Handbook of Zoology
Echinodermata

Volume 1:
Echinoidea

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Foreword

Sea urchins (class Echinoidea) belong to the phylum Echinodermata together with sea lilies (class Crinoidea), starfishes (class Asteroidea), brittle stars (class Ophiuroidea), and sea cucumbers (class Holothuroidea). Their calcite skeleton provided them with an excellent fossil record since they first evolved, some 450 million years ago.

Today, this highly diverse and very successful group of marine invertebrates is distributed from the tropics to the poles and from the intertidal zone to the deep sea down to more than 5,000 m. About 900 species are described to date.

To most people, echinoids are known as decorative skeletons in souvenir shops or from eating their gonads as sushi. Beachcombers, snorkelers, and divers enjoy their bizarre forms or beautiful colors – or they keep long-lasting impressions after having touched the sharp and sometimes venomous spines.

For ecologists, echinoids are an important component of the marine benthic community with conspicuous influence in complex food webs regulating the diversity and abundance of plants and animals.

The focus of this book is to give an overview on described echinoid species and represent them with images. Short chapters give an introduction into the biology, ecology, and phylogeny. This is the first of two volumes, and it deals with pentameral (regular) echinoids; a second volume on the bilateral (irregular) species will soon follow.

The two volumes were generated from a book publication: *Sea Urchins: A Guide to Worldwide Shallow Water Species* (published in 2005 by Heinke & Peter Schultz Partner Scientific Publications), followed by the supplement volumes: *Sea Urchins II. Worldwide Irregular Deep Water Species* (2009) and *Sea Urchins III. Worldwide Regular Deep Water Species* (2011). All these three volumes had a limited distribution and are out of print.

Contents

Abbreviations

In the text, museums or collections are abbreviated. The following abbreviations were used:

AWI	Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany
MfN	Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitäts-Forschung, Berlin, Germany
NHM	Natural History Museum, London, UK
NIWA	National Institute for Water and Atmospheric Research Ltd., Wellington, New Zealand
ZMUC	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Denmark
ZMH	Zoologisches Museum, Centrum für Naturkunde, Hamburg, Germany
ZSM	Zoologische Staatssammlung München, Germany

1 Introduction and general morphology

Sea urchins, Echinoidea, belong to the Echinodermata. The other four classes of this phylum comprise the sea cucumbers (Holothuroidea), sea lilies (Crinoidea), starfish (Asteroidea), and brittle stars (Ophiuroidea). They live exclusively in marine environments from the poles to the equator and from intertidal zones to depths of more than 5,000 m. Fossil echinoids date as far back as the Late Ordovician Period, about 450 million years ago.

Superficially, extant sea urchins can be divided into two groups: the "regulars", with a circular test and pentameral symmetry living on the sediment (Fig. 1.1 A), and the bilaterally symmetrical "irregulars", mainly living in the sediment (Fig. 1.1 B). The regulars itself consists of two subclasses, separated by fundamental differences in morphology and phylogeny, the Cidaroidea (Fig. 1.2) and the Euechinoidea. Besides the somewhat strange Echinothurioida ("leather urchins"), the regular Acroechinoids (Fig. 1.3), with eight orders, and the irregular Acroechinoids (Irregularia), with six orders (Figs. 1.4 and 1.5), belong to Euechinoidea.

1.1 Body plans of major groups of sea urchins

The calcareous shell of the sea urchin (test or corona) is built of ten double columns of plates: five in the ambulacra (white), perforated by one or more pairs of pores or single ones, and five in the alternating interambulacra (shaded in blue). The perforated ambulacra (A) are labeled from I to V; the interambulacra (IA) are labeled from 1 to 5 (see Figs. 1.2 and 1.3).

In irregular echinoids, this principal plan is modified and the test is bilaterally symmetrical with two equal sides (see Figs. 1.4 and 1.5). The anus has moved from the upper side out of the apical system to the posterior or oral side.

1.2 General morphology

Echinoids have a hollow, more or less globular test built by an internal skeleton covered by a skin. The plates of

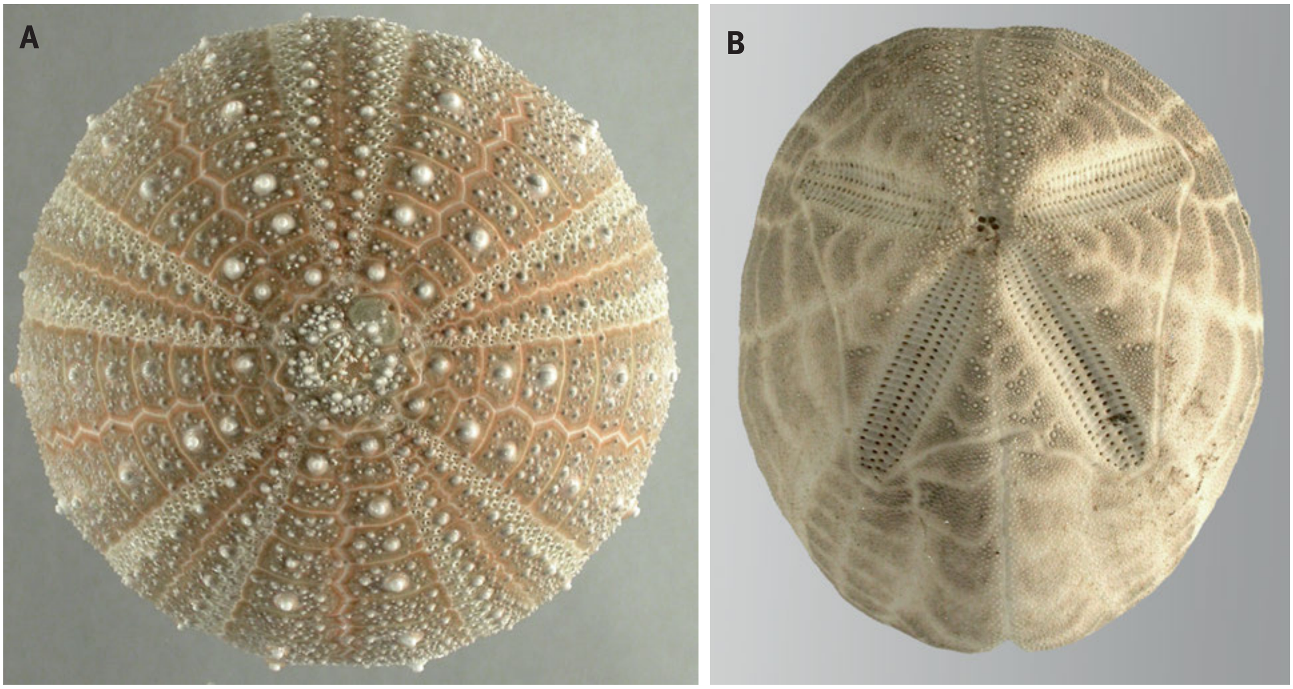
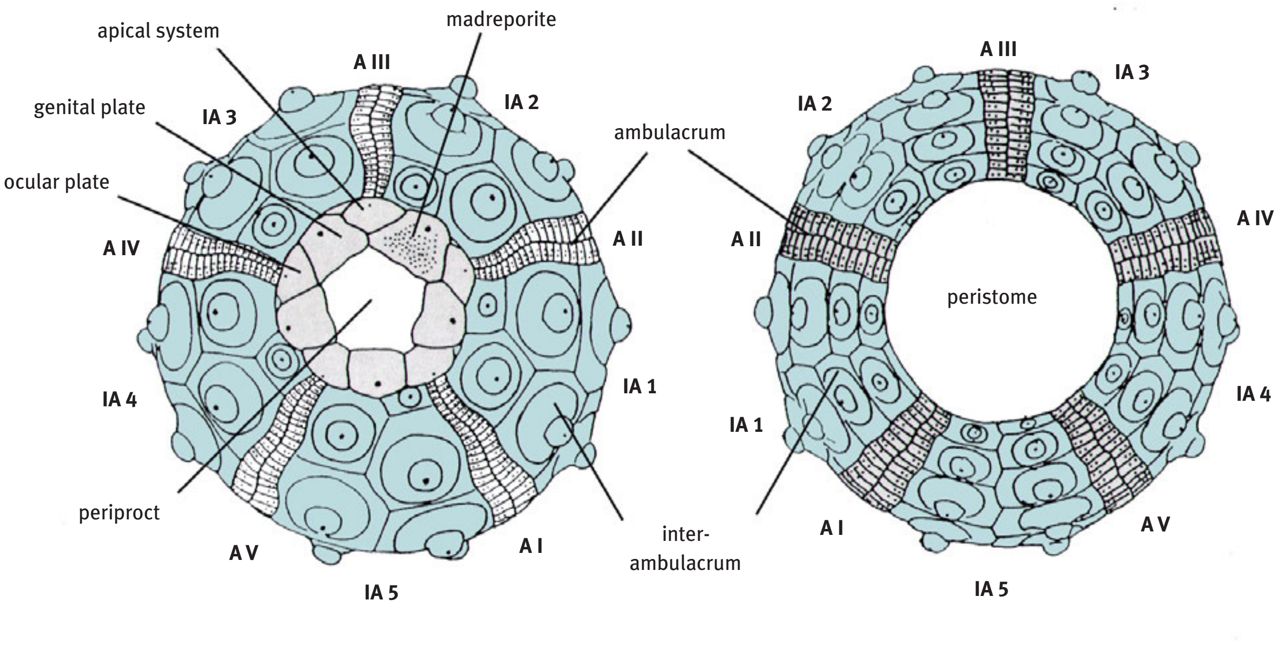


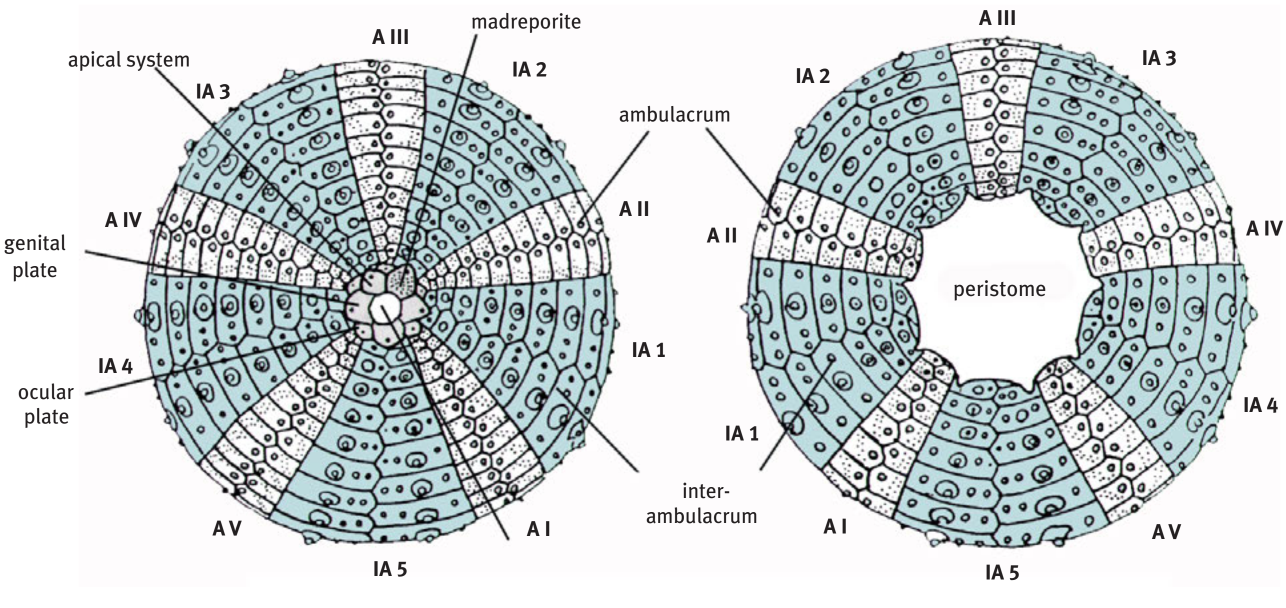
Fig. 1.1: (A) Regular sea urchin with pentameral symmetry. *Echinus gilchristi* Bell, 1904. (B) Irregular sea urchin with bilateral symmetry. *Metalia spatagus* Linné, 1758.



upper side
aboral

underside
oral

Fig. 1.2: Regular sea urchin: diagrammatic plan of a Cidaroid.



upper side
aboral

underside
oral

Fig. 1.3: Regular sea urchin: diagrammatic plan of a regular Acroechinoid.

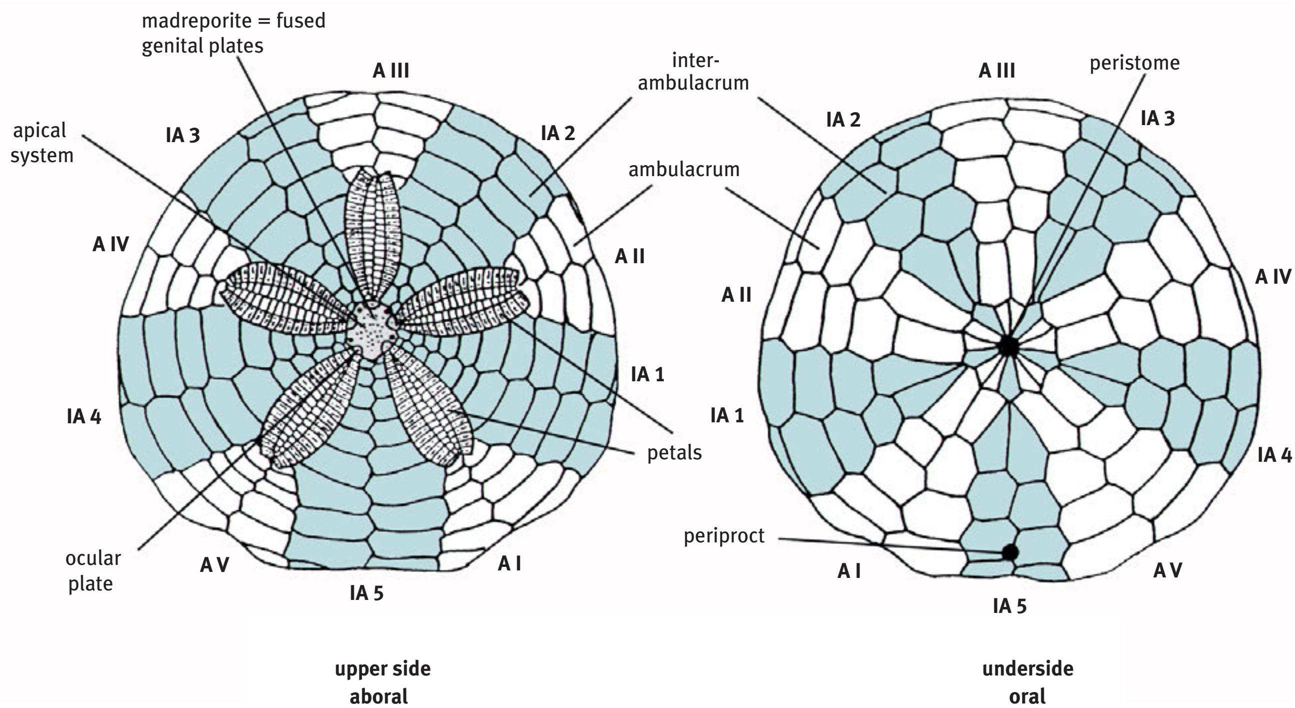


Fig. 1.4: Irregular sea urchin: diagrammatic plan of a Clypeasteroid (“sand dollar”).

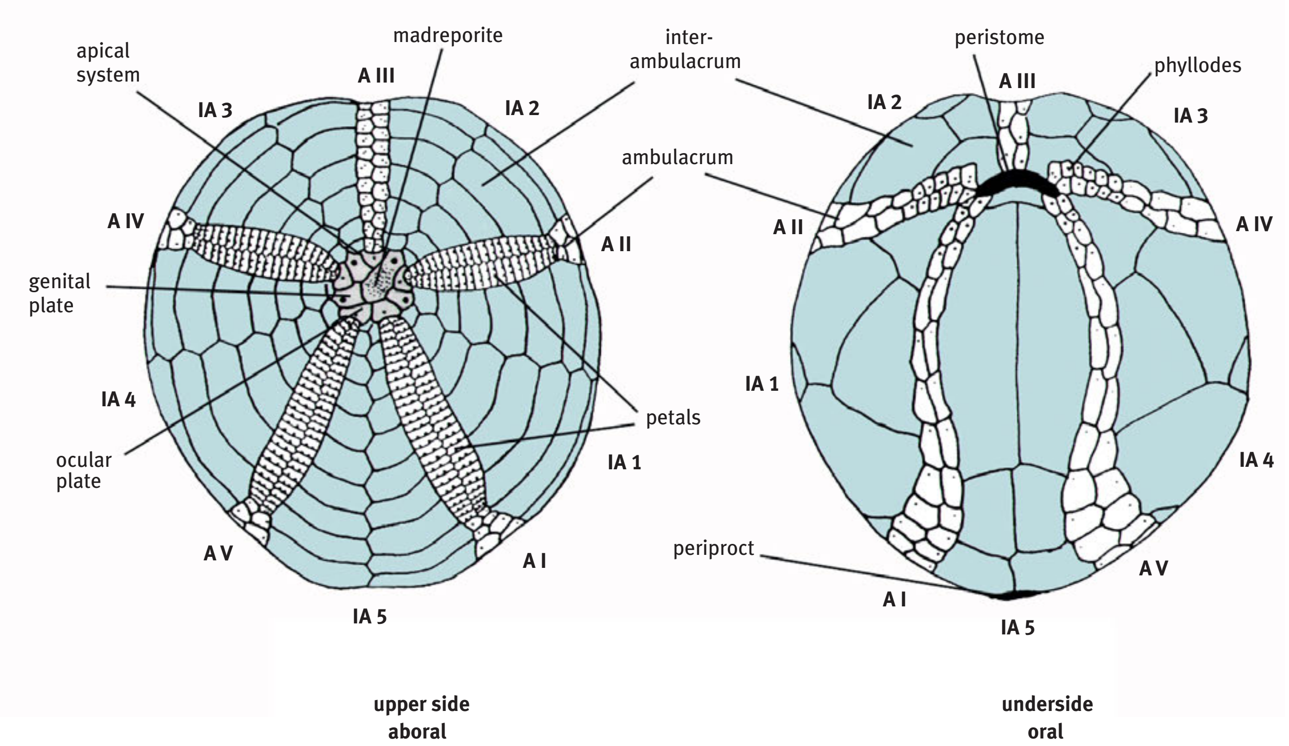


Fig. 1.5: Irregular sea urchin: diagrammatic plan of a Spatangoid (“heart urchin”).

