

Sea Urchins



Sea Urchins



**a guide
to worldwide shallow water species**

Heinke Schultz

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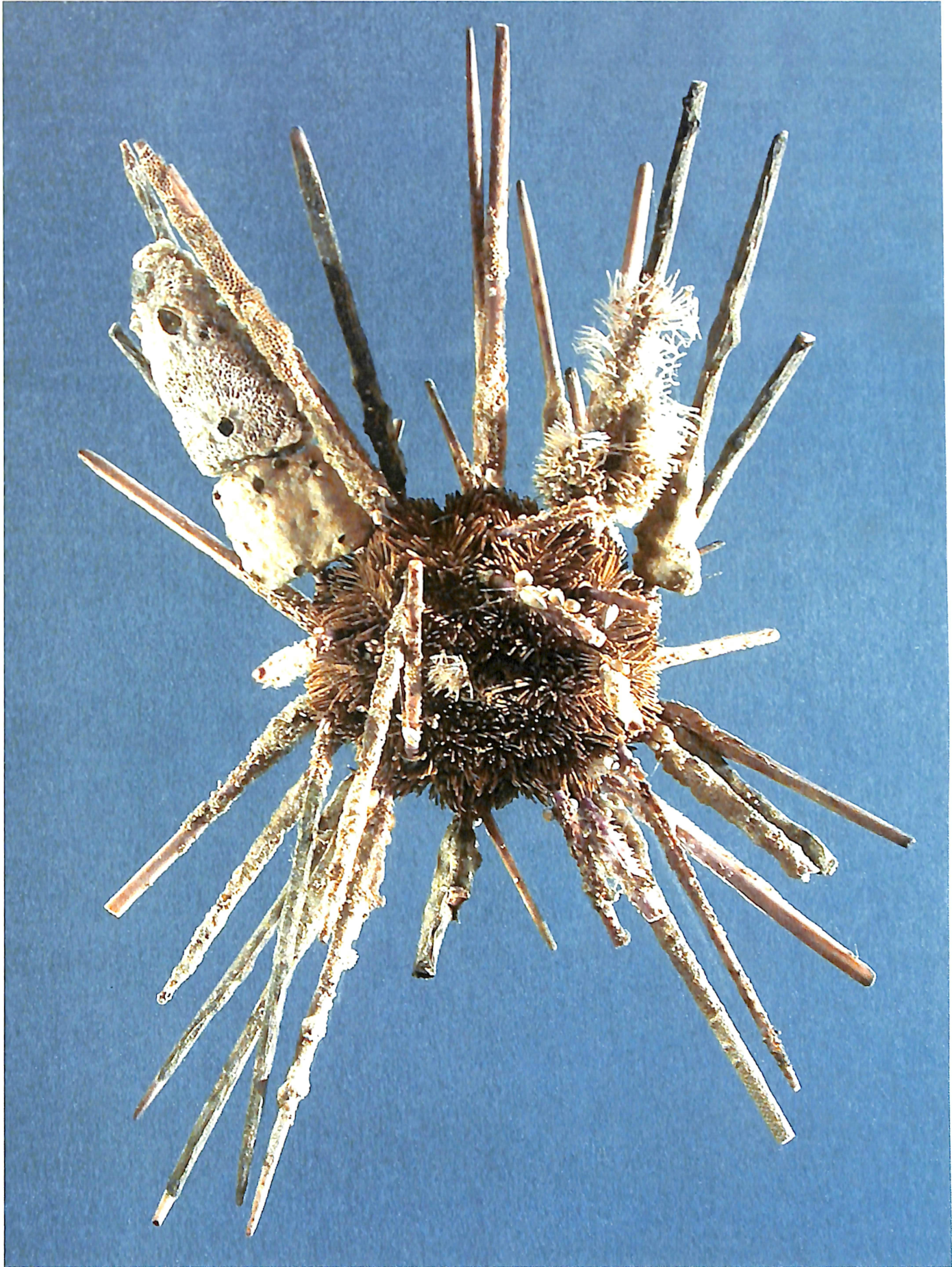
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Notocidaris mortenseni (Koehler 1900). **Weddell Sea. AWI**
The spines of the Antarctic cidarid are overgrown by numerous incurring organisms.

