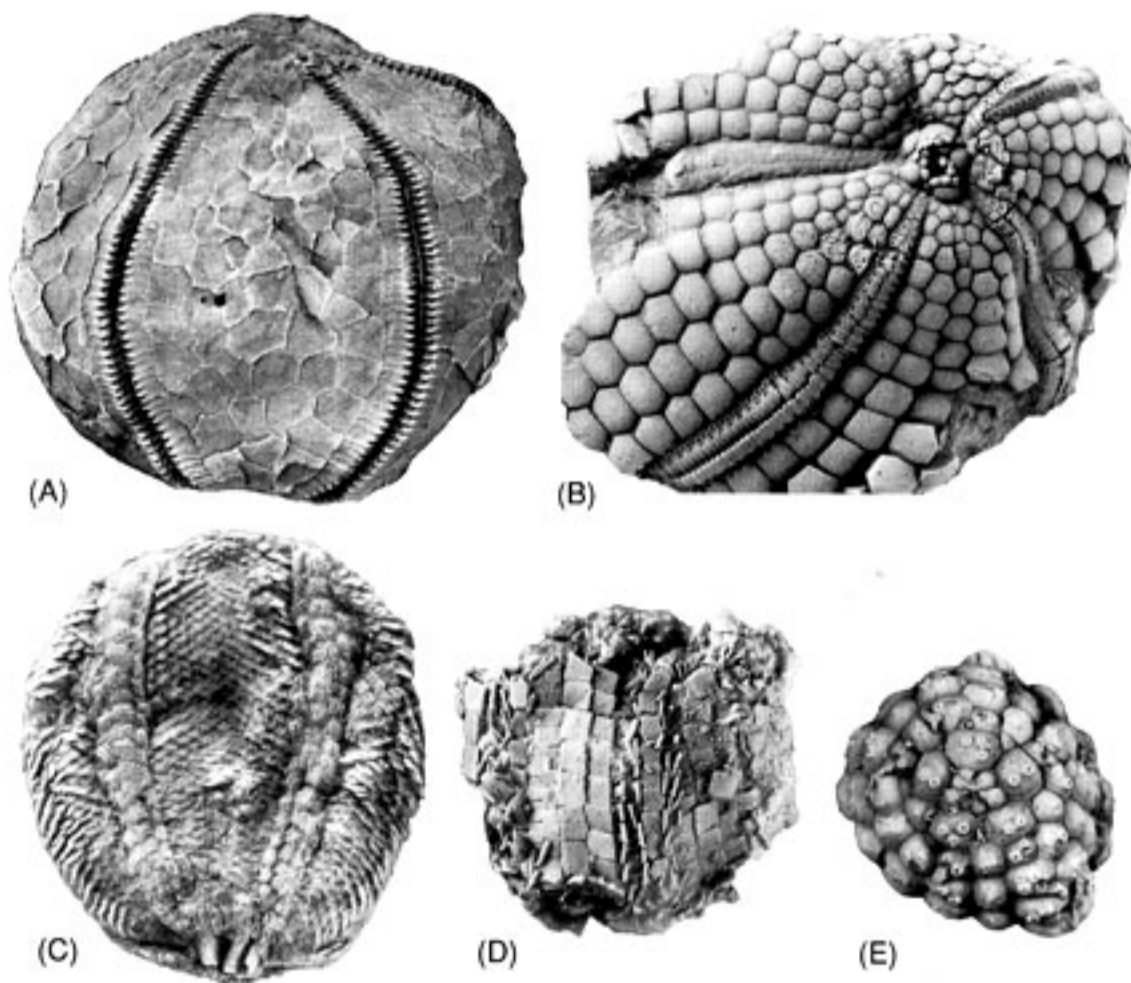
Although Palaeozoic echinoids mostly retain a pentaradiate pattern of alternating ambulacral and interambulacral zones, the precise way their test



**Figure 3** Test of a modern echinoid (*Echinus*) broken open to show the internal lantern and perignathic girdle.



**Figure 4** Modern echinoids with their complement of spines attached. (A) the cidaroid *Cidaris*; (B) the echinoid *Heterocentrotus*.