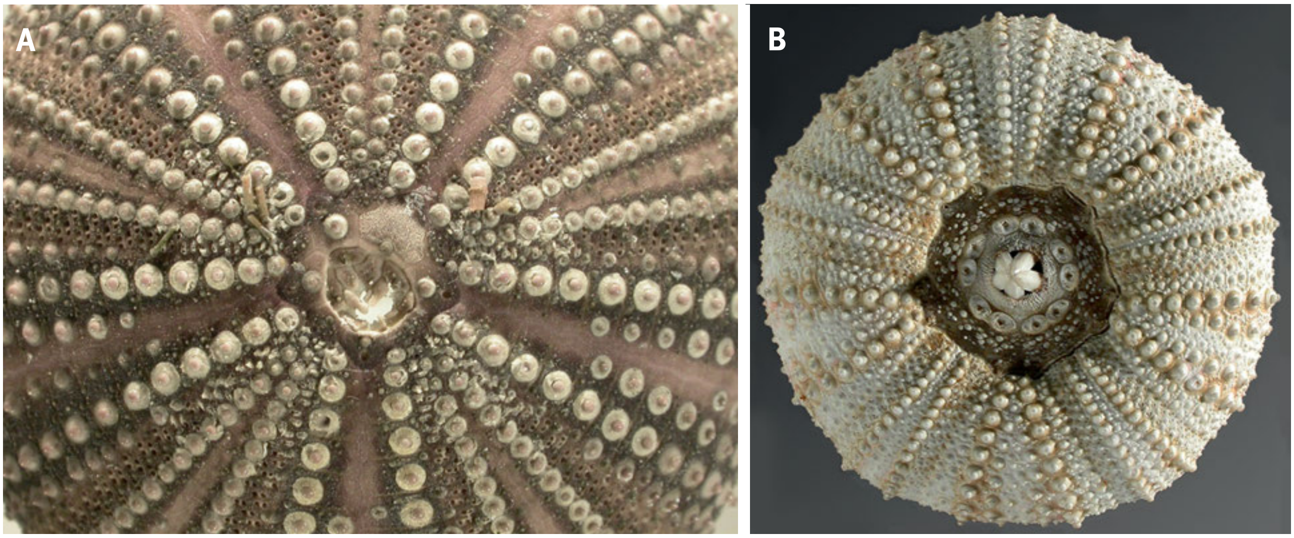


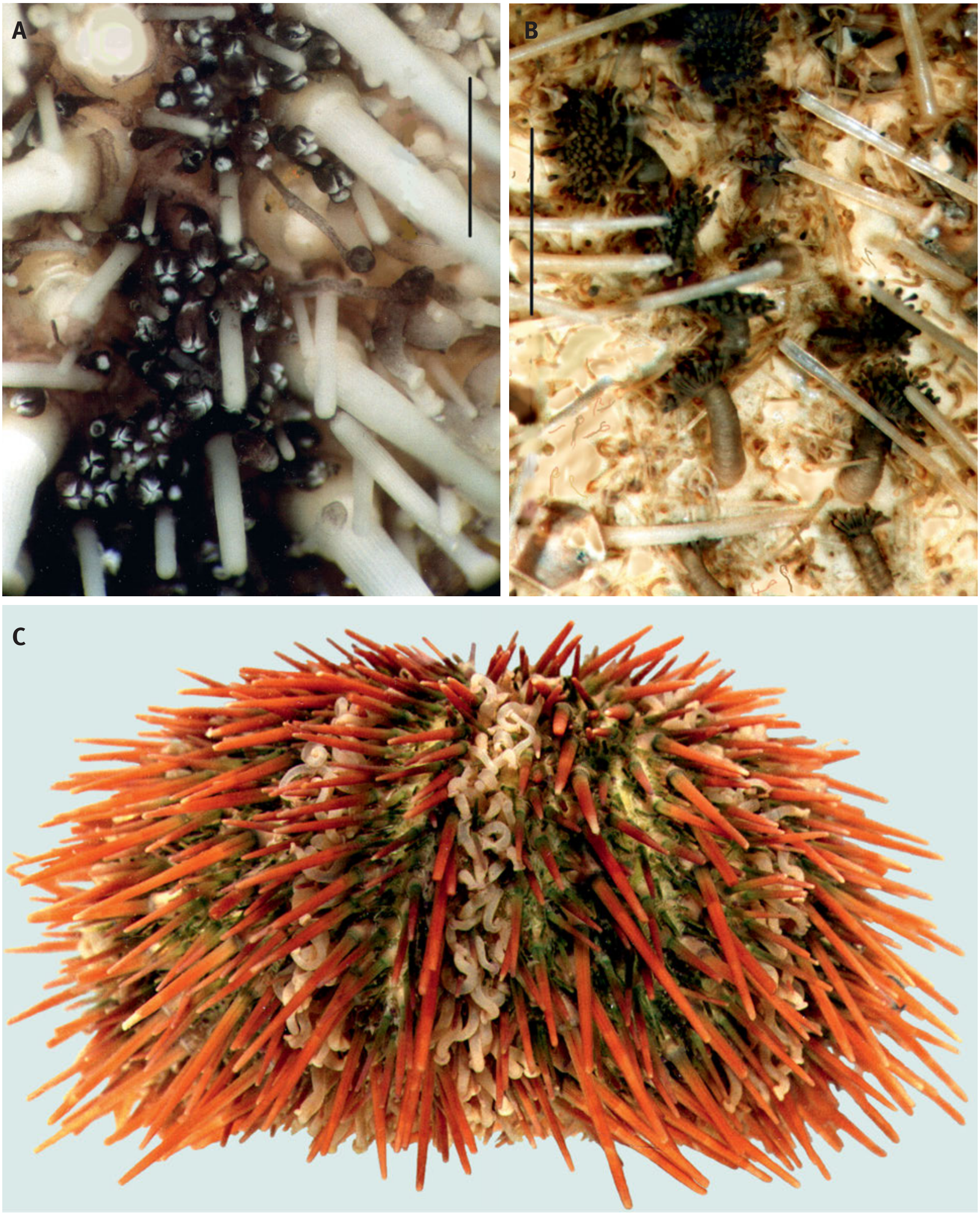
Fig. 1.6: (A) Regular Acroechinoid: upper side (aboral), the columns of plates radiate from the apical system. *Lytechinus variegatus* (Lamarck, 1816). (B) Underside (oral): the columns of plates converge at the peristome. In the center opens the mouth with the teeth (called "Aristotle's lantern"). *Gracilechinus elegans* (Düben & Koren, 1844).

the ten double columns are equipped with one or more tubercles of various sizes, which carry spines or other specialized structures. On the upper side (aboral, Fig. 1.6), the apical system is positioned. It is composed of up to 10 plates, 5–2 genital plates, penetrated by gonopores, from which eggs or sperm are released during spawning, and five ocular plates. One genital plate is a more or less densely perforated sieve plate (madreporite). Through the pores of the madreporite, the internal water vascular system is connected to the exterior. The five ocular plates at the summit of each ambulacrum are pierced by a single tube foot, which is the terminal extension of the radial water vessel (Fig. 1.8). The periproct within the ring of apical plates is in life covered by a flexible membrane, with the opening of the anus more or less in the center (Figs. 1.2 and 1.3).

In irregulars, the ambulacral pores are concentrated on the aboral side in leaf-shaped areas (petals); on the oral side, they are crowded around the mouth (phyllodes) or in well-defined fields. In heart urchins, the peristome has shifted to the anterior, while the posterior interambulacrum is strongly elongated. The surface of the test is densely covered by more or less uniform tubercles set with small fur-like spines (Figs. 1.4 and 1.5).

The columns of plates converge on the oral side, opposite to the apical disc, at the mouth (peristome). In life, the peristome is covered by a flexible membrane with embedded platelets of variable size and density. In cidaroids and echinothurioids, the double series of ambulacral plates with pore pairs continue over the peristome to the central mouth. Between these rows, there may be non-ambulacral plates. In all other regular groups (Fig. 1.6 B), the peristomial membrane has only five pairs of buccal plates, each bearing one single tube foot. The remainder of the membrane is more or less scattered with small platelets. The mouth opens in the center of the peristomial membrane. All regular groups of echinoids have external teeth, which form part of a rather

► **Fig. 1.7:** External appendages. (A) Wormlike tube feet (podia) are arranged in two rows in each ambulacrum, protruding from the pore pairs. Their thin walls function as a surface for gaseous exchange. Their distal end is developed as a sucking disc and contains sensory organs. The tubes of the podia are very extensible. *Parechinus angulosus* (Leske, 1778); test diameter with spines, 45 mm; Cape Town, South Africa. (B) Penicillate tube feet with many finger-like digits are positioned in the oral ambulacra picking up food particles and directing them into the mouth (upward). Scale: 5 mm. *Amphipneustes bifidus* Mortensen, 1950. (C) The median area of the ambulacra is set with numerous white-tipped pedicellariae, which have poison glands developed at the base of their thick valves. Scale: 2 mm. *Tripneustes ventricosus* Lamarck, 1816.


A
B
C

complicated jaw apparatus, called “Aristotle’s lantern” (or simply “lantern”) (Fig. 1.9). In the irregular cassiduloids, teeth are only found in very young specimens; in adults, they are lost; in clypeasteroids, they are modified to internal grinding organs, and in the Atelostomata, they are completely absent.

1.2.1 External appendages

The body surface of sea urchins is equipped with a variety of appendages: the spines, made of calcite, are very conspicuous. Each of them is connected to the test by a muscular collar, and is articulated to a round tubercle. Other connecting tissues can lock the spine erect. Once this tissue is activated, it is easier to break the spine than to move it. In cidarids, there are a few large primary spines, which are encircled at the base by a palisade of secondary spines. The cidarid spines have an outer layer of calcite, and they are more or less overgrown by foreign organisms, foraminifers, sponges, small molluscs, etc. In all other echinoids, the mass of primary, smaller secondary and tiny miliary spines is covered by living skin and never becomes encrusted.

The tube feet (podia) (Figs. 1.7 B and C) are delicate tubes of soft tissue, which penetrate through two small holes from the inner of the test, where they are connected to the water vascular system. They are very extensible and move hydraulically. The podia may end distally with a suckered disc or in finger-like processes. They are used for locomotion, sensory perception, respiration, and the manipulation of nearby objects.

The pedicellariae (Fig. 1.7 A) are tiny, stalked, pincer-like valves, more or less densely scattered among the spines. They serve to ward off small organisms or predators by means of sharp teeth and/or poison glands and to keep the surface of the test clean. The various shapes of these microscopic structures are important for distinguishing species.

The buccal sacs emerge at the peristomial edge (buccal notches) of the interambulacra. Five pairs are arranged around the mouth. They are direct extensions from the internal body cavity and compensate for internal volume changes when the jaws are moved in and out of the rigid test. In former times, they were thought to be gills for respiration.

The sphaeridia are microscopic, stalked, club-shaped structures on the underside of the test and are developed in all echinoids except of Cidarids. They are thought to act as organs of balance.

1.2.2 Internal organs

The water vascular system (Fig. 1.8) consists of a tube connected through the pores of the sieve plate (madreporite) to the exterior. It leads downward to the ring canal, which encircles the lower part of the intestine coming from the mouth. From the ring canal, five branches (radial canals) radiate, underlying the median suture of the ambulacral plates. Ampullae are attached to the radial canals and joined through a pore or a pair of pores to the external tube feet. Each radial canal ends in a single ocular tentacle, piercing through the ocular plate in the apical system.

The hemal system is a type of “blood” circulatory system. The main tubes roughly follow the water vascular system and the gut, but give rise to branches that reach the gonads and other internal organs to supply them with nutrition. The spongy axial organ is involved with functions of the hemal system, but what precise function it may have is not clear.

1.2.3 Digestive system

The tube-like esophagus emerges from the top of the jaw apparatus (if present) and leads to the stomach. The stomach leads into an intestine that performs a loop inside the test and back again forming a second loop. The latter ends in the anus that exits through the center of the periproctal membrane (Fig. 1.10).

The gonads are five (in regulars) to two (in some irregulars) interradially placed organs, which are each connected by a gonoduct to the genital pore (gonopore) in the corresponding apical plates. The sexes are separate.

A central nervous system is lacking; there are neither ganglia nor a brain. Nevertheless, all echinoids have an extensive subepithelial net of nerves that serve in coordination of external appendages and sense reception. Nerve tracks around the gut and associated with the internal organs allow echinoids to coordinate locomotion, nutrition, sensation, and reproduction.

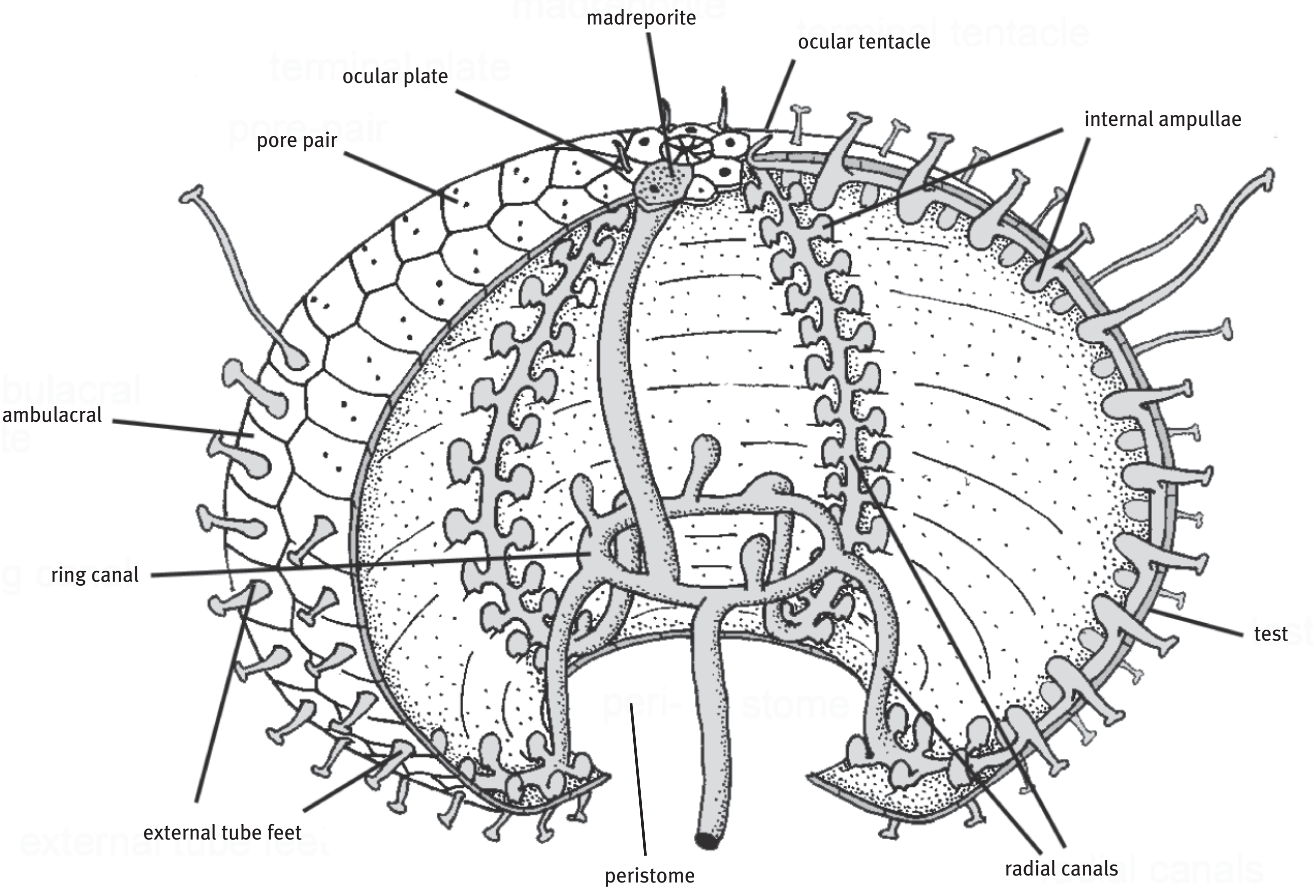


Fig. 1.8: Schematic drawing of the water vascular system.

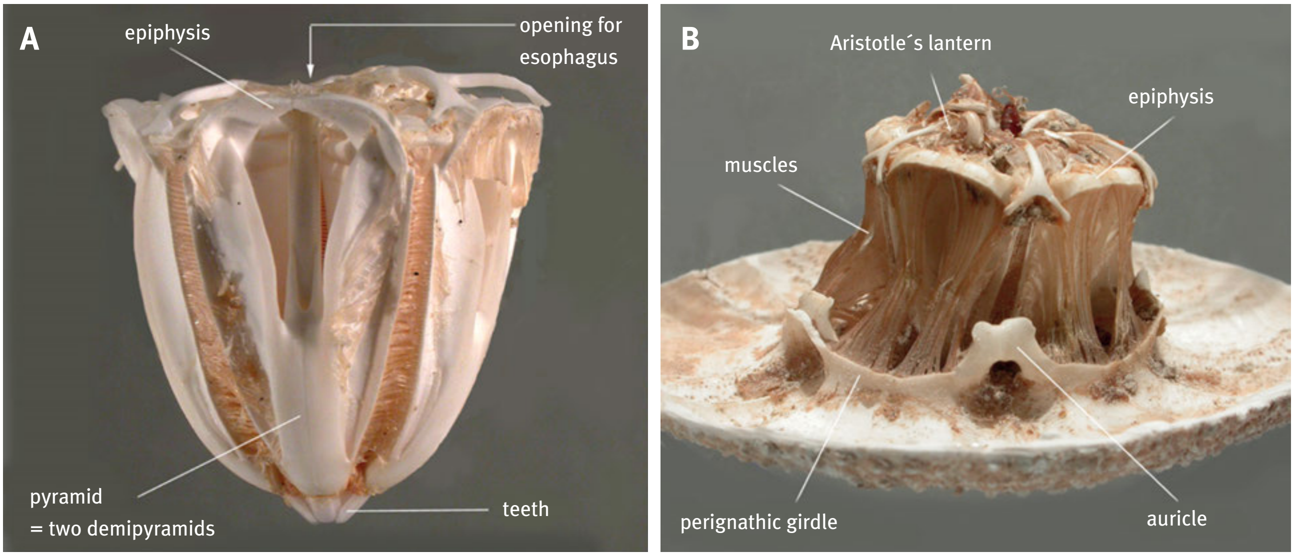


Fig. 1.9: Aristotle's lantern (jaw apparatus) of camarodont echinoid. (A) Internal view of lantern: the muscles for moving the lantern are connected to the perignatic girdle. (B) The lantern is built of five pyramids (=10 demipyramids), which are overbridged by the epiphysis to strengthen the construction in camarodonts. Height of lantern 28 mm (*Pseudoboletia maculata*).