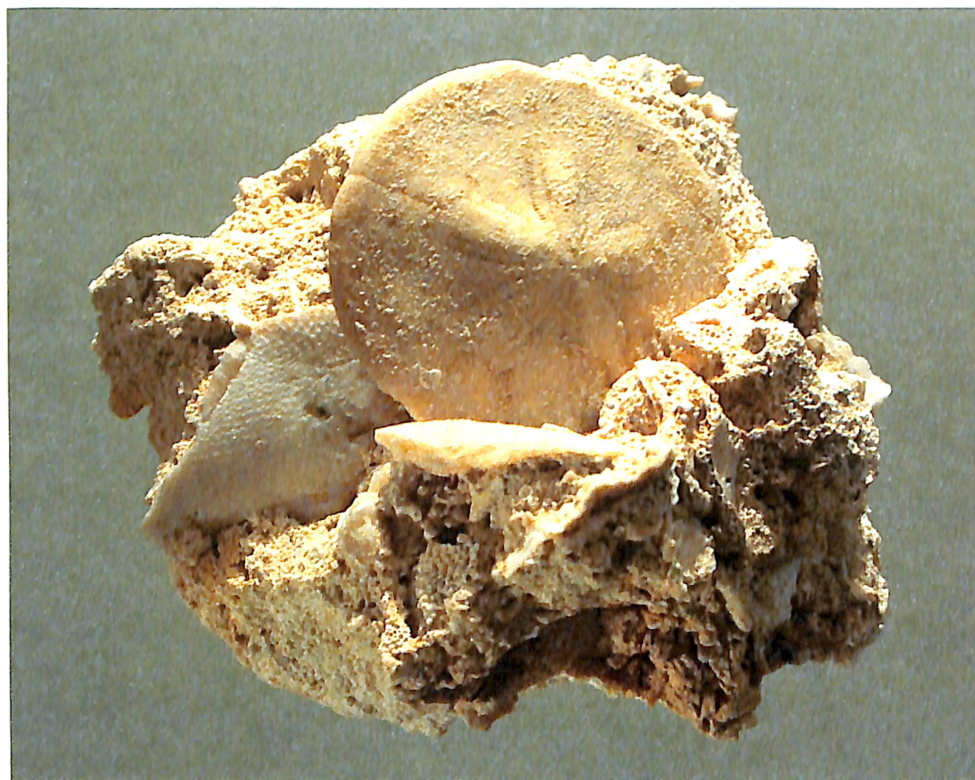
Preface

Today sea urchins are a highly diverse and remarkably successful group of marine invertebrates found living from the poles to the tropics and from the intertidal zone down to depths of more than 5000 m. Most people will have at some time in their lives encountered sea urchins in rock pools or while snorkelling in shallow water. Those that live on the surface protect themselves with a formidable array of spines that deters all but the most determined predator. But there is also a largely unseen diversity of forms living buried beneath the sea floor or hidden away in crevices and beneath algal fronds.

Sea urchins possess a calcite skeleton that has provided them with an excellent fossil record since they first evolved, some 450 million years ago. This skeleton is tough while the animal is alive but becomes much more fragile and easily broken once the soft tissue binding the plates has decayed. Their skeleton is remarkable for its five-fold symmetry, something that has made echinoids particularly attractive to collectors over the centuries. As a palaeontologist I have grown used to working on the wonderfully symmetrical skeleton of sea urchins. Yet it is often easy to forget that, in life, these animals can be even more stunningly beautiful. Many are vividly coloured and patterned though this colouration quickly fades and is lost in museum specimens and in fossils.

This book provides a much-needed guide to the modern shallow water species and will be of a boon to amateur and professional alike. No such overview has previously been attempted since the great monographs of Theodore Mortensen in the first half of the 20th century, and there the illustrations fail to capture their splendour. At last we have a publication that does justice to these amazing animals.

Andrew B. Smith
Department of Palaeontology,
The Natural History Museum,
London SW7 5BD, UK



Monostychia australis Laube 1869; **Blanchetown, South Australia. Tertiary, Early Miocene (Batesfordian).** The fossil clypeasteroid has been embedded 11 Million years ago amongst corals and fragments of molluscs. The species is endemic to southern Australia.

Foreword

At the seaside, when snorkeling or diving, one will find living sea urchins occasionally in shallow or deep water in reefs, in tide pools, on rocks or between sea-weed. The tests of dead individuals may lie as flotsam along the strandline, to be discovered when one walks along the beach. Some swimmers or beachcombers get a long lasting impression from them – after having stepped on their sharp spines. - Decorative tests and spines are used in shell craft and are sold as souvenirs, such as the flat white skeletons of the famous sand dollars, or the often beautifully coloured globes of regular sea urchins.