**Figure 5** Representative fossil Palaeozoic echinoids. (A) *Aulechinus* (internal mould) from the Upper Ordovician of Scotland ( $\times 1$ ). (B) *Maccoya* from the Carboniferous of England ( $\times 0.5$ ). (C) *Lepidesthes* from the Carboniferous of the USA ( $\times 1$ ). (D) *Bromidechinus* from the Upper Ordovician of the USA ( $\times 1$ ). (E) *Bothriocidaris* from the Upper Ordovician of Estonia ( $\times 3$ ).

is constructed shows a huge amount of variation (Figure 5). Only the Permian genus *Miocidaris* has a test constructed of 10 ambulacral and 10 interambulacral columns like that of post-Palaeozoic echinoids. In all others the number of columns of plates, both ambulacral and interambulacral, varies tremendously. Some, such as *Palaechinus* and *Aulechinus* (Figure 5A) have biseriate ambulacra and multiple columns of non-ambulacral plates. Others, such as *Proterocidaris* and *Lepidesthes* (Figure 5C), have very wide ambulacra of up to 20 columns of plates, and narrow interambulacra. *Bothriocidaris*

(Figure 5E) has no interambulacral plates at all, but there is an imperforate series of ambulacral plates. Primitive echinoids also, interestingly, have the radial water vessel enclosed within the ambulacral plates rather than being fully internal, as it is in all post-Palaeozoic forms. A lantern is present, but the teeth are very primitive in structure and no Palaeozoic echinoid has a perignathic girdle. Finally, plating is imbricate (Figure 5D) and so the test rapidly fell apart at death so that even partially articulated specimens are rare except in Lagerstätte deposits.

## Echinoid Palaeobiology

### Locomotion and Burrowing

Regular echinoids are vagile benthos, moving by means of their oral spines over the sea floor and using their tube-feet to climb and grip hard substrata. In forms living in high-energy, rocky, shore environments, the oral tube-feet that provide grip are highly muscular and also densely packed, an adaptation that is easily recognizable from fossil tests. Only a few regular echinoids, notably cidaroids and arbaicoids, evolved specialized aboral respiratory tube-feet: for the most part tube-feet are undifferentiated. Spines would have been the primary means of locomotion in Palaeozoic echinoids, although some of the most primitive presumably used their tube-feet.

Irregular echinoids rely entirely on their spines for locomotion, and most burrow into unconsolidated sediment. This raises a number of problems: locomotion is harder, and circulation of oxygenated water and removal of waste products more difficult, particularly in finer-grained, more impermeable sediments. Infaunal echinoids have highly specialized aboral tube-feet for gaseous exchange and these regions form characteristic petals on the surface of the test (Figure 1B). However, only heart urchins have successfully adapted for life in fine-grained sediments. In order to do this they have specialized aboral tube-feet that are used to build and maintain an open shaft to the surface down which fresh water can be drawn. Water is drawn into the burrow by bands of highly ciliated spines, termed fascioles. These fascioles also generate a mucous coat that is held over the tips of the spines and prevents fine-grained sediment from falling between the spines. The mucous coat thus allows heart urchins to maintain a water-filled space within the burrow.

The traces of burrowing echinoids have been described in rocks from the late Lower Cretaceous onwards.

### Feeding

Regular echinoids feed using their lantern. Palaeozoic echinoids had relatively weak lantern musculature and feeding must have largely involved scooping material from the sea floor. With stronger lanterns echinoids were able to utilize new food sources and could rasp encrusting organisms from hard substrata. Echinoid tooth bite marks first appear as trace fossils in the late Triassic, at about the same time that well-developed perignathic girdles and stronger lanterns evolved. During the Mesozoic the biting force that lanterns could exert was further increased through the development of teeth with a stronger T-shaped

cross-section, and the stronger and more extensive bracing of hemipyramids. Mesozoic and Tertiary echinoids were mostly either algivores or predatory on sessile organisms.