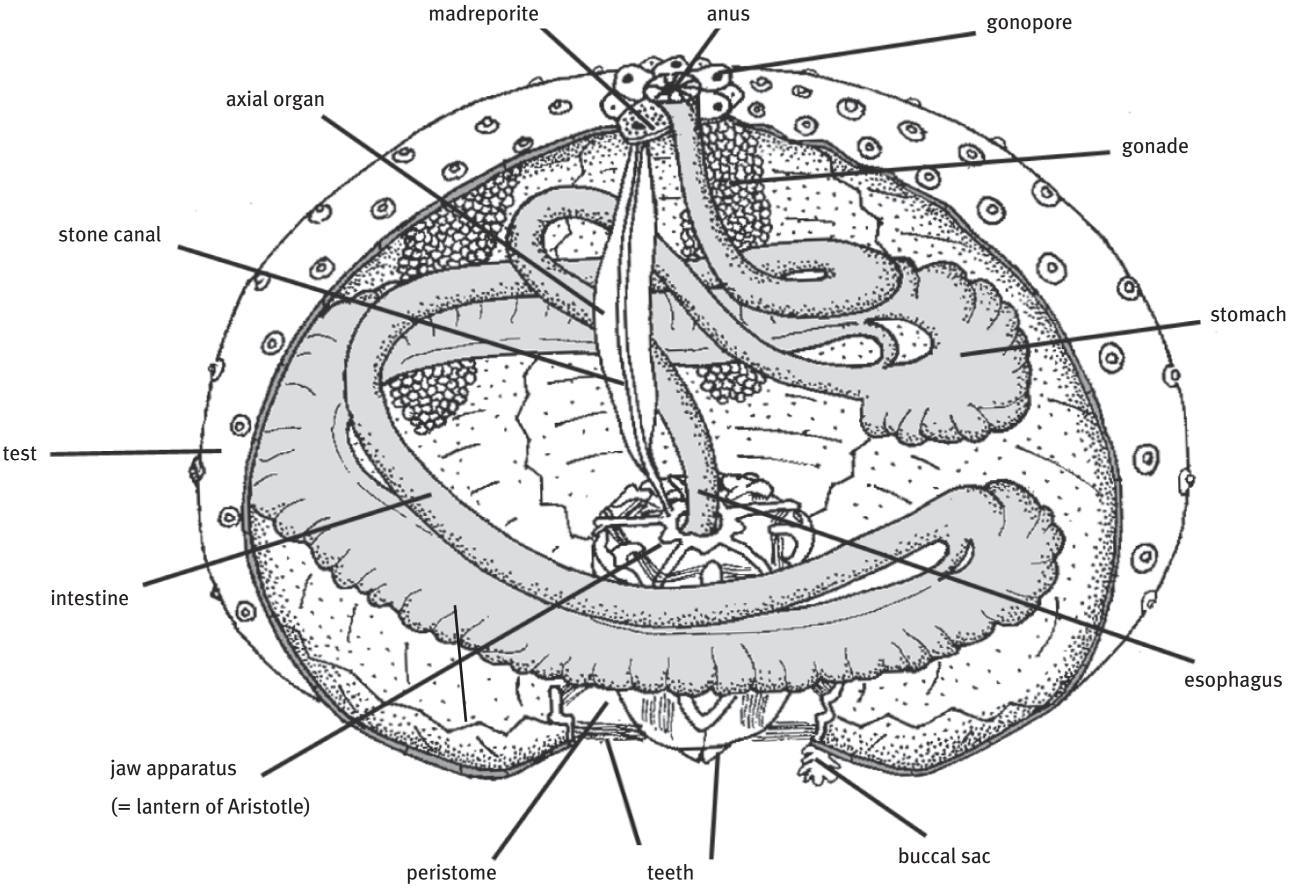


Fig. 1.10: Digestive system of sea urchins (modified after Storch & Welsch 1994).

2 Echinoid biology

2.1 General biology

According to the differences in shape, regular and irregular sea urchins differ considerably in lifestyle. While the former live epifaunally, on rocks or solid sandy bottoms, the latter are mostly found infaunally, among gravels or in sands or even mud.

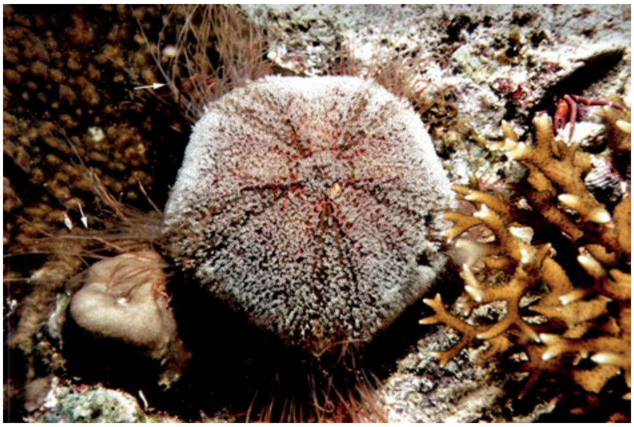


Fig. 2.1: The greatly expanded tube feet (white arrows left) in the five ambulacra explore the vicinity of the animal. The surface of the upper side is densely covered by pedicellariae, the valves of which have developed small blisters, filled with poison. *Tripneustes gratilla* Linné, 1758 Safaga, Egypt, Red Sea (photo by H. and I. Rauch).

2.1.1 Locomotion

Sea urchins generally use their oral spines for locomotion. Regulars move in any direction according to their pentameral symmetry, while the sensitive, highly extendable tube feet examine the vicinity (Fig. 2.1). They are able to hold onto vertical walls and "climb" on steep rocks using the sucking discs of their tube feet. All sea urchins, except the members of the family Arbaciidae, are able to right themselves by means of their tube feet, when waves have overturned them.

The irregular echinoids are unidirectional, they move forward with ambulacrum III forward and leading. With the help of strong, often spatulate spines, they plough or burrow through the sediment (Fig. 2.2 A). In contrast to the regulars, they usually have short, dense, overlapping spines to prevent sediment from falling onto the test and so maintain a water-filled gap around themselves.

2.1.2 Respiration

Respiration takes place mainly across the thin walls of the tube feet. Fluid is constantly circulating from the internal ampullae through one pore into the external tube feet and back through the other pore. In epifaunally living regular

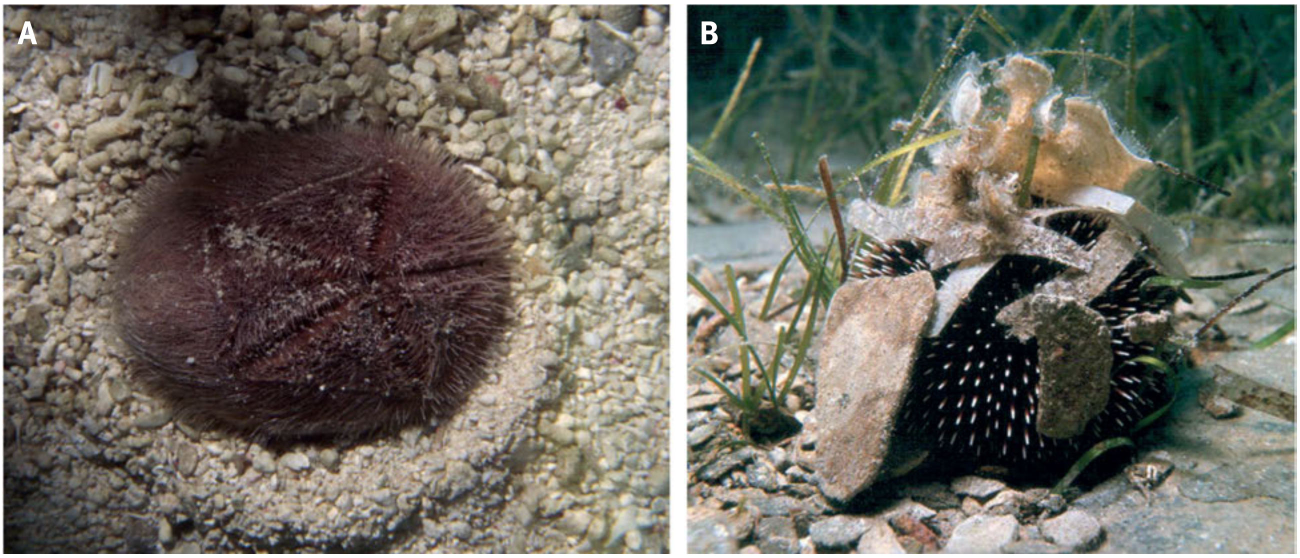


Fig. 2.2: (A) An irregular echinoid is going to burrow into the sediment. *Metalia spatagus* Linné, 1758, Bohol, Philippines.
(B) Many sea urchins cover their upper side with organic debris or small gravel particles, which the suckered discs of the tube feet hold tight. This way, the animals camouflage themselves to protect their tests against direct light. *Sphaerechinus granularis* (Lamarck, 1816), Turkey (photos by H. Moosleitner).

sea urchins, the efficiency of the "normal" suckered podia is sufficient. Irregular echinoids, which live in sediment, where oxygen is less available, have developed specialized podia with enlarged surfaces and extremely thin walls to increase respiratory efficiency. These tube feet are concentrated in leaf-shaped areas (petals) on the adapical side. Many groups are equipped with bands of tiny ciliated spines (fascioles), which create, through coordinated motion, a current of oxygen-rich water over the petals and ventilating the entire surface. Waste water is directed to the rear of the animal, where other fascioles wash it into the sanitary funnel, together with fecal material.

2.1.3 Defense, predators, and camouflage

In regular echinoids, the dense and spiky spines are used for defense. In cidarids, the large interambulacral plates are set with large primary spines. The alternating ambulacra are narrow, and the plates carry small secondary spines covering and protecting the delicate podia of the pore zones, which are arranged in one pore pair per plate.

In the regular Acroechinoidea, the ambulacral plates are fused to larger compound plates providing space for larger secondary spines. On the other side, the primary spines become smaller and much more numerous, and therefore, the sea urchin gets a better all-round defense.

In echinothurioids, the needle-like spines have large, fleshy sacs at their distal end, which contain a very effective poison. In addition, they are equipped with numerous large pedicellariae with sharp teeth. In the family Toxopneustidae, the valves of the pedicellariae themselves have poison glands, which are powerful enough to repel large predators like sea stars, hence their name.

Using their aboral suckered podia, many groups cover themselves with pieces of algae or shells for protection against light (camouflage) (Fig. 2.2 B). The camouflage may help avoid predation, as the sea urchin is hidden below a cluster of dead debris. In cidarids, the setting of foreign organisms on the spines may also have a masking effect, but some of them try to avoid over-heavy settling by the development of fine hairs and thin, sharp thorns. One sponge is able to remove the calcium from cidarid spines, which become soft and useless and fall off. All echinoids have an astonishing capacity for healing wounds and regenerating parts that are damaged or lost. Fish, birds, crabs, and even snails with their soft body are the main predators of spiny echinoids.

An example, the large gastropode *Cypraecassis rufa* Linné, 1758 emerges a cushion of mucus on which it creeps over the sharp, finely thorny spines. Then it leads its snout through the spines to the surface of the test, drills it, and discharges the animal (Fig. 2.3).

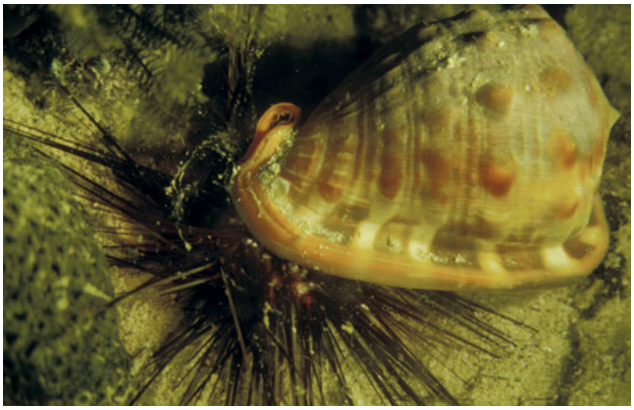


Fig. 2.3: A large gastropod preys upon a diadematoid sea urchin by means of a mucus cushion against the sharp spines. Length of snail 18 cm. *Cypraecassis rufa* Linné, 1758, Lembeth strait, Sulawesi, Indonesia (photo by R. Kraft).

Irregular sea urchins avoid predators by living "out of sight". But certain predacious snails search out buried urchins and feed on them, drilling through the test with their radula. Consequently, some irregulars have developed thickened tests or long spines at the aboral side for defense.

2.1.4 Feeding

Regular echinoids graze with their sharp teeth on sessile organisms such as algae or sea weed, hydroids, foraminifers, sponges, or young echinoderms. They bite off pieces of algae, which are then manipulated into the mouth with help of the circum-oral tube feet. Irregulars are primarily deposit feeders, feeding on the fine organic material (detritus) that has sunken to the sea bottom.

The flat sand dollars, the Clypeasteroida, prefer the detritus-rich layer just beneath the sediment. While the uppermost sand is transported over the test – the dense spine canopy making sure grains do not fall onto the test skin – enormous numbers of tiny oral tube feet on the oral side pick up small particles encrusted with organisms. These particles are placed into the food grooves, where they are moved by small spines like on a "conveyor belt" toward the mouth. Cassiduloids swallow large quantities of sediment for its relatively poor organic content. The indigestible sand is continuously discharged from the anus.

In spatangoids, the podia concentrated around the mouth are equipped with many finger-like appendages (Figs. 1.7 and 2.12 A). They are able to pick up selectively organic particles from the sediment in their burrow.

Other penicillate tube feet, situated at the center of the upper side, collect food from the surface of the sea bottom, bring it down a vertical funnel and place it into the deep furrow of the anterior side of the test. Mucus-producing spines transport the particles down to the mouth isolated from the surrounding sand by an arc of larger spines.

2.1.5 Human consumption

The gonads of the sea urchins have been eaten by humans since prehistoric times. In some tropical regions, they are an important component of diet.

In Japan and other countries, they are considered as delicacy, and they are harvested on a large scale in Chile or along the west coast of America. But the stock has already greatly diminished, and overfishing can radically change the ecosystem, as the grazing echinoids control the growth of the algae. Consequently, aquaculture of sea urchins has developed in recent years, with the trend to rear specimens with more uniform and more attractively colored gonads.

2.2 Reproduction

In echinoids, the sexes are separated. According to the group, they have 2 to 5 gonads, which open through the gonopores in the genital plates. The males release the sperm and then the females disperse the tiny eggs into the open water, where the eggs are fertilized. In temperate climatic zones, spawning is often triggered by the temperature, and there exist annual cycles; in the tropics, spawning occurs more often.

The tiny embryo grows into a transparent larva (“echinopluteus”) with two or more movable arms, supported by calcareous rods and bordered by ciliated bands for food collection and locomotion (Fig. 2.4 A–D).