In general, most people will tend to encounter sea urchins on their holidays, when diving around the Maledives, swimming at the coast of Florida or trekking along the beach of northern California. However, a book on sea urchins to those who are interested in these animals is missing.

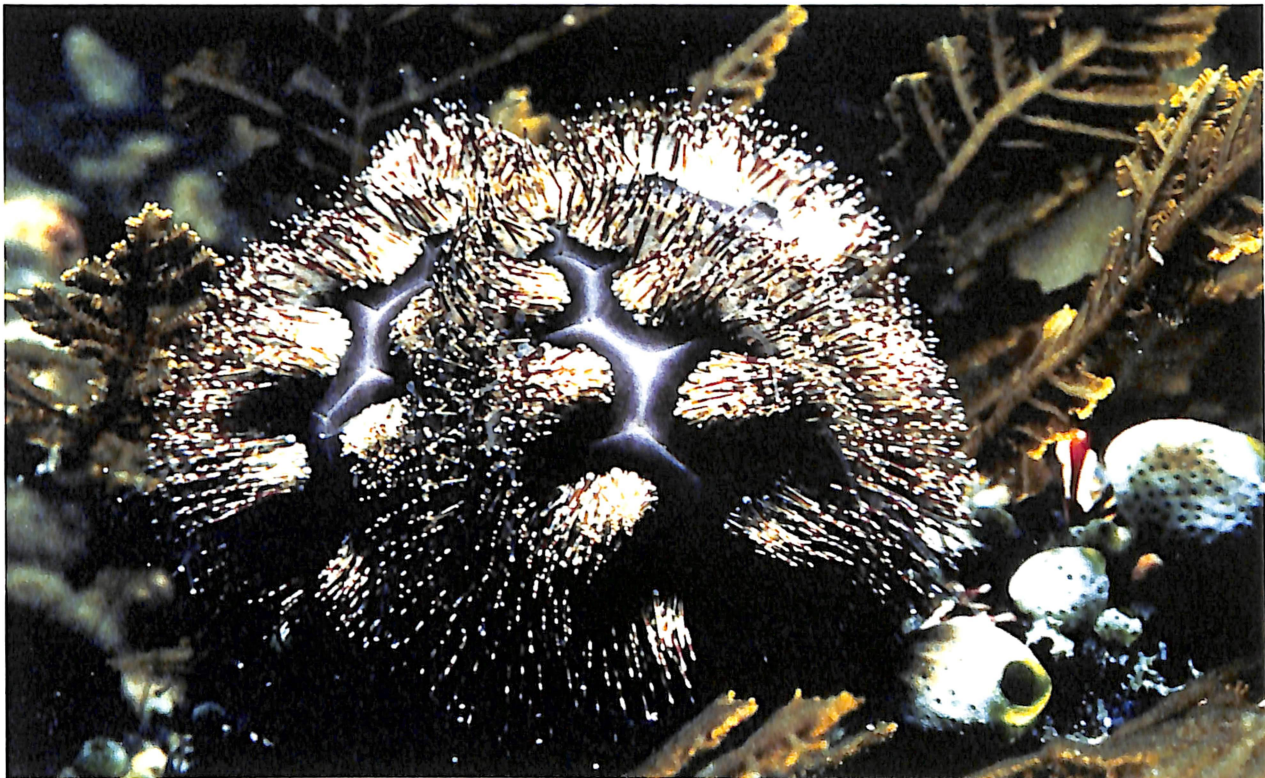
This book sets out to compile the sort of information on echinoids that allows the reader to determine the species of this group of echinoderms and to understand their behaviour.

I have dealt with most of the more or less commonly known sea urchins living in shallow water. But I have also included some species or groups which are really extraordinary, either in life-style, as the brood-protecting sea urchins of the Antarctic, or in beauty, as the species of *Coelopleurus*.

I wanted to display the astonishing diversification of these intrincating, beautiful and bizarre, living animals !!

I am grateful for each comment, improvement or addition. Please do not hesitate to contact me, for instance by my home-page: www.sea-urchins.com (Contact)

Heinke Schultz, Hemdingen, January 2005



Microcyphus rousseaui Agassiz & Desor 1847. Hurghada, Egypt, Red Sea.