Deposit feeding may have evolved in the Carboniferous, when echinoids such as *Proterocidaris* evolved large numbers of massive oral tube-feet whose most likely function was in detritus gathering. However, this clade became extinct towards the end of the Permian and deposit feeding was not adopted again by echinoids until the Early Jurassic. The evolution of irregular echinoids in the Jurassic is really the story of adaptation towards improved deposit feeding. Some irregular echinoids (cassiduloids) are bulk sediment swallowers, passing a continuous stream of sediment through the gut in order to extract the small quantities of organic matter it might contain. Others (spatangoids and holasteroids) evolved as selective deposit feeders using specialised tube-feet to pick out organic-rich detritus. Sand dollars are rather special in that they appear to be using their aboral spine canopy as a sort of sieve to separate fine organic material from amongst the sand grains. The finer particles fall between the spines and are swept towards the mouth and entrapped in mucous strings that run towards the mouth. These food grooves are easily visible even on a denuded test.

### Predation and Defence

Echinoids today are preyed upon by a variety of animals (including humans), and predation has, presumably, been a major factor since the Devonian, when the first echinoids with long, lance-like spines evolved. Long, sharp spines (Figure 4A) are effective deterrents to many predators, but alternative strategies have also been evolved. Cidaroids have spines that are not covered in a living tissue, and that, consequently, can become heavily encrusted with algae and sessile organisms. This encrustation on flattened, paddle-shaped spines provides very effective camouflage. An alternative ploy has been to develop very thick club-shaped spines that cannot easily be snapped or broken off (Figure 4B). A few regular echinoids have abandoned spines in favour of poisonous pedicellariae as their first line of defence. *Toxopneustes* has a very short, uniform coating of spines and their highly venomous pedicellariae are almost as long. The aboral surface of this animal thus presents a formidable battery of dense, poisonous pedicellarial jaws.

Spines can also provide a first level of protection against impact in high-energy environments, and both in the Jurassic and in the Tertiary echinoids evolved that were short, stout and umbrella-like, forming a tessellate pavement over the surface of the test.

## Reproduction

In echinoids the sexes are separate, but it is usually impossible to tell the sexes apart visually. Reproduction occurs by broadcast spawning: eggs and sperm are released into the water column where fertilization takes place. The fertilized egg then develops into a planktonic larva termed pluteus, which feeds in surface waters for a few weeks before metamorphosing into the adult form and settling to the bottom. A small number of species, most from high-latitude, do not pass through a planktonic larval stage, but develop directly. In such cases the female produces large yolk-rich eggs that are brooded on the test. Females then have special brood pouches termed marsupia where the eggs are protected, and these form sunken zones around the gonopore openings. Sexual dimorphism first evolved in the Late Cretaceous and was particularly prevalent in Australian faunas in the Early Tertiary.

## Geological History

The closest living relative of the echinoids are holothurians (*see Fossil Invertebrates: Echinoderms (Other Than Echinoids)*) and their ancestry presumably lies amongst the 'asterozoan' taxa of the Early Ordovician. When echinoids first appear in the Upper Ordovician, there were already three very different body forms. Bothriocidarids have a small globular test composed of thick plates of the ambulacral series only (Figure 5E), lepidocentrids have narrow biserial ambulacra and wide zones of irregularly arranged imbricate interambulacral plates (Figure 5A), and *Bromidechinus* has biserial interambulacra and triserial ambulacra (Figure 5D). Clearly the earliest phase in the history of echinoids has yet to be uncovered.

During the Lower Palaeozoic, echinoids remained a minor component of marine benthic communities, never becoming diverse or abundant. By the Devonian one lineage had developed enlarged adoral tube-feet and appears to have specialized as a deposit feeder, and this group thrived through to the Permian before going extinct. In the Carboniferous another important group, the archaeocidarids, made their appearance. Archaeocidarids have a single large tubercle on each interambulacral plate and possessed long highly muscular spines. On functional grounds they were probably the first active predators. *Miocidaris*, the only Palaeozoic echinoid with the test architecture of post-Palaeozoic forms, evolved directly from *Archaeocidaris* by reduction of plating columns in each interambulacral zone.