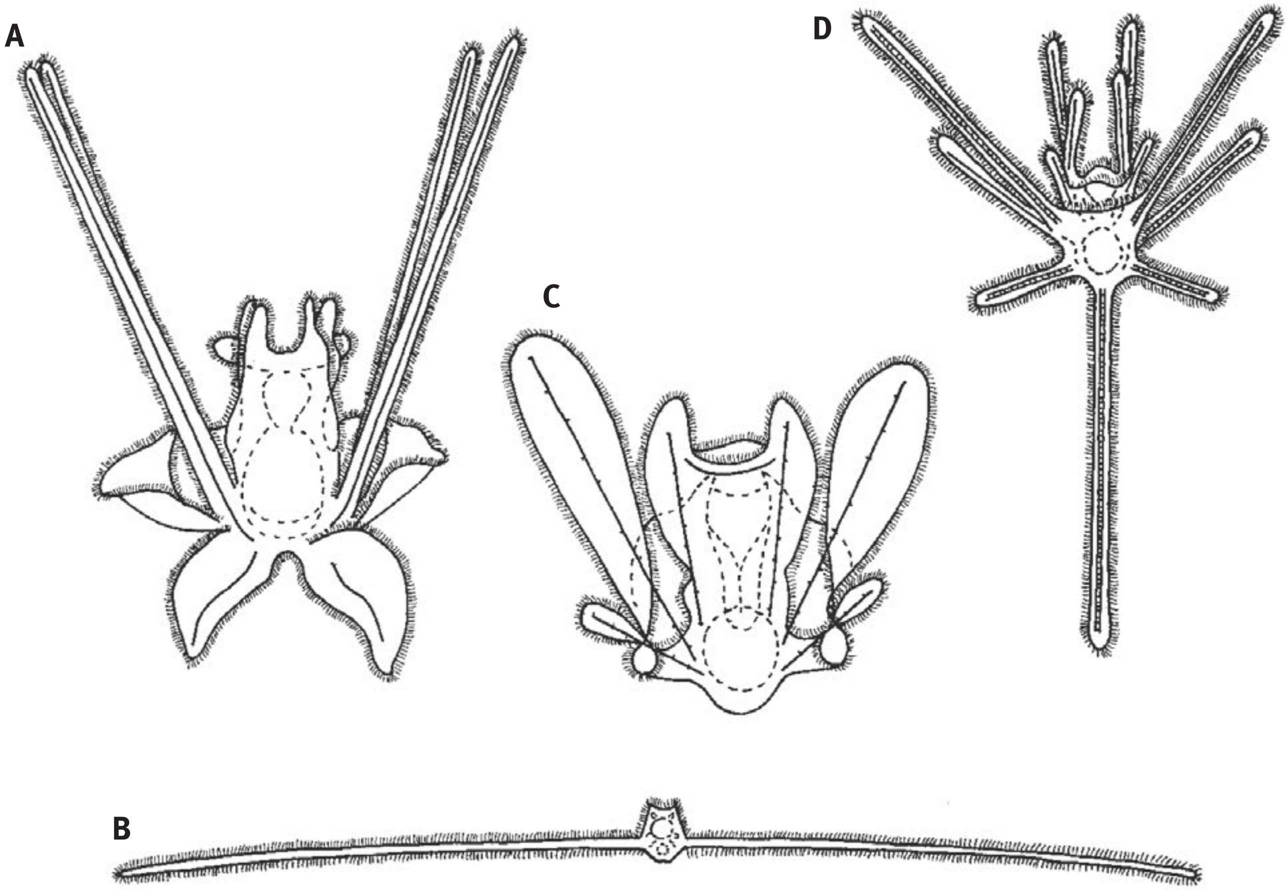


Fig. 2.4: (A–D) Echinopluteus larvae: (A) *Eucidaris thouarsi*, about 1.5 mm. (B) *Diadema antillarum*, 10 mm. (C) *Clypeaster humilis*, about 0.8 mm. (D) *Lovenia elongata*, about 2.5 mm (A, Mortensen 1928; B–D, Mortensen 1931). The arms of the transparent larva are bordered by short, dense bands of tiny hairs, the cilia. The coordinated beating of these cilia causes the locomotion. The bilaterally symmetric larvae have developed a mouth, a gut, and an anus, and they feed actively on planktonic organisms.

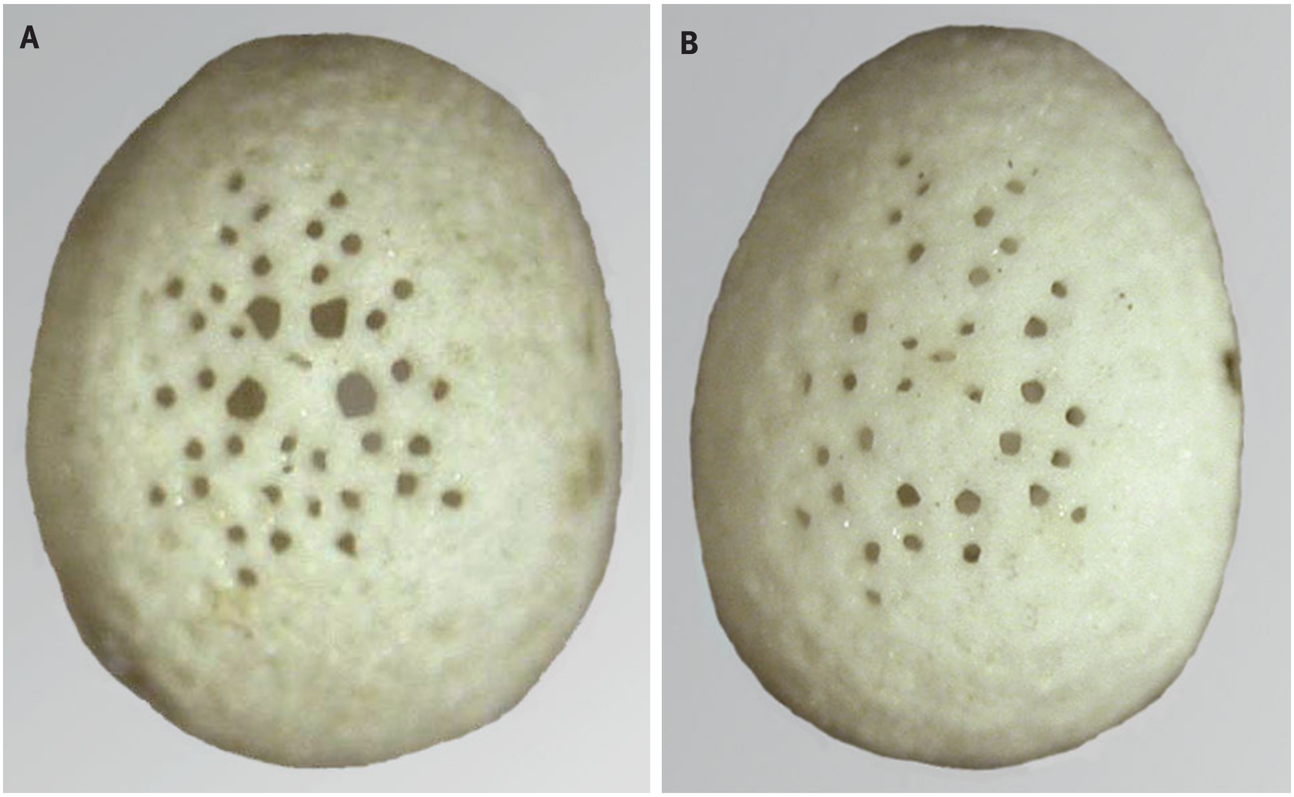


Fig. 2.5: *Fibularia japonica*, Central Japan, Pacific: sexual dimorphism. (A) The female has four large gonopores (length of female, 5 mm). (B) The male has small gonopores (length of male, 5.5 mm).

The larva lives in the plankton, actively feeding on microorganisms (a condition termed “planktotrophic”). But they are also prey for other animals. This stage can last some days or up to some months, and the larva drifts widely with the sea currents. Then it sinks to the sea floor and undergoes a complicated metamorphosis, radically changing its morphology from bilateral to pentameral symmetry and consequently changing its lifestyle from a pelagic filter feeder to a benthic grazer or infaunal detritus feeder.

About two thirds of all living species develop through a larval stage, but in various echinoids belonging to different orders, more specialized modes of reproduction have evolved. The females release fewer but larger eggs, which are filled with yolk, the nourishment during the development of the young. Having no mouth or anus, they are not able to feed (“lecitotrophic”). After being fertilized by the male sperm, the embryo grows directly into a small sea urchin. The larval stage and the metamorphosis are more or less abbreviated or completely lacking. In these species, the difference between the sexes (“sexual dimorphism”) is visible (Fig. 2.5 A, B). The females have distinctly larger gonopores than the male.

Thus, there are principally two different strategies for reproduction:

1. Millions of tiny eggs develop into actively feeding echinopluteus larvae, which drift far away before they sink down onto a suitable substrate, undergoing metamorphosis. The great majority of them are preyed on by other animals in the plankton.
2. Relatively few, large, yolky eggs develop to non-feeding embryos with either rudimentary or no larval features. They stay only for very few days in the plankton before becoming sessile and passing through a largely abbreviated metamorphosis or they are housed in the brood pouches of the female until they are able to feed independently. The distribution of these juveniles is restricted, but a large number of them survive. Additionally, there occur intermediates, e.g. in the abbreviated larval stage of *Heliocidaris erythrogramma* (Williams & Anderson 1975).

In some groups of directly developing sea urchins, brood protecting has evolved; the young are attached to or, even more sheltered, held inside the body of the female parent. This mode of reproduction is particularly common in Antarctic species, but it also occurs in some

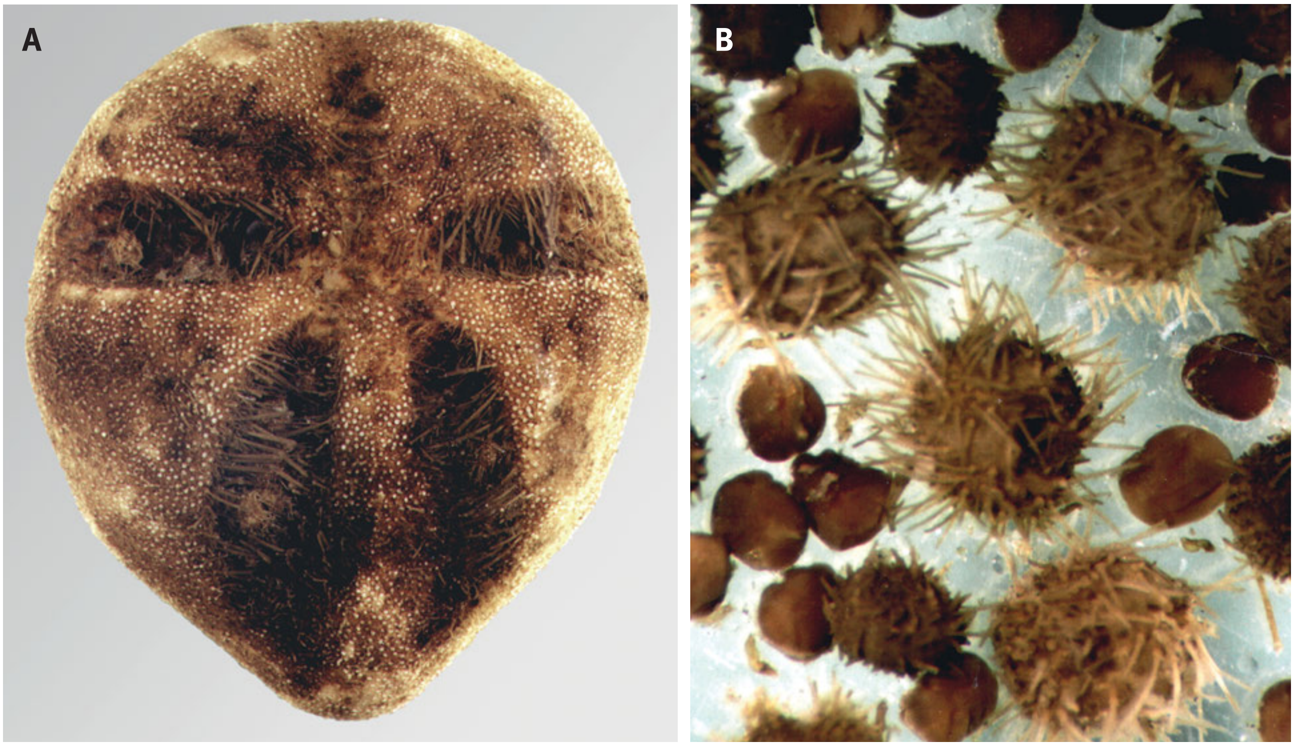


Fig. 2.6: *Amphipneustes marsupialis*. (A) Aboral side of a female, test length 54 mm; Weddell Sea, Antarctica. In the broad, deep brood pouches of the female, the young grow up beneath a layer of spines. The eggs are hidden in the lowermost corner, the older juveniles lie between the spines. (B) Eggs and embryos. The young occur in three stages, as eggs, short-spined embryos, and long-spined juveniles. The latter are almost ready to leave the mother. Test diameter of a large juvenile, 3.3 mm.

tropic species. In Antarctic schizasterids, the young grow very slowly in deep brood pouches (marsupia), living on the yolk from the egg (Fig. 2.6 A, B). In the well-studied *Abatus cordatus*, endemic to the Kerguelen Islands in the southern Indian Ocean, this stage lasts 8½ to 9 months. Then the young are able to feed actively and they leave the female (Magniez 1979, 1983).

In brood-protecting cidarids – the predominant number of them also from Antarctica – the juveniles are housed in a recess created by the flexible peristomial membrane. The eggs are manipulated from the gonopores in the apical disc to the underside by means of pedicellariae and small spines, being fertilized on the way (Barker 1984, *Goniocidaris umbraculum*). In *Austrocidaris*, the embryos are held on the depressed apical disc. The two most advanced modes of reproduction have developed in the Antarctic, too.

In *Aporocidaris incerta*, the reproduction apparatus has been strongly altered: the gonoducts do not lead from the gonads to gonopores piercing the genital plates in the apical disc to emerge eggs or sperm. In females, the gonoducts end in large pores in the interambulacral median sutures on the oral side or even at the edge of the peristome. In males, relatively small gonopores are transferred halfway down the interambulacral midline (Mortensen 1909, 1928, Lockhart unpublished PhD thesis 2006) (see page 78).

It is self-evident that the position of the gonopores on the oral side is advantageous for the success of reproduction because the perilous transfer of the eggs from the gonopores on the apical side to the brood chamber on the peristome is avoided.

In the holasteroid *Antrechinus mortenseni*, Family Urechinidae, the apical plates are modified in invaginating to an inner chamber, into which the fertilized eggs are deposited. Here they grow, in staggered stages, nourished by the initial yolk in the egg. When the embryos are fully developed, the center of the apical disc opens to let the young pass into the free water (Mooi & David 1996).

2.3 Growth

As a sea urchin grows, new plates are added at the outer edge of the ocular plates (Fig. 2.7). In very young specimens, the apical plates cover the whole upper side, but

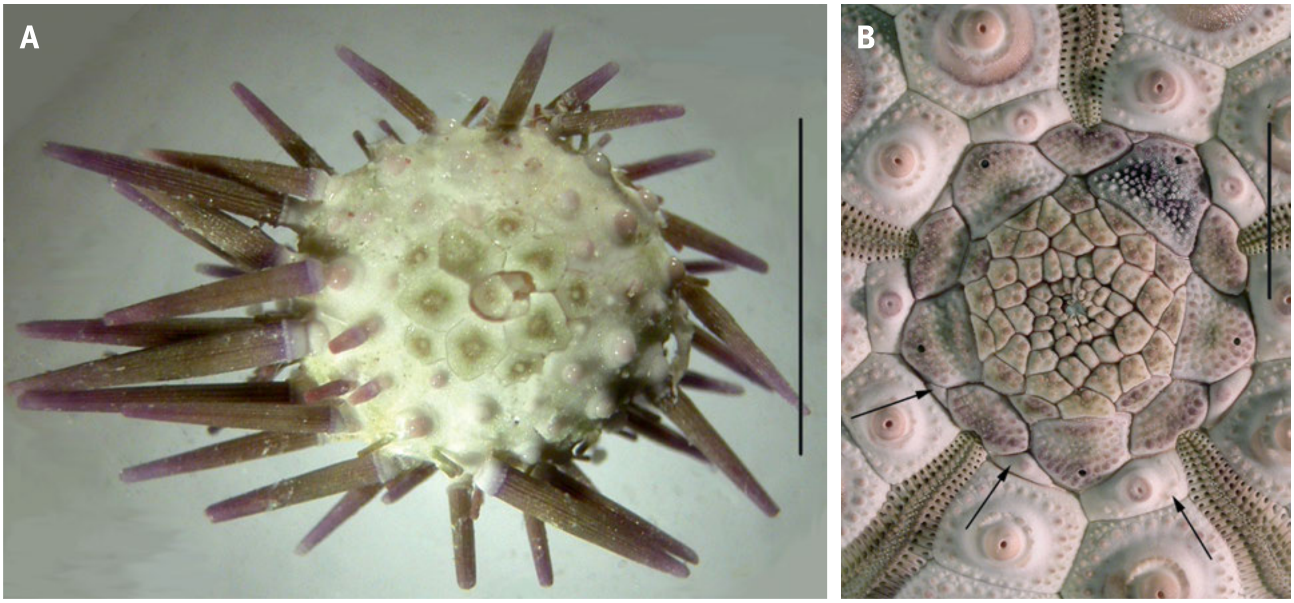


Fig. 2.7: Growth of echinoids. (A) The apical system of the young *Echinometra mathaei* is very large relative to the size of the test. Scale: 4 mm. (B) New plates are created at the outer edge of the ocular plates of *Prionocidaris*, the ambulacral plates in the center, and the two adjacent interambulacral ones at either side (arrows). The plates grow in size and are incorporated into the columns (right arrow). Scale: 10 mm.

as growths proceeds, the apical system becomes smaller relatively to the size of the test.

The plates themselves increase in size, showing more or less concentric growth rings, only exceptionally visible. Depending on variable rates of growth at the edges, the shape of an individual plate is formed and consequently the shape of the test between the apical system and the peristome.

In irregular echinoids, the periproct of very young specimens still touches the apical system, but it shifts during growth to the rear or to the oral side.

A sea urchin is considered mature when the gonopores have broken through the genital plates, although the adult still grows considerably in size. Most echinoids live several years. However, in colder water, they have a longer life expectancy: e.g. *Sterechinus neumayeri* from the Antarctic Weddell Sea may live 75 years (Brey 1991).

2.4 Evolution and phylogeny

Echinoids first appear in the Upper Ordovician, about 450 million years ago. Various forms with flexible, imbricating plates evolved (Fig. 2.8 A, B). They had tube feet for gathering food, which was scooped into the mouth by the teeth. By the end of the Palaeozoic, the group had dangerously declined in diversity. Only two lines with very few species survived the Permian-Triassic crisis: the miocidarids and the triadocidarids, from which later in the Triassic, the first modern Euechinoidea evolved. In the Lower Jurassic, echinoids underwent a spectacular adaptive radiation, many diverse forms arose, which occupied various ecological niches.

The cidarids (Fig. 2.9) are an offshoot of late Palaeozoic miocidarids, and thus, the oldest extant group with the most primitive features – but not at all a “model in decline”. In Antarctica, they were able to develop one of the most advanced modes of reproduction, brood protecting. With more than 120 Recent species, they are still “successful”, living on hard grounds like coral blocks or boulders or on solid sandy bottoms in relatively sheltered waters – much the same ecological niche as in the Triassic. There was “no need” to change their morphology.

The cidarids are the sister-group of the Euechinoidea, which comprises the echinothurioids, a rather peculiar group with flexible, imbricating plates and some other features of former, Palaeozoic echinoids – and the Acroechinoidea.

The acroechinoids include today approximately three quarters of all sea urchins. They are divided into three major groups, the regular Diadematacea and Echinacea and the Irregularia. As in the cidarids, the constructional plan of the regulars has remained remarkably “stable” since the Upper Triassic or Lower Jurassic. Their pentamery allows them to move on their oral spines in all directions, while the sensory tube feet explore the nearby environment. The feces, released from the periproct on the upper side, are washed away by water currents.

Acroechinoids have principally the same lifestyle as at the start of their evolution, which is restricted by the balance among the five virtually identical sections of the test.

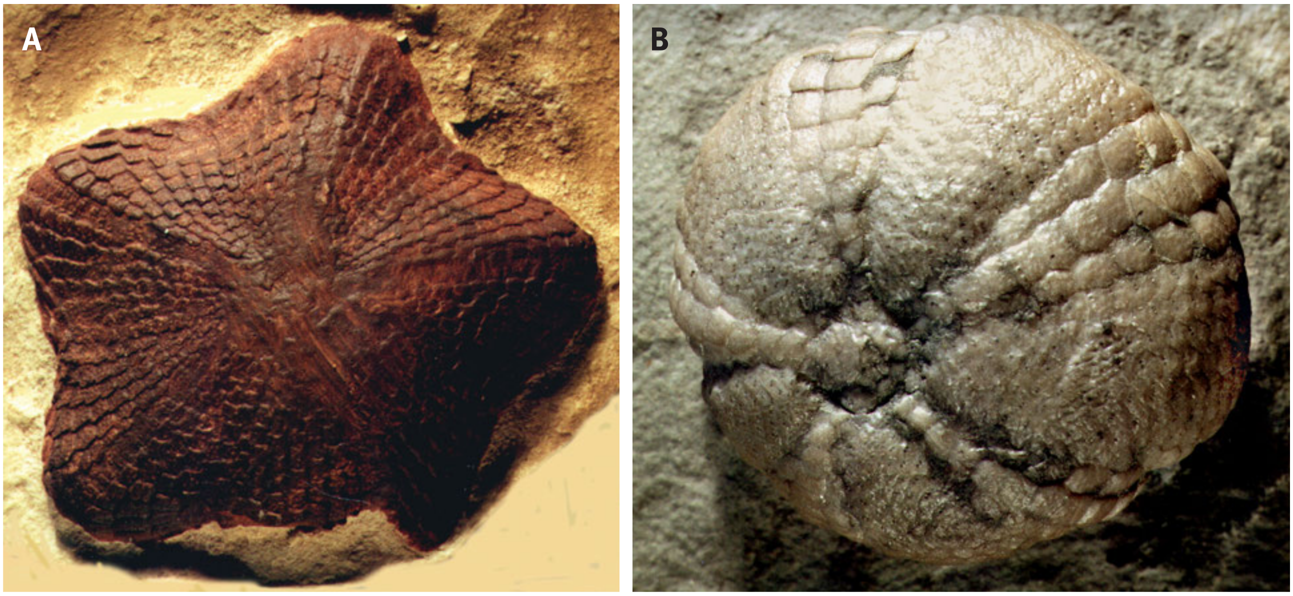


Fig. 2.8: Early forms of echinoids. (A) *Hyattechinus pentagonus* Jackson, 1912. Aboral side, diameter 49 mm; Lower Carboniferous, Pennsylvania, USA (cast of an external mold, coll. HVT). The broad interambulacra are covered with many columns of imbricating plates. The ambulacra are very narrow. (B) *Lepidesthes wortheni* Jackson, 1896. Aboral side, diameter 38 mm; Lower Carboniferous, Indiana, USA (coll. HVT). The ambulacra are broad and set with numerous pore pairs. There are three columns of plates in each interambulacrum.

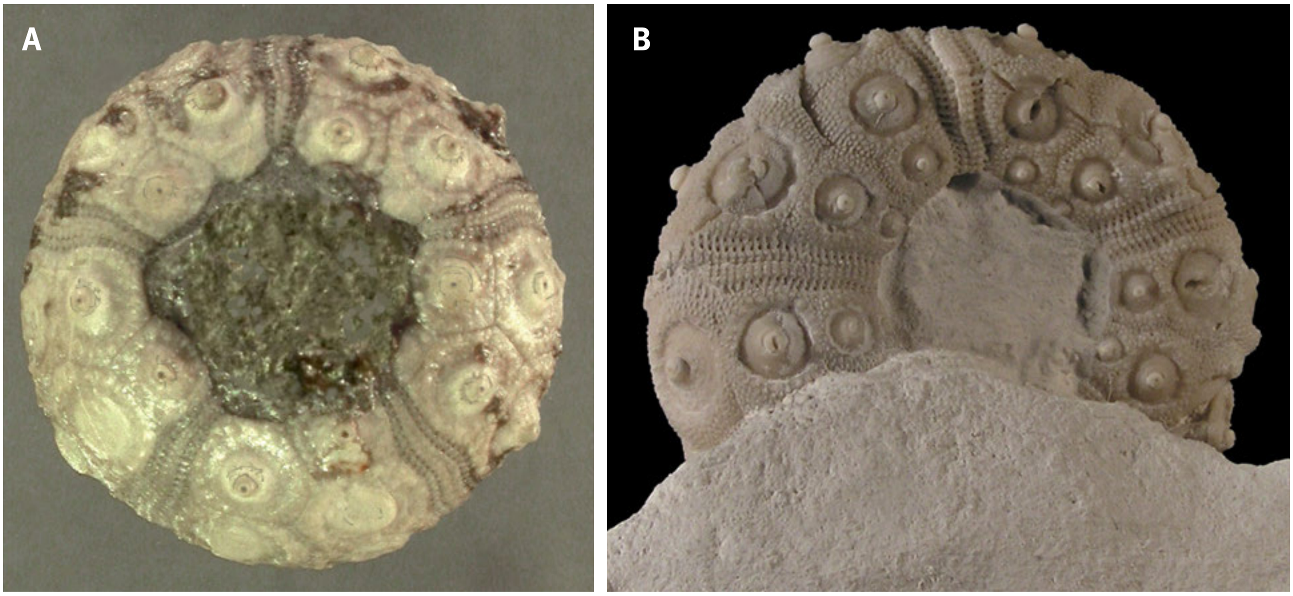


Fig. 2.9: Fossil Cidaroids. (A) *Paracidaris jeanneti* (Lambert, 1924). Aboral side, test diameter 18 mm; Upper Triassic, Hindelang, Germany (coll. HVT). (B) *Stereocidaris sceptrifera.* Oral side on a piece of chalk, diameter 28 mm; Upper Cretaceous, Criel, Normandy, France (photo by H. Friedhoff). *Paracidaris* lived approximately 200 million years ago, *Stereocidaris* 70 million. Both cidarids show the same morphology as Recent forms: few prominent tubercles with large areoles in the broad interambulacra, the ambulacra being very narrow.

Changes or “improvements” were relatively small and took place mainly with respect to nutritional, respiratory, and defensive functions: in the teeth, in the ambulacral plating with their pores and in the shape and arrangement of the spines and the tubercles.

In cidarids, the solid-plated test gives the necessary rigidity for the strong muscles of the jaw apparatus – Aristotle’s lantern – and the teeth were used for a more powerful plucking or rasping. Acroechinoids developed both lighter and more maneuverable lanterns

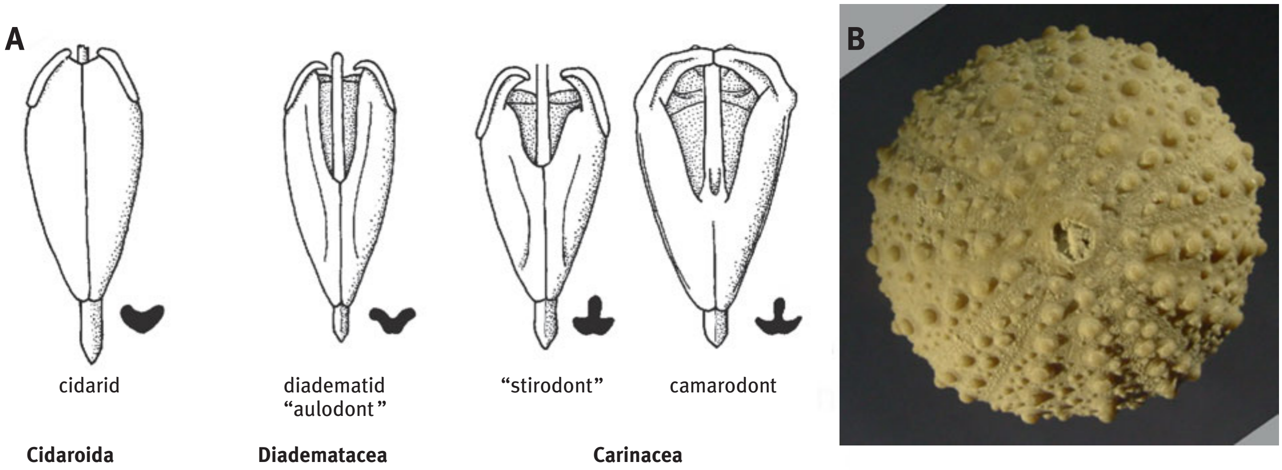


Fig. 2.10: (A) Evolution of Aristotle's lantern: cidarids and "diademataceans" have teeth with an U-shaped cross section. The Carinacea evolved mechanically stronger keeled (or T-shaped) teeth, at first more simple typs ("stirodont", term no longer in use). Later in evolution in the Camarodonta the plates of the jaw apparatus (pyramids) are connected by a bow (epiphysis), which further increases their strength. Cross sections of teeth are shown in solid black (after A. B. Smith 1984). (B) Acroechinoid regular echinid. *Phymechinus mirabilis* L. Agassiz, 1846. Aboral side, diameter 41 mm. Upper Jurassic (about 160 million years), France: in ambulacra and interambulacra, two series of subequal tubercles are developed, which in life would have been set with numerous spines for defense.

that allow them to take advantage of new food sources and therefore to colonize previously unexploited habitats.

Another innovation comprises the ambulacral plating. The regular Acroechinoidea developed compound ambulacral plates with more space for larger secondary spines, and therefore a better all-round defense. The number of pore pairs did not decrease essentially.

The four orders, formerly summarized under the name Diadematacea (see Chapter 4.3.), and echinaceans are distinguished by their lantern. The mechanically stronger, keeled teeth (stirodont) of the latter must have given them an advantage over the diademataceans with their "aulodont" jaw apparatus (Fig. 2.10 A). Their "bite" could be harder and they could graze more efficiently on encrusting organisms.

In the Cretaceous, the camarodont lantern evolved in the Temnopleuroida, and by the end of that period, many groups of echinaceans with stirodont lanterns had become extinct and were mostly replaced by camarodont echinoids. In the following Tertiary, the most recent, regular group, the Echinoida, evolved, being specialized for life on rocky bottoms in shallow water with stronger wave activity.

The third group of Acroechinoidea, the Irregularia, evolved in the early Jurassic from tiny opportunistic regulars like *Eodiadema* Duncan, 1889. They made the adaptive breakthrough to living and feeding on loose mobile sediment. In this new habitat, changes in lifestyle and morphology progressed step by step: the first irregular echinoids were simply adapted for locomotion over unconsolidated sedimentary bottoms by having broader, flattened oral sides with shorter, but more numerous spines. Later, they may have lived semi-infaunally, shallowly digging, before they become adapted for burrowing. They ploughed unidirectionally(!) through the sediment, while waste material was channeled through a depressed anal groove toward the posterior end of the test. The bilateral symmetry, i.e. the antero-posterior polarity with two equal sides, allowed the evolution of shapes, structures, and specializations, which were new to echinoids.

Early irregulars like the Pygasteroida and the Holectypoida could only live in coarse sediments, remaining more or less stationary. They had to return to the surface, perhaps at night, to feed using only their lantern. But very quickly, by the end of the Lower Jurassic, species had evolved that were able to collect the food with their suckered tube feet of the oral side (Fig. 2.12 A). On the upper side of the test, the podia in the ambulacra were modified into specialized respiratory tube feet, which extracted oxygen from the surrounding water through their thin body walls.

The dense uniform spine canopy enabled cassiduloids and disasteroids to move into finer sediments, and soon, the two groups were adapted to different niches. The cassiduloids developed specialized spines and tube feet around the peristome to increase the quantity of sediment that could be ingested (Fig. 2.11). Teeth were no

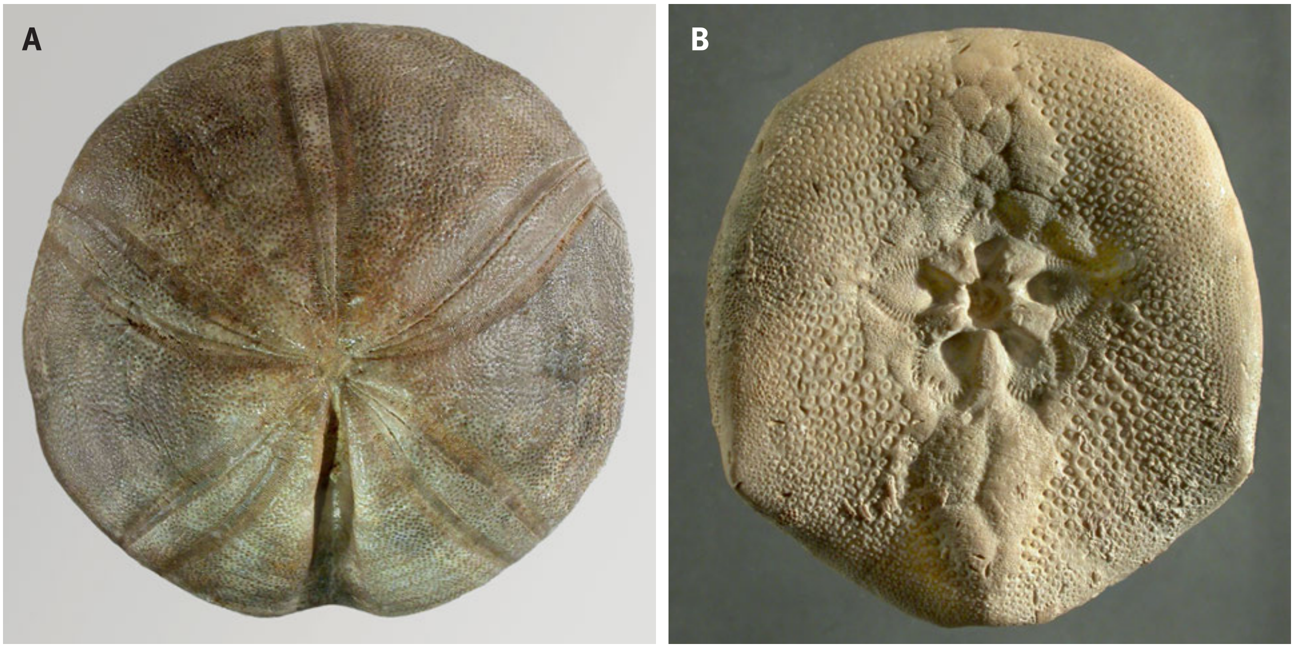


Fig. 2.11: (A) Cassiduloid *Clypeus plotii* Leske, 1778. Aboral side, length 102 mm; Middle Jurassic, England (coll. HM). With the five narrow ambulacra, the test still resembles in appearance that of a regular echinoid. But as the periproct has moved out of the apical system, lying immediately posterior in a deeply depressed groove, the echinoid is bilaterally symmetrical with a clearly defined anterior and posterior. (B) Cassiduloid *Hardouinia mortonis* Michelin, 1855. Oral side, length 51 mm; Upper Cretaceous, USA. The mouth is encircled by large podia, penetrating through pores, conspicuously arranged like leaves. The prominent tooth-like areas are set with spines. Both the spines and the tube feet are specialized to shovel large quantities of sediment into the peristome.

longer necessary; only in early ontogenetic stages are they still present. Thus, the cassiduloids were able to colonize sediments with a relatively low organic content.

The disasteroids by contrast evolved tube feet ending in discs with numerous finger-like digits, which allowed them to collect selectively fine-grained, organic particles by mucous adhesion. The evolution of these penicillate podia was an important innovation, and the disasteroids subsequently gave rise to the Holasteroida and Spatangoida in Late Jurassic to Early Cretaceous, both of which inherited this kind of tube foot (Fig. 2.12 A, B).

The spatangoids especially became much better adapted for burrowing, and they were able to live infaunally even within fine muddy sediments. They evolved fascioles, bands of ciliated tiny spines that create a current of fresh water over the respiratory podia and the whole surface. The tube feet of the anterior ambulacrum no longer served for respiration but became differentiated for funnel building, selection of food, or sensory reception. On the oral side, the posterior interambulacral plates enlarged and became set with strong spines for excavating. Burrowing in sediments thus led to the evolution of new feeding and food transporting techniques in tandem with morphological changes.

The spatangoids diversified during the Tertiary, often into niches previously held by holasteroids, and today, they are found in almost all grades of sediment, burrowing down to depths of 20 cm below the sea bottom. The holasteroids lack funnel-building tube feet.

Generally, in contrast to the spatangoids, they have never been particularly successful burrowers (Fig. 2.12 B). After their severe decline at the Cretaceous-Tertiary boundary, they became restricted mainly to deep-sea environments, where they have evolved an efficient method of scooping up the surface detritus layer by scooping it directly along the oral groove into the vertical mouth – without using any specialized spines or tube feet.