The modern crown group was initiated and had already begun to diversify before the end of the

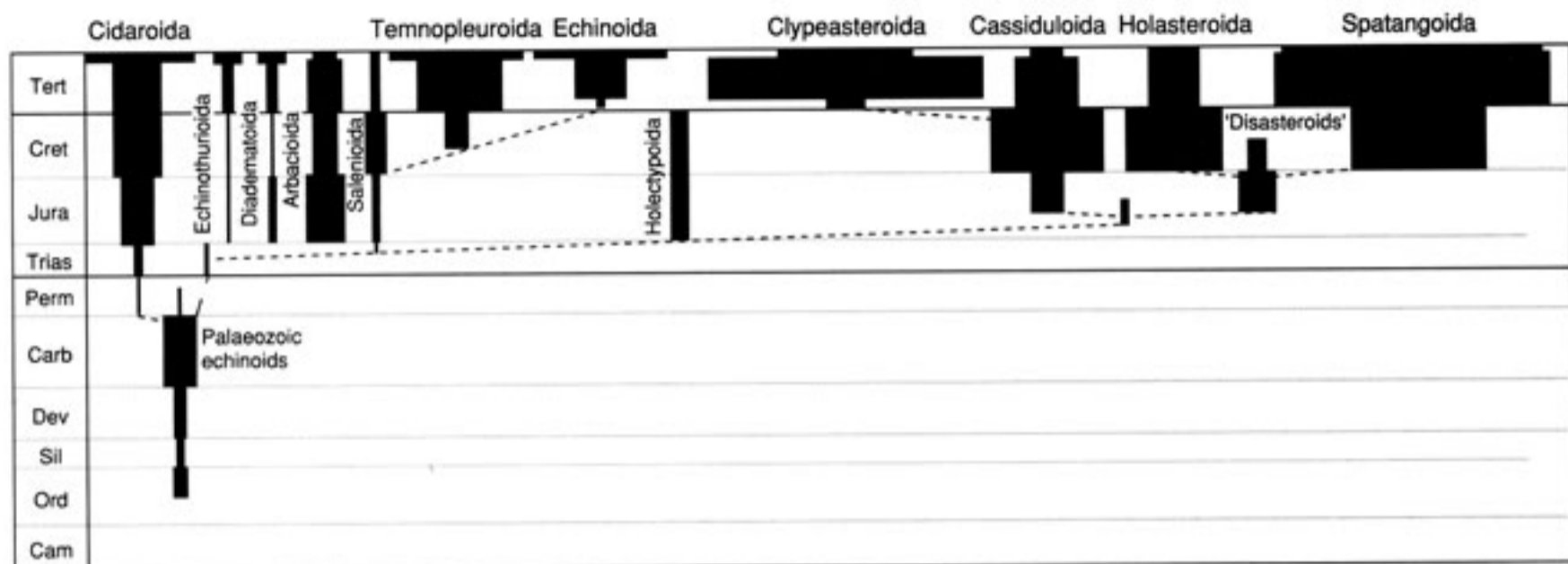
Permian, with both a cidaroid and a non-cidaroid lineage passing into the Triassic. The cidaroids (Cidaroidea) developed rigid test plating in the Triassic and have been an important constituent of deeper-water, shelf communities ever since. Despite attaining a modest diversity, cidaroids have always remained very conservative in their morphology.

Small non-cidaroid forms flourished in reefal settings in the Late Triassic, but it was not until the early Jurassic that the other lineage (Euechinoidea) started to diversify in a major way. Irregular echinoids make their first appearance in the Lower Jurassic and rapidly evolved as deposit feeders. The earliest irregular echinoids still possessed a lantern like that of regular echinoids, but by the Middle Jurassic both cassiduloids and spatangoids had evolved. Cassiduloids specialized as bulk sediment feeders using dense tube-feet for handling sediment particles. Sand dollars arose in the Early Tertiary from cassiduloid ancestors and specialized for life in the near-shore. Unique amongst echinoids, they developed large numbers of microscopic tube-feet to each ambulacral plate and adopted a very singular method of sediment sifting to obtain their food. Spatangoids and holasteroids on the other hand evolved a special kind of tube-foot around the mouth for selective deposit feeding. Modern heart urchins first appear at the base of the Cretaceous and have diversified more or less constantly since then. The end-Cretaceous extinction (*see Mesozoic: End Cretaceous Extinctions*) affected echinoids selectively, with deposit feeders being hardest hit. Regular echinoids also thrived throughout the Mesozoic, although today's major modern groups did not become established until the Late Cretaceous.