In the early Tertiary, the Clypeasteroida evolved from some form of cassiduloids. With their flat tests, equipped with very numerous short, differentiated spines, they are adapted to move through the detritus-rich uppermost layer of the sediment. Enormous numbers of tiny tube feet with suckered discs, arranged in broad areas all over the strongly enlarged ambulacra, collect fine organic material from among the sand grains. These particles are laid into food

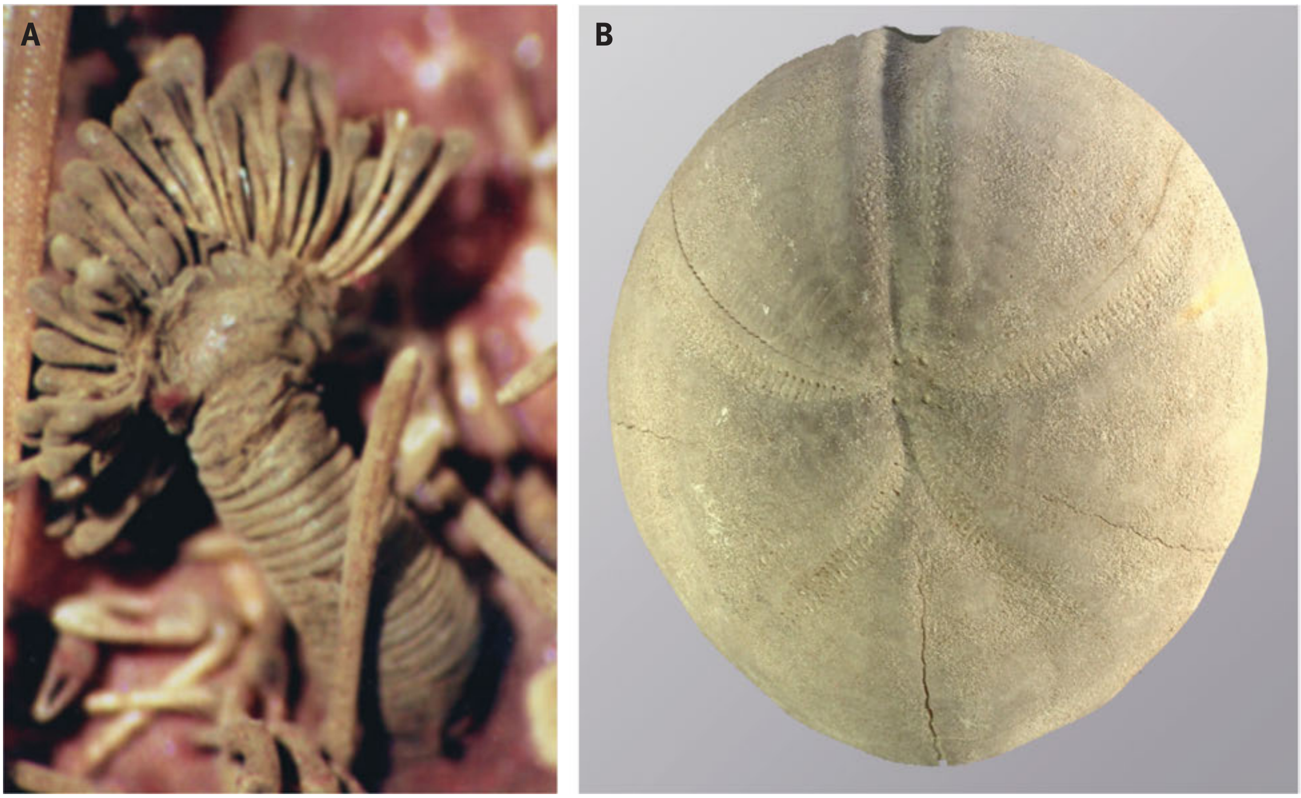
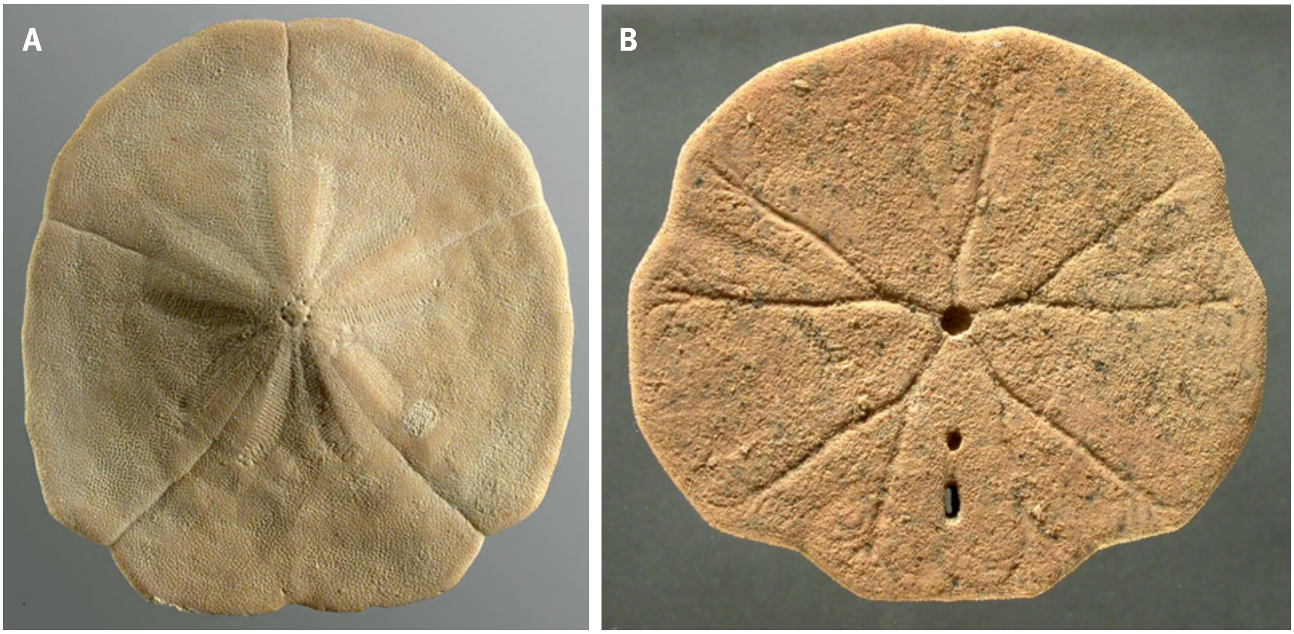


Fig. 2.12: (A) Penicillate podium of extant spatangoid, *Amphipneustes lorioli* Koehler, 1901, length 3 mm; Weddell Sea, Antarctica. AWI. The finger-like processes at the distal end of the extensible tube foot are specialized for food grasping supported by internal, calcareous rods. The contracted shaft has a length of 2 mm; the digits at the disc are 1 mm long. (B) Holasterid *Hemipneustes striatoradiatus* (Leske, 1778). Aboral side, length 84 mm; Upper Cretaceous, Netherlands (coll. HvN). In each petal, slit-like pore pairs are developed, and the tube feet were elongated and leaf-shaped with a strongly enlarged surface for more efficient gaseous exchange. The anterior furrow was overarched by spines to protect and cover the mucous string with its food particles.



grooves to be transported in a mucous string toward the mouth to be crunched by the broadly winged, internal teeth (Fig. 2.13 A, B). Obviously, this innovation was very efficient, for within 15 to 20 million of years these sand dollars with their flat discs had expanded all over the world.

Thus, the evolution of crucial new morphological features has led to the adoption of new modes of life or has allowed access to new habitats. After each adaptive breakthrough, a more or less rapid radiation and diversification in morphology follows, until the possibilities of the new niches are exhausted.

Literature: Kier 1974, 1982; Phelan 1977; Smith 1984, 2004; David 1988; Hendler et al. 1995; Smith et al. 2005; Kroh & Smith 2010; Smith & Kroh 2011.

◄ **Fig. 2.13:** (A) Clypeasteroid *Monostychia australis* Laube, 1869; aboral side, test length 42 mm; Tertiary, Miocene, South Australia. The ambulacra are broad, each marked by a food groove, which leads round the margin to the central mouth. (B) Clypeasteroid *Monophoraster darwini* (Desor, 1847). Oral side, test length 58 mm; Tertiary, Miocene, Argentina. The branched food grooves spread over the surface. The periproct is situated between the peristome and the small anal lunule).

3 Classification and systematics

Sea urchins were long classified in the traditional hierarchical system used since Linné (1758). In the course of time, the order into classes, orders, families, and genera became finer and finer by addition of supertaxa, infrataxa, or subtaxa, etc. Increasingly more specimens were discovered and examined, and modern technology of sampling and microbiological investigation revealed more detailed characteristics including genetic, reproductive, and ecological aspects. By means of computer programs, it is possible to handle enormous quantities of data creating cladistics trees (e.g. Kroh & Mooi 2010, Smith & Kroh 2015), and analyses of gene sequences or entire genomes supplement such analyses. Such analyses are not always congruent, and therefore, it was chosen here to use the classification from the *World Echinoidea Database* (version 3.0) (slightly simplified). It is part of WoRMS (the World Register of Marine Species) and incorporates many recent advances in echinoid systematic:

Class Echinoidea Leske, 1778
Subclass Cidaroidea Smith, 1984
Order Cidaroida Claus, 1880
- Family Cidaridae Gray, 1825
- Subfamily Cidarinae Mortensen, 1928
  - Genus *Acanthocidaris* Mortensen, 1903
  - Genus *Calocidaris* H. L. Clark, 1907
  - Genus *Centrocidaris* A. Agassiz, 1904
  - Genus *Chondrocidaris* A. Agassiz, 1863
  - Genus *Cidaris* Leske, 1778
  - Genus *Compsocidaris* Ikeda, 1939
  - Genus *Eucidaris* Pomel, 1883
  - Genus *Hesperocidaris* Mortensen, 1928
  - Genus *Kionocidaris* Mortensen, 1932
  - Genus *Lissocidaris* Mortensen, 1939
  - Genus *Phyllacanthus* Brandt, 1835
  - Genus *Plococidaris* Mortensen, 1909
  - Genus *Prionocidaris* A. Agassiz, 1863
  - Genus *Stylocidaris* Mortensen, 1909
  - Genus *Tretocidaris* Mortensen, 1903
- Subfamily Ctenocidarinae Mortensen, 1928
  - Genus *Aporocidaris* A. Agassiz & H. L. Clark, 1907
  - Genus *Ctenocidaris* Mortensen, 1910
  - Genus *Homalocidaris* Mortensen, 1928
  - Genus *Notocidaris* Mortensen, 1909
  - Genus *Rhynchocidaris* Mortensen, 1909
- Subfamily Goniocidarinae Mortensen, 1928
  - Genus *Austrocidaris* H. L. Clark, 1907
  - Genus *Goniocidaris* Desor, in Agassiz & Desor
  - Genus *Ogmocidaris* Mortensen, 1921
  - Genus *Psilocidaris* Mortensen, 1927
  - Genus *Rhopalocidaris* Mortensen, 1927
  - Genus *Schizocidaris* Mortensen, 1903
- Subfamily Stereocidarinae Lambert, 1900
  - Genus *Phalacrocidaris* Lambert, 1902
  - Genus *Stereocidaris* Pomel, 1883
- Family Histocidaridae Lambert, 1900
  - Genus *Histocidaris* Mortensen, 1903
- Family Psychocidaridae Ikeda, 1936
  - Genus *Psychocidaris* Ikeda, 1935

Subclass Euechinoidea Bronn, 1860
Order Echinothurioida Claus, 1880
- Family Kamptosomatidae Mortensen, 1934
  - Genus *Kamptosoma* Mortensen, 1903
- Family Phormosomatidae Mortensen, 1934
  - Genus *Hemiphormosoma* Mortensen, 1934
  - Genus *Paraphormosoma* Mortensen, 1934
  - Genus *Phormosoma* Thomson, 1872
- Family Echinothuriidae Thomson, 1872
  - Genus *Araeosoma* Mortensen, 1903
  - Genus *Asthenosoma* Grube, 1868
  - Genus *Calveriosoma* Mortensen, 1934
  - Genus *Hapalosoma* Mortensen, 1903
  - Genus *Hygrosoma* Mortensen, 1903
  - Genus *Sperosoma* Koehler, 1897
  - Genus *Tromikosoma* Mortensen, 1903

Infraclass Acroechinoidea Smith, 1981
Order Aspidodiadematoida Kroh & Smith, 2010
- Family Aspidodiadematidae Duncan, 1889
  - Genus *Plesiodiadema* Pomel, 1883
  - Genus *Aspidodiadema* A. Agassiz, 1878

Order Diadematoida Duncan, 1889
- Family Diadematidae Gray, 1855
  - Genus *Astropyga* Gray, 1825
  - Genus *Centrostephanus* Peters, 1855
  - Genus *Chaetodiadema* Mortensen, 1903
  - Genus *Diadema* Gray, 1825
  - Genus *Echinothrix* Peters, 1853
  - Genus *Eremopyga* A. Agassiz & H. L. Clark, 1908
  - Genus *Goniodidema* Mortensen, 1939
  - Genus *Lissodiadema* Mortensen, 1903

Order Micropygoida Kroh & Smith, 2010
Family Micropygidae Mortensen, 1903
Genus *Micropyga* A. Agassiz, 1879

Order Pedinoida Mortensen, 1939
Family Pedinidae Pomel, 1883
Genus *Caenopedina* A. Agassiz, 1869

Carinacea Kroh & Smith, 2010
Superorder Calycina Gregory, 1900
Order Salenioida Delage & Hérouard, 1903
Family Saleniidae L. Agassiz, 1838
Genus *Salenocidaris* A. Agassiz, 1869
Genus *Bathysalenia* Pomel, 1883

Superorder Echinacea Claus, 1876
Order Stomopneustoida Kroh & Smith, 2010
Family Glyptocidaridae Jensen, 1982
Genus *Glyptocidaris* A. Agassiz, 1864
Family Stomopneustidae Pomel, 1883
Genus *Stomopneustes* L. Agassiz, 1841

Order Arbacioida Gregory, 1900
Family Arbaciidae Gray, 1855
Genus *Arbacia* Gray, 1835
Genus *Arbaciella* Mortensen, 1910
Genus *Coelopleurus* L. Agassiz, 1840
Genus *Dialithocidaris* A. Agassiz, 1898
Genus *Habrocidaris* A. Agassiz & H. L. Clark, 1907
Genus *Podocidaris* A. Agassiz, 1869
Genus *Pygmaeocidaris* Döderlein, 1905
Genus *Tetrapygus* L. Agassiz, 1841

Order Camarodonta Jackson, 1912
Family Parasaleniidae Mortensen, 1903
Genus *Parasalenia* A. Agassiz, 1863

Infraorder Temnopleuridea Kroh & Smith, 2010
Family Temnopleuridae A. Agassiz, 1872
Genus *Amblypneustes* L. Agassiz, 1841
Genus *Erbechinus* Jeannet, 1935
Genus *Holopneustes* L. Agassiz, 1841
Genus *Mespilia* Desor in Agassiz & 1846
Genus *Microcyphus* L. Agassiz, 1846
Genus *Opechinus* Desor, 1856
Genus *Paratrema* Koehler, 1927
Genus *Printechinus* Koehler, 1927
Genus *Pseudechinus* Mortensen, 1903
Genus *Salmaciella* Mortensen, 1942
Genus *Salmacis* L. Agassiz, 1841
Genus *Temnopleurus* L. Agassiz, 1841
Genus *Temnotrema* A. Agassiz, 1863
Family Trigonocidaridae Mortensen, 1903
Genus *Asterechinus* Mortensen, 1942
Genus *Desmechinus* H. L. Clark, 1923
Genus *Genocidaris* A. Agassiz, 1869
Genus *Hypsiechinus* Mortensen, 1903
Genus *Prionechinus* A. Agassiz, 1879
Genus *Trigonocidaris* A. Agassiz, 1869

Infraorder Echinidea Kroh & Smith, 2010
Family Echinidae Gray, 1825
Genus *Dermechinus* A. Agassiz, 1879
Genus *Echinus* Linné, 1758
Genus *Gracilechinus* Fell & Pawson, 1966
Genus *Polyechinus* Döderlein, 1905
Genus *Sterechinus* Koehler, 1901
Genus *Stirechinus* H. L. Clark, 1912
Family Echinometridae Gray, 1855
Genus *Caenocentrotus* H. L. Clark, 1912
Genus *Colobocentrotus* Brandt, 1835
Genus *Echinometra* Gray, 1825
Genus *Echinostrephus* A. Agassiz, 1863
Genus *Evechinus* Verrill, 1871
Genus *Heliocidaris* L. Agassiz & Desor, 1846
Genus *Heterocentrotus* Brandt, 1835
Genus *Selenechinus* de Meijere, 1903
Genus *Zenocentrotus* H. L. Clark, 1931
Family Parechinidae Mortensen, 1903
Genus *Loxechinus* Desor, 1856
Genus *Paracentrotus* Mortensen, 1903
Genus *Parechinus* Mortensen, 1903
Genus *Psammechinus* L. Agassiz & Desor, 1846
Family Strongylocentrotidae Gregory, 1900
Genus *Hemicentrotus* Mortensen, 1942
Genus *Mesocentrotus* Tatarenko & Poltaraus, 1993
Genus *Pseudocentrotus* Mortensen, 1903
Genus *Strongylocentrotus* Brandt, 1835
Family Toxopneustidae Troschel, 1872
Genus *Cyrtechinus* Mortensen, 1942
Genus *Goniopneustes* Duncan, 1889
Genus *Gymnechinus* Mortensen, 1903
Genus *Lytechinus* A. Agassiz, 1863
Genus *Nudechinus* H. L. Clark, 1912
Genus *Pseudoboletia* Troschel, 1869
Genus *Sphaerechinus* Desor, 1846
Genus *Toxopneustes* L. Agassiz, 1841
Genus *Tripneustes* L. Agassiz, 1841

4 Taxonomy: systematic descriptions

4.1 Subclass Cidaroidea Smith, 1984

4.1.1 Order: Cidaroida Claus, 1880

Introduction: The Cidaroids, the oldest group of extant echinoidea, live in sheltered environments in reefs, on hard grounds such as rocks or corals, or on firm sand. Most of them inhabit waters deeper than 50 m. By daylight, they hide beneath coral blocks or in crevices, emerging at night walking on their oral spines and grazing on encrusting organisms like algae and microscopic animals.

The large primary spines themselves provide a habitat of many other animals or algae, mostly bryozoans, calcareous algae, small molluscs, and even sessile sea cucumbers. The spines are not covered by living skin (epithelium), as in all other sea urchins. Only near the base, within the reach of the pedicellariae, the setting of foreign organisms is not to be found. Some species have evolved a fur-like hair canopy over the lower shaft, which serves for anti-fouling.

Other species have developed broad spines, which seem to be an "invitation" for encrusting organisms to settle, serving as camouflage against predators.

The cidaroids with their pentameral symmetry show rather few distinct features, which have remained in the main stable for hundreds of million years. Differences are mostly only evident in the shape of the primary spines and the pedicellariae. Denuded tests are often difficult to distinguish.

Remark: Many of the original descriptions by L. and A. Agassiz, H.L. Clark, Döderlein, Mortensen, and others were based on a single or at most on very few specimens, and slightly distinguishing characteristics were often pointed out as basis for new species or varieties.

The order is characterized by the following features (Fig. 4.1, 4.2):

Test: Strong, lacking buccal notches.

Ambulacra: Very narrow, plates simple, pore pairs in a single series, small marginal tubercles on interporiferous zone (secondaries) carrying small spines.

Interambulacra: One large primary tubercle per plate carrying a single large spine.

Peristome: Perforated ambulacral plates continuing to mouth opening; apophyses in interambulacral position; teeth unkeeled.

Superfamily Cidaridea Gray, 1825

Primary tubercles perforated; globiferous pedicellariae present.

This family is subdivided into four subfamilies, roughly characterized by the following features:

Cidarinae: Primary tubercles non-crenulate or with just traces of crenulation on aboral tubercles; no pits or grooves; scrobicular tubercles distinctly larger than the extrascrobicular ones.

Ctenocidarinae: Scrobicular tubercles not much larger than extrascrobicular ones, globiferous pedicellariae without end tooth; the species live almost exclusively in Antarctic and subantarctic waters.

Goniocidarinae: Pits and grooves in horizontal sutures, globiferous pedicellariae with end tooth.

Stereocidarinae: Non-functional primary tubercles on the adapical interambulacral plates.

Superfamily Histocidaroidea

Consisting of two families:

Histocidaridae Lambert, 1900. Primary tubercles perforated and strongly crenulated; scrobicular ring not complete, no cortical hair on primary spines; globiferous pedicellariae absent.

Psychocidaridae Ikeda, 1936. Coarse primary spines with club-shaped shaft; no interradial plates on peristome; tubercles generally without perforation. Only a single extant genus with one species.

4.1.1.1 Family Cidaridae Gray, 1825

Subfamily Cidarinae Mortensen, 1928

The subfamily contains 15 genera:

Acanthocidaris Mortensen, 1903. Three species, Indo-Pacific.

Calocidaris H. L. Clark, 1907. Monospecific, Caribbean.

Centrocidaris A. Agassiz, 1904. Monospecific; Pacific Central America.

Chondrocidaris A. Agassiz, 1863. Two species, Indo-West and Central Pacific.

Cidaris Linné, 1758. Five species, restricted to the Atlantic.

Compsocidaris Ikeda, 1939. Monospecific, West Pacific.

Eucidaris Pomel, 1883. Four species, in tropical waters.

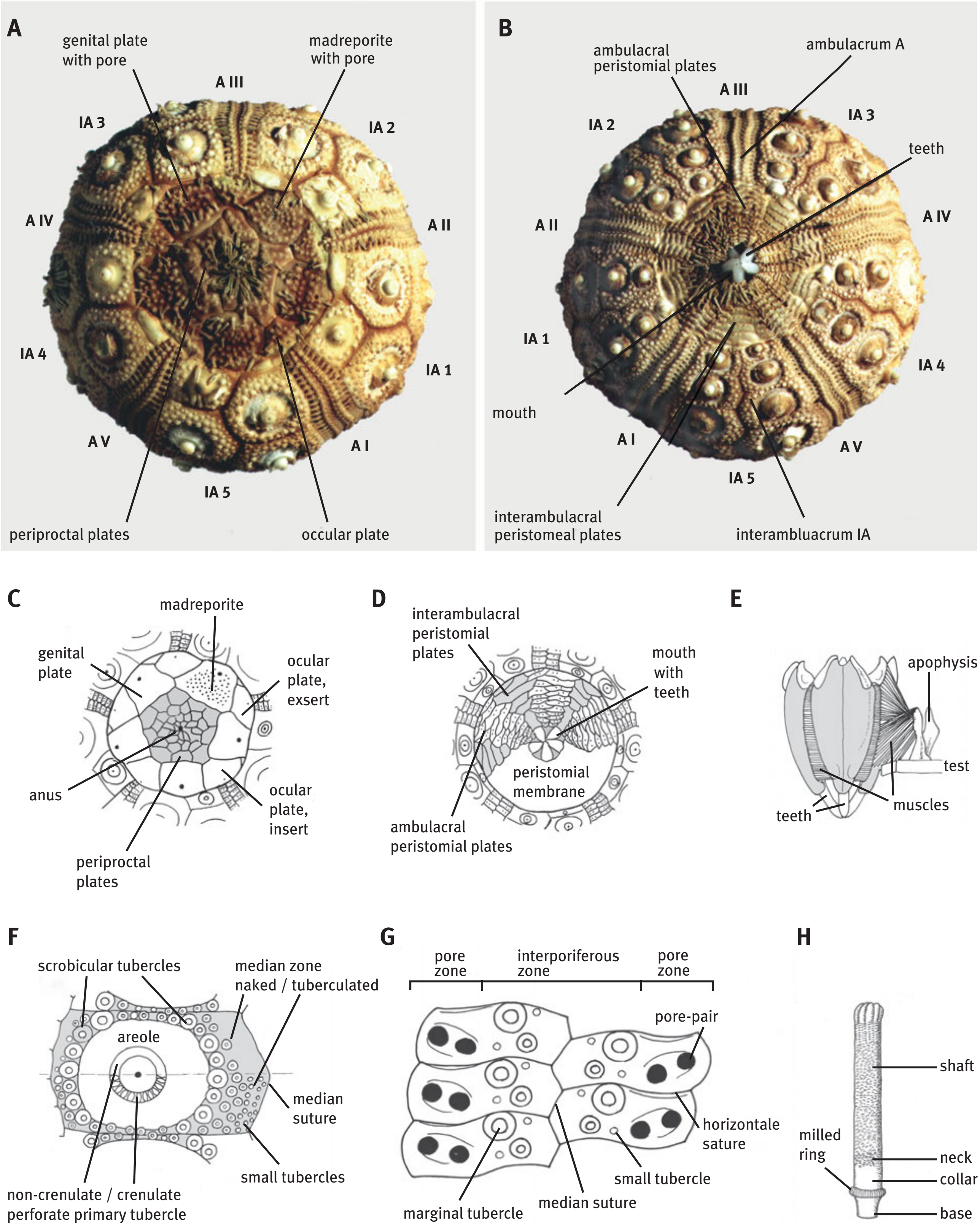
Hesperocidaris Mortensen, 1928. Five species, East Pacific.

Kionocidaris Mortensen, 1932. Monospecific, South Africa.

Lissocidaris Mortensen, 1939. Two species, Indo-Pacific.

Phyllacanthus Brandt, 1835. Seven species, Indo-Pacific.

Plococidaris Mortensen, 1909. Monospecific, Indo-Pacific.


A
genital plate with pore
madreporite with pore
A III
IA 3
IA 2
A IV
A II
IA 4
IA 1
A V
A I
IA 5
periproctal plates
occular plate
B
ambulacral peristomial plates
ambulacrum A
A III
IA 2
IA 3
teeth
A II
A IV
IA 1
IA 4
mouth
A I
A V
IA 5
interambulacral peristomeal plates
interambluacrum IA
C
madreporite
genital plate
ocular plate, exsert
anus
ocular plate, insert
periproctal plates
D
interambulacral peristomial plates
mouth with teeth
peristomial membrane
ambulacral peristomial plates
E
apophysis
test
muscles
teeth
F
scrobicular tubercles
median zone naked / tuberculated
areole
median suture
small tubercles
non-crenulate / crenulate perforate primary tubercle
G
pore zone
interporiferous zone
pore zone
pore-pair
horizontale sature
small tubercle
median suture
marginal tubercle
H
shaft
milled ring
neck
collar
base

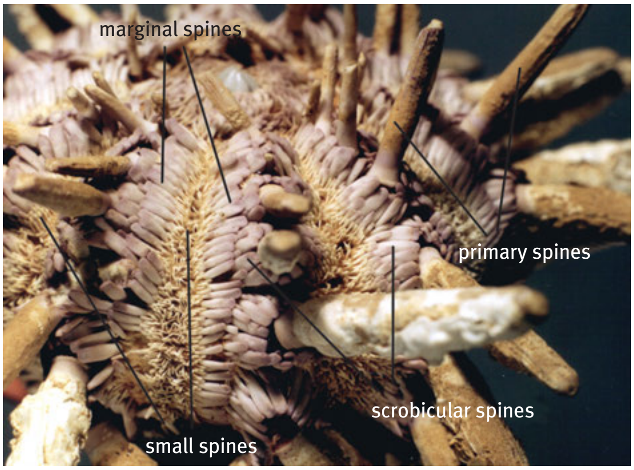


Fig. 4.2: (A) Diagram of cidaroid primary spine. At the milled ring, strong muscles are attached that lead to the areole. (B) Teeth of cidaroid. The jaw apparatus, also called "Aristotle's lantern", is massive; the strong muscles moving the teeth are supported by paired processes (apophyses) at the inner side of the test in interambulacral position (modified after Märkel 1979). (C) Cidaroid spines: the cidaroid echinoids are provided with three kinds of spines associated with tubercles. One large primary spine is carried by a large primary tubercle on each interambulacral plate. Secondary spines are distinctly smaller and are carried by smaller tubercles. They comprise (i) scrobicular spines encircling the base of the primary spine on the interambulacra like a palisade; the associated tubercles surround the areole; (ii) marginal spines in the ambulacra cover the pore zones – the associated tubercles form a regular series; (iii) Small spines are distributed on the remaining areas of the test to differing densities.

Prionocidaris A Agassiz, 1863. Nine species, Indo-Pacific.
Stylocidaris Mortensen, 1909. Numerous species in tropical and temperate waters.
Tretocidaris Mortensen, 1903. Two species, Atlantic.

Genus *Acanthocidaris* Mortensen, 1903

This genus is characterized by having very conspicuous primary spines with a broad, long, and more or less flattened collar, which is ornamented by longitudinally arranged darker or lighter spots. The primary tubercles are distinctly crenulated.

Acanthocidaris curvatispinis Bell, 1892. Indo-West Pacific, Mauritius to Japan and Australia.
Acanthocidaris hastigera A. Agassiz & H. L. Clark, 1907. Hawaii.
Acanthocidaris maculicollis de Meijere, 1904. Type locality Indonesia, Sunda Islands.

Remark: Rowe & Hoggett (1986) compared many specimens from Australian waters and Hawaii, and they recognized the large range of variation in spine ornamentation and color. They suppose all three species may be synonymous.

Acanthocidaris curvatispinis Bell, 1892 (Fig. 4.3 A–C)

Test: High, flattened above and below; test diameter may reach 61 mm.

Apical system: About half the test diameter, ocular plates usually insert, covered regularly by small tubercles, which sometimes show a radial prolongation.

Ambulacra: Sinuous, pore pairs horizontal; marginal tubercles small, median zone with a few scattered tubercles, slightly sunken.

Interambulacra: 9 plates in a column; primary tubercles perforate and distinctly crenulated, strongest adapically; areoles separated except near the peristome.

Primary spines: Long, tapering, and flattened, with blunt tip; collar very broad and long, ornamented with longitudinally arranged spots or nodes; shaft with fine, more or less distinct longitudinal ridges; oral primaries curved, serrated along the sides; collar often longer than the shaft.

◄ **Fig. 4.1:** Cidarids:(A) Aboral side with apical system. (B) Oral side with peristome: The five ambulacra are narrow and more or less sinuous. They consist of a double row of numerous small, simple plates, each perforated by one pore-pair. The plate series continue over the peristomial membrane to the mouth. They are labelled A I to A V. The five broad double series of the interambulacra are built of a few large plates each set with one large tubercle. They are labelled from IA 1 to IA 5. As the madreporite is always situated in IA 2, the other plates can be determined. (C) Aboral side with apical system: The genital and ocular plates are arranged in a ring, encircling the periproct. The ocular plates may reach the periproctal edge (insert) or not (exsert). The periproct is covered with plates, the opening of the anus more or less in the centre. (D) Oral side with peristome: The peristome is closed by a membrane, which is covered by five series of perforated ambulacral plates, and interambulacral plates, which develop to different degrees. In the centre the mouth opens with five teeth (called "Aristotle's lantern"). (E) Teeth of cidaroid. The jaw apparatus is massive, the strong muscles moving the teeth are supported by paired processes (apophyses) at the inner side of the test in interambulacral position. (Modified after Märkel 1979.) (F) One interambulacral plate: The primary tubercle is surrounded by a large areole, bordered by the scrobicular tubercles. The platform of the tubercle may be smooth or crenulated. The space at the median zone of the plate may be naked or set with small tubercles. The smooth surface of the areoles is where the muscles of the spines attach. (G) Ambulacral plate: Two series of pore-pairs make up the pore zones at the outer parts of the plates. The interporiferous zone expands along the median suture and is more or less set with tubercles. (H) Diagram of cidaroid primary spine. At the milled ring strong muscles are attached that lead to the areole (see in F).

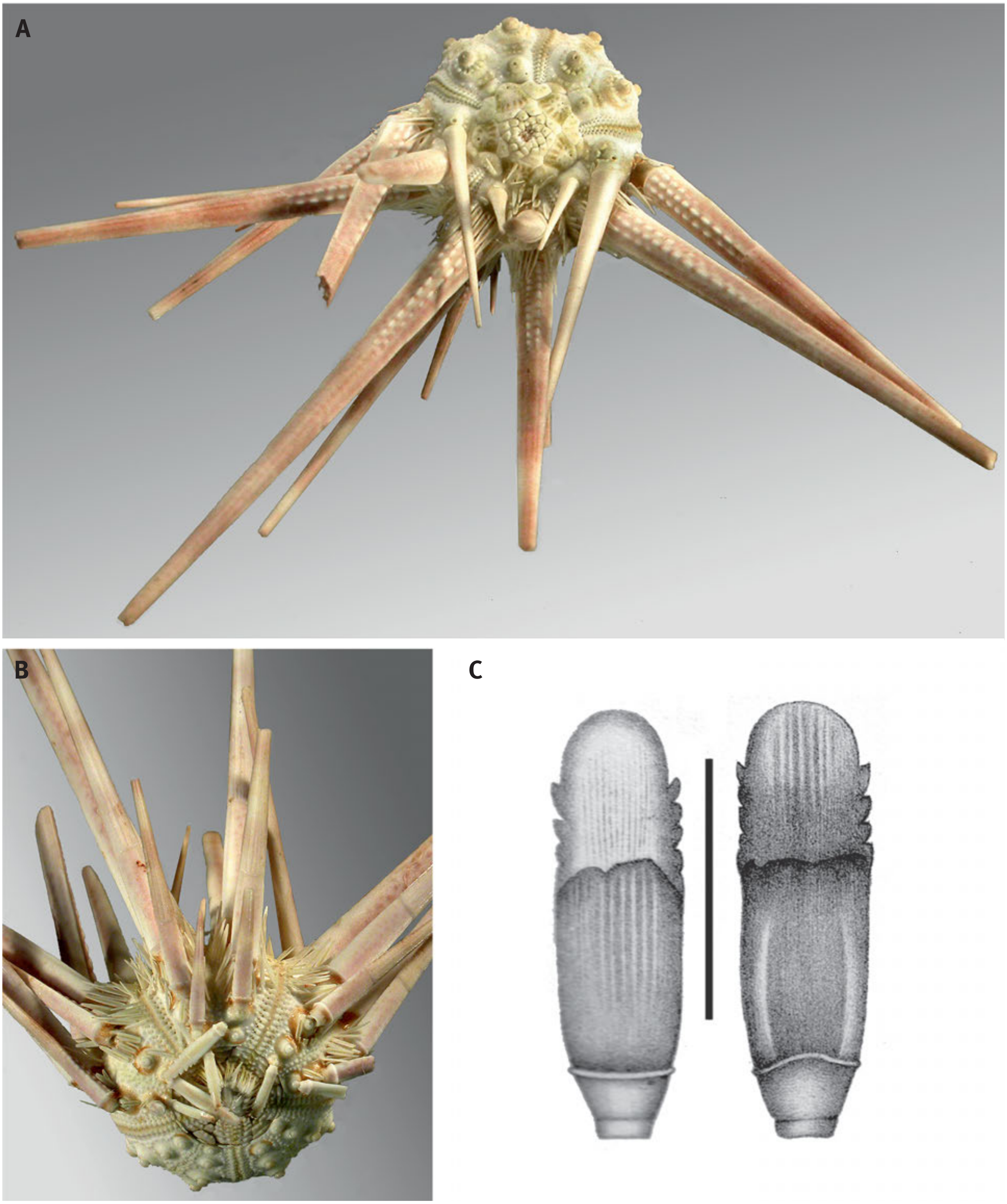


Fig. 4.3: (A–C) *Acanthocidaris curvatispinis*. Aboral side with long primary spines, diameter of test 14 mm; Port Louis, Mauritius. ZMUC. (B) Oral side. (C) Primary spines of the oral side: (left: upper side; right: underside). Scale: 5 mm. (A) From A. Agassiz & H.L. Clark (1907).