## Phylogeny and Classification

Major groups and their characteristic features are listed below and their geological ranges are shown in Figure 6:

- Cidaroida (Figure 1A) (Permian – Recent): regular echinoids with simple ambulacral plating and interambulacra with a single large primary tubercle; teeth U-shaped in cross-section.
- Echinothurioida (Jurassic – Recent): regular echinoids with hollow spines and an imbricate plated test; tubercles perforate and non-crenulated; teeth U-shaped in cross-section.
- Diadematoidea (Jurassic – Recent): regular echinoids with rigid, thin-plated test, compound ambulacra and perforate and crenulated tuberculation; teeth U-shaped in cross-section.
- Pedinoidea (Figure 2F) (Triassic – Recent): regular echinoids with perforate non-crenulate tubercles,



**Figure 6** Stratigraphic range charts for the major groups of echinoid. Width of bars is proportional to taxic (genus level) diversity. The dashed lines show their phylogenetic relationships.

compound ambulacral plating and teeth U-shaped in cross-section.

- Arbacioida (Figure 2I) (Jurassic – Recent): regular echinoids with imperforate, non-crenulate tubercles, compound ambulacral plating and teeth T-shaped in cross-section.
- Salenioida (Figure 2E) (Jurassic – Recent): regular echinoids with imperforate tubercles, compound ambulacral plating and teeth T-shaped in cross-section. The apical disc is large and cap-like and has extra plates incorporated into it.
- Temnopleuroidea (Figure 2G) (Upper Cretaceous – Recent): regular echinoids with compound ambulacral plating, imperforate tuberculation that is either crenulated or non-crenulate, and teeth T-shaped in cross-section. The test surface is often highly ornamented with pits.
- Echinoida (Figure 2H) (Upper Cretaceous – Recent): regular echinoids with compound ambulacral plating, imperforate, non-crenulate tuberculation and teeth T-shaped in cross-section.
- Holoctypoida (Jurassic – Cretaceous): irregular echinoids with a large functional lantern, no petals, and peristome with buccal notches. The periproct is large and tuberculation relatively coarse.
- Cassiduloida (Jurassic – Recent): irregular echinoids with no lantern and small peristome; tube-feet concentrated around the mouth to form phyllodes; aboral ambulacra petaloid; spines fine and dense.
- Clypeasteroida (Figure 2B) (Palaeocene – Recent): irregular echinoids, often flattened and disc-like, characterized by having petals, a fully internal lantern and small peristome and very many microscopic tube-feet to each ambulacral plate.
- Holasteroida (Figure 2C, D) (Cretaceous – Recent): ovate to heart-shaped irregulars, but may be more

elongate; no lantern; apical disc elongate with ocular plates II and IV meeting behind anterior genital plates.

- Spatangoida (Figures 1B, 2A) (Cretaceous – Recent): ovate to heart-shaped irregulars; no lantern; apical disc compact.

## See Also

**Fossil Invertebrates:** Echinoderms (Other Than Echinoids); Crinoids. **Lagerstätten.** **Mesozoic:** End Cretaceous Extinctions. **Sedimentary Environments:** Reefs ('Build-Ups'). **Trace Fossils.**

## Further Reading

- Kier PM (1965) Evolutionary trends in Paleozoic echinoids. *Journal of Paleontology* 39: 43–465.
- Kier PM (1974) Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *Journal of Paleontology* 48(supplement 5): 1–95.
- Lewis DN and Donovan SK (1998) Fossils explained 23: Palaeozoic echinoids. *Geology Today November/December*: 235–240.
- Smith AB (1984) *Echinoid Palaeobiology*, p. 199. London: George Allen & Unwin.
- Smith AB and Savill JJ (2002) *Bromidechinus*, a new Middle Ordovician Echinozoa (Echinodermata), and its bearing on the early history of echinoids. *Transactions of the Royal Society of Edinburgh* 91: 137–147.
- Smith AB, Littlewood DTJ, and Wray GA (1996) Comparative evolution of larval and adult life history stages and small subunit ribosomal RNA amongst post-Palaeozoic echinoids. In: Harvey PH, Leigh Brown AJ, Smith JM, and Nee S (eds.) *New Uses for New Phylogenies*, pp. 234–254. Oxford: Oxford University Press.
- Smith AB (2004) *The Echinoid Directory*. World Wide Web electronic publication. [www.nhm.ac.uk](http://www.nhm.ac.uk).