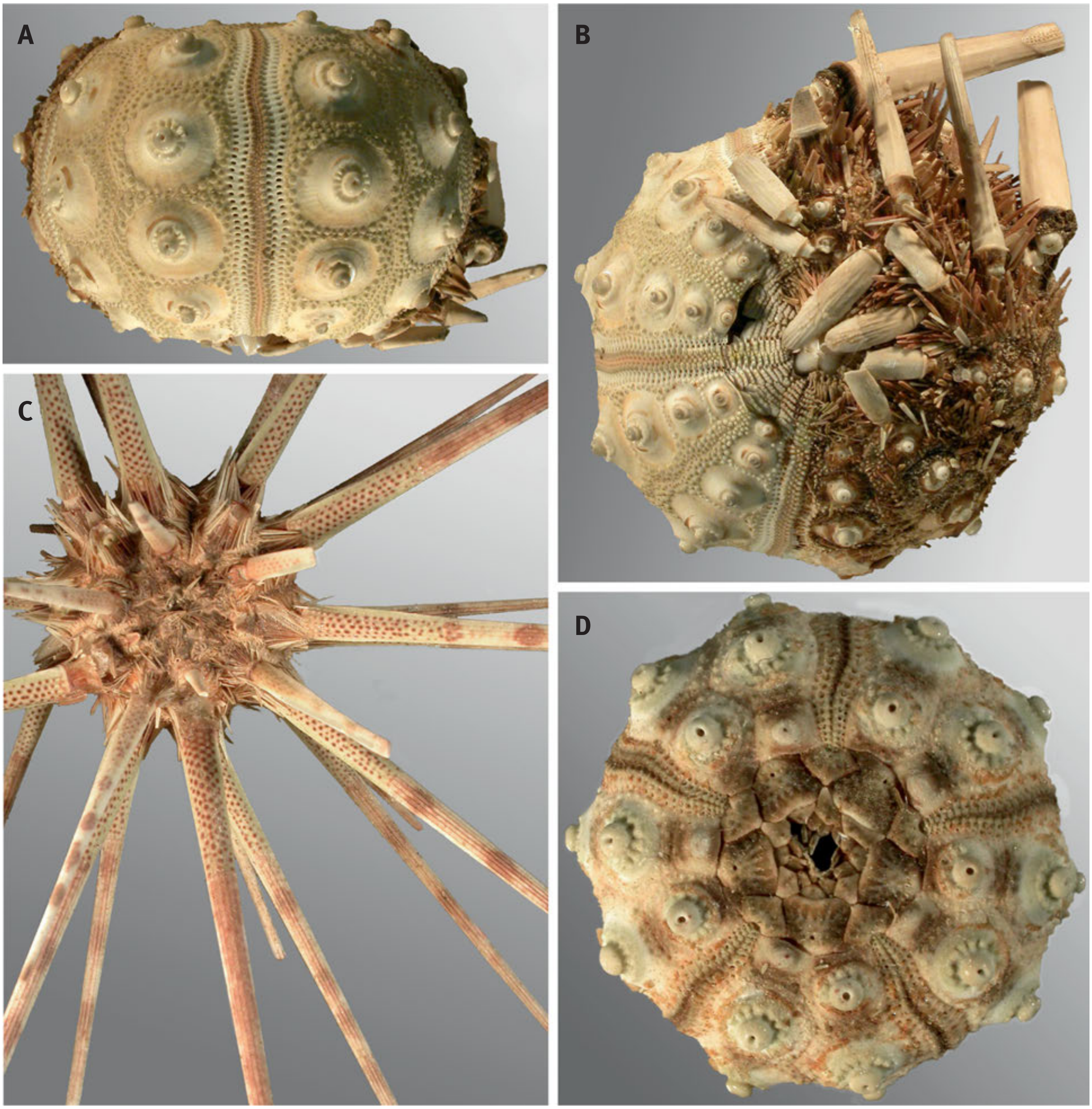


Fig. 4.4: (A, B) *Acanthocidaris hastigera*. (A) Side view, diameter of test 45 mm; Hawaii. ZMUC. The primary tubercles are strongly crenulated. (B) Oral side. (C, D) *Acanthocidaris maculicollis*. (C) Aboral side, diameter 21 mm; Cebu, Philippines. ZMUC. (D) Aboral side with spines, test diameter 20 mm; Philippines. ZMUC.

Secondary spines: Flattened, not appressed, but rather erect.

Color: The patterns on the collar and on the shaft are formed mainly of darker brown or reddish spots on a white, creamy, or olive green ground. Additionally, there are darker lines in brown or olive green along the midlines of ambulacra and/or interambulacra or spots between the aboral primary tubercles and on the genital plates. Secondary spines yellowish.

Distribution: *Acanthocidaris curvatispinis* is wide-spread in the Indo-West Pacific: from Mauritius through the Malayan Archipelago and the Philippines to Japan, then to Australia (Western Australia, along the tropical northern to the southeastern coast of New South Wales). Bathymetric range 40 to 355 m.

Acanthocidaris hastigera A. Agassiz & H. L. Clark, 1907
(Fig. 4.4 A, B)

Very similar to *Acanthocidaris curvatispinis*.

Test: Diameter may reach 52 mm. *Acanthocidaris hastigera* differs in the brown color of its secondary spines, the collar appears to be a little longer than in *A. curvatispinis*.

Distribution: Probably endemic to the Hawaiian Islands, 57 to 355 m.

Acanthocidaris maculicollis de Meijere, 1904 (Fig. 4.4 C, D)
This species resembles very much *A. curvatispinis*. Often, the collar of the primary spines is set with red spots and the shaft may be banded.

Distribution: Type locality: Indonesia, Sunda Islands, at depths of 69 to 94 m.

Genus *Calocidaris* H. L. Clark, 1907

This monospecific genus is characterized by entirely smooth and shiny primary spines.

Calocidaris micans Mortensen, 1903 (Fig. 4.5 A, B)

Test: Relatively high, up to 75 % of test diameter, not flattened above or below.

Apical system: Madreporite not larger than other genital plates, plates densely tuberculated; ocular plates just exsert or just insert.

Ambulacra: Interporiferous zone at ambitus with four series of almost equal-sized tubercles, inner tubercles adorally and adapically smaller than marginal ones and more irregular; poriferous zone narrow.

Interambulacra: Areoles large and round, scrobicular tubercles well differentiated, reaching the upper and lower edge of plates; median zone depressed toward midline, extrascrobicular tubercles in horizontal series; aboral primary tubercles faintly crenulated at upper side.

Primary spines: Long and slender, up to 3 times the diameter, but usually 1.5 times, tapering gently to the tip,

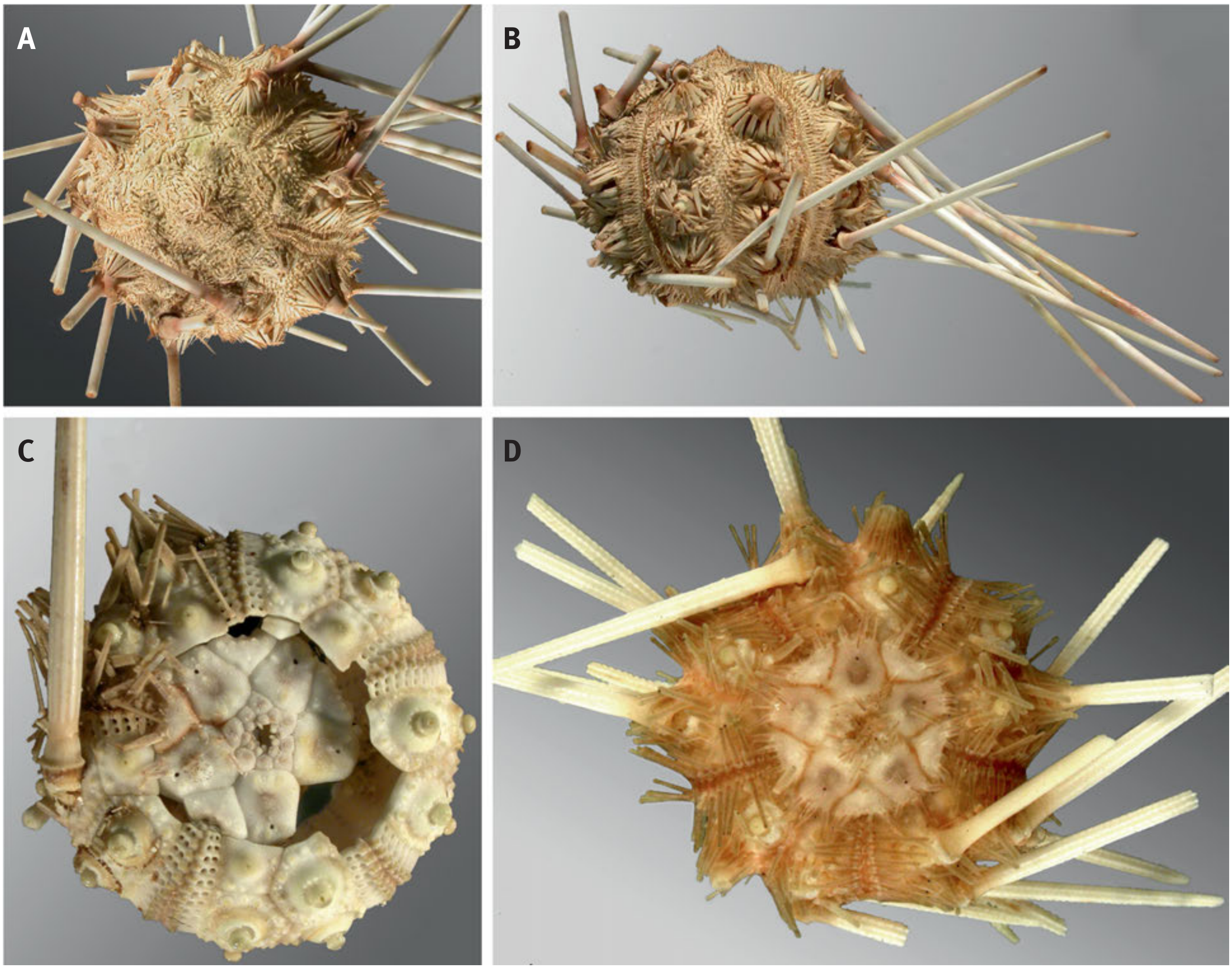


Fig. 4.5: (A, B) *Calocidaris micans*. (A) Aboral side, diameter 49 mm, longest spine 90 mm; Havana, Cuba. ZMUC. (B) Side view: the scrobicular spines are much larger than the other secondaries. (C, D) *Centrocidaris doederleini*. (C) Oral side, diameter of test 14 mm; Galapagos Islands. ZMUC. (D) Aboral side with spines, diameter of test 12 mm; Galapagos Islands. ZMUC.

totally smooth and shiny, lacking hairs or granules; above the ambitus, set with about 16 glassy zones slightly elevated longitudinally, visible only to the aided eye; below the ambitus, they form faint, glassy ridges; oral primaries flattened with ridges and thin edges.
Secondary spines: Scrobiculars long and appressed; other secondaries much smaller and pointed at the tip.
Color: Test and secondary spines light brown to beige; primary spines white with faintly red brown tip, collar red brown or pink, neck and shaft light olive; cleaned test white with very slight olive tint.
Distribution: West Indies and Gulf of Mexico at a depth of 200 to 330 m.
Biology: Recent deep-sea submersible expeditions in the Bahamas revealed interactions between *Calocidaris micans* and the stalked crinoid *Endoxocrinus parrae* (Gervais in Guérin 1835). The in situ observations suggest that these sea urchins, often occurring in "meadows" of sea lilies, prey on live crinoids, which respond by shedding the distal stalk portions and rapidly crawling away (Baumiller et al. 2008).
Literature: Mortensen 1903, 1910; Phelan 1970; Coppard & van Noordenburg 2007.

Genus *Centrocidaris* A. Agassiz, 1904

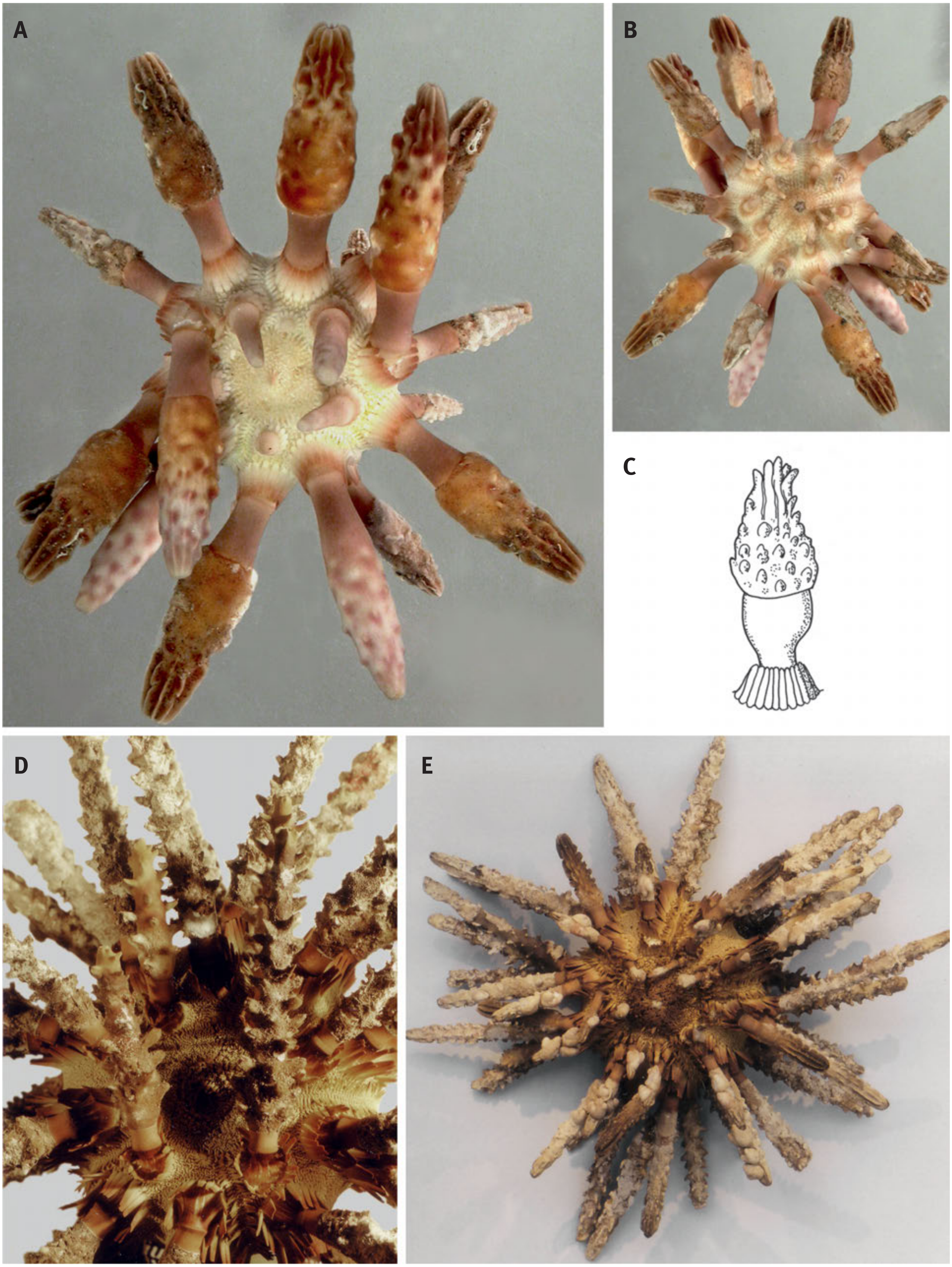
This monospecific genus is characterized by its high and rather naked genital plates.

Centrocidaris doederleini A. Agassiz, 1898 (Fig. 4.5 C, D)
Test: Small, not exceeding 30 mm; low, flattened above and below.
Apical system: Ocular plates exsert, genital plates remarkably high and narrow; consequently, the periproct is small; all plates rather naked, some small tubercles along the outer edges, a single usually in the middle of the genital plates.
Ambulacra: Almost straight, relatively broad, in width almost half of interambulacra; interporiferous zone twice the width of pore zone; marginal tubercles regular and contiguous, usually a single inner tubercle per plate, narrow naked midline.
Interambulacra: Areoles large and shallow, almost completely filled by the boss; adorally coalescing; scrobicular tubercles slightly larger than marginal tubercles; median space with a single series of extrascrobicular tubercles and a distinct naked midline.
Peristome: Smaller than apical system.
Primary spines: In length, about 1–1.5 times the test diameter; slender, cylindrical; aborally with indication of about 10 low ridges, cortical hair well developed, forming a dense meshwork covered by a glabrous crust appearing totally smooth; below the ambitus, set with more or less distinct fine teeth, oral primaries serrated.
Secondary spines: Long, very slender, club-shaped, not appressed.
Globiferous pedicellariae: Stem of globiferous pedicellariae with limb.
Color: Primary spines white, collar yellowish; secondaries greenish with a faint darker midline; naked median space in ambulacra and interambulacra in life dark purple to red violet; apical system white with dark purple to brown sutures; denuded test white with greenish-olive tint and brown to violet-red interporiferous zones in ambulacra.
Distribution: West coast of central America, Cocos and Galapagos Islands. Depth 91 to 550 m.
Literature: Mortensen 1928; Lessios 2005.

Genus *Chondrocidaris* A. Agassiz, 1863

This genus, consisting of two species, is characterized by strongly sculptured primary spines.

Chondrocidaris brevispina H. L. Clark, 1925 (Fig. 4.6 A–C)
Test: Flattened above, horizontal diameter of test reaches 55 mm.
Apical disc: Ocular plates exsert, whole apical system covered with very small, glassy tubercles, with a circle of larger ones around the anus.
Ambulacra: Rather sinuate; marginal tubercles regular, median space covered with small spines, the tubercles being glassy; pores equal-sized and conjugate.
Interambulacra: Distinctly separated areoles, median space closely covered with very small tubercles of uniform size, leaving no naked or sunken median or horizontal lines; scrobicular tubercles well differentiated.
Peristome: Distinctly larger than apical system, rather conically protruding.
Primary spines: In length, less than diameter of test in adult, relatively longer in young specimens; long vase-shaped collar, which may reach a length of 15 mm in large specimens, sharply separated from the shaft carrying coarse thorns, developing into longitudinal ridges toward the tapering or flaring distal end; in well-preserved specimens, the shaft is set with a thick coat of fur-like hair.
Secondary spines: Scrobicular spines ca. 3 mm long, with distinct longitudinal ridges, truncated at the distal end; marginal spines rounded at the point; all of them strongly appressed.
Color: Test and spines are rather variable, mostly olive green, more rarely yellow, the collar and shaft of spines more or less coral-red, younger specimens are generally lighter.
Distribution: This species lives probably throughout the whole Malayan Archipelago and eastward to the South Pacific Islands such as Samoa at depths of 10 to 15 m.
Literature: Guille et al. 1986.


A
B
C
D
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