The test has zones with densely packed short spines, and alternating, zigzag like naked areas, which are actually covered by microscopic pincer shaped structures. (Photo by H. and I. Rauch)

Acknowledgements

Many people were so kind to support me so that this book could be done:

First of all I want to thank Andrew B. Smith, The Natural History Museum, London, for the enormous, time-intensive task of reviewing the whole text (!), for improving my English and for checking the echinology. It was the best thing to happen to my book and to me !

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Thanks to Rich Mooi, California Academy of Sciences, San Francisco, who has followed and supported my "echinological career" for many years, and who has always answered my questions, even if they were rather stupid.

Thanks to Hilke Ruhberg and Peter Stiewe, that I could work in the echinoid collection of the Zoological Institute and Museum of the University of Hamburg. Without this illustrative material, and the experience and knowledge I could acquire there, I would have never begun the book.

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And last but not least I want to thank my husband Peter for his endless encouragement during these stressful years. He was the first who was sure that I was able to write this book, even before I myself dared to think about it. I am very grateful to him for doing the peripheral works such as the index, content and lists, the preparations for the printing – and that he has solved all the large and small problems with the PC and the programs. Without this help I would sometimes have been driven to despair.

And I thank my mother for her interest and sponsorship of the basic lecturer.

I am very grateful to all of you !!
Heinke Schultz

Introduction

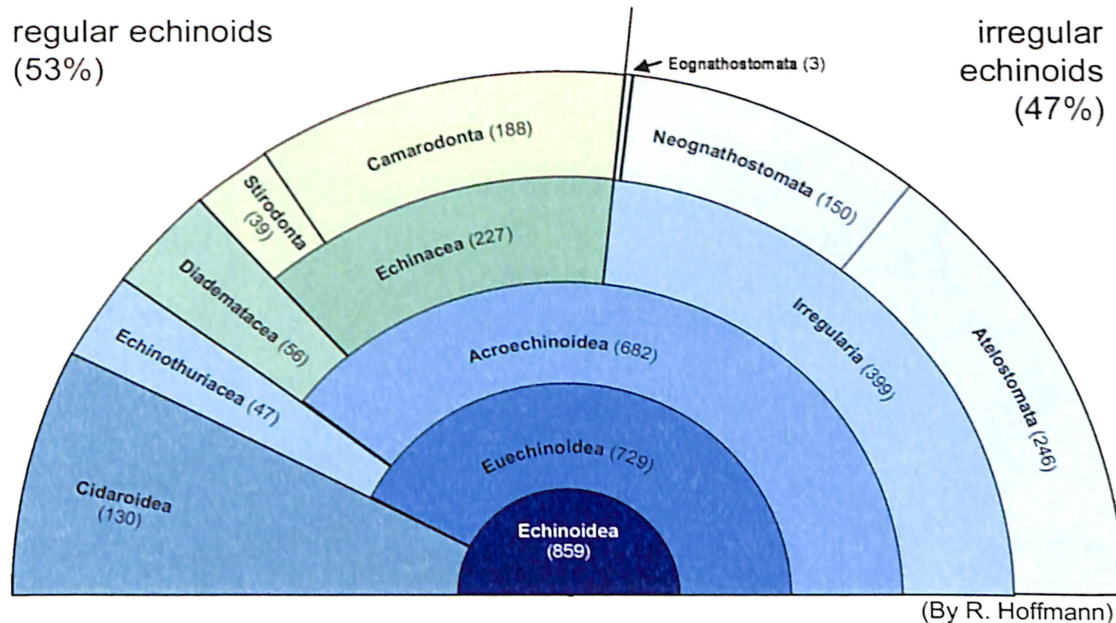


Fig. 1. The relations of the major divisions of Recent echinoids.
The numbers indicate the number of species (after Mortensen 1927 – 1951).

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 brittlestars (Ophiuroidea). They live exclusively in marine environments from the poles to the equator and from intertidal zones to depths of more than 5.000 meters. Fossil echinoids date as far back as the Late Ordovician Period, that is about 450 million years.

Superficially extant sea urchins can be divided into two groups: the “regulars” with a globose test and pentamerall symmetry, and the bilaterally symmetrical “irregulars”. But based on closer inspection fundamental differences in structure separate the subclass Cidaroida from the subclass Euechinoidea. To this later subclass belong besides the somewhat strange Echinothurioida (“leather urchins”), the regular Acroechinoids (Diadematacea and Echinacea) with seven orders, and the irregular Acroechinoids (Irregularia) with six orders. (See also classification and phylogenetic tree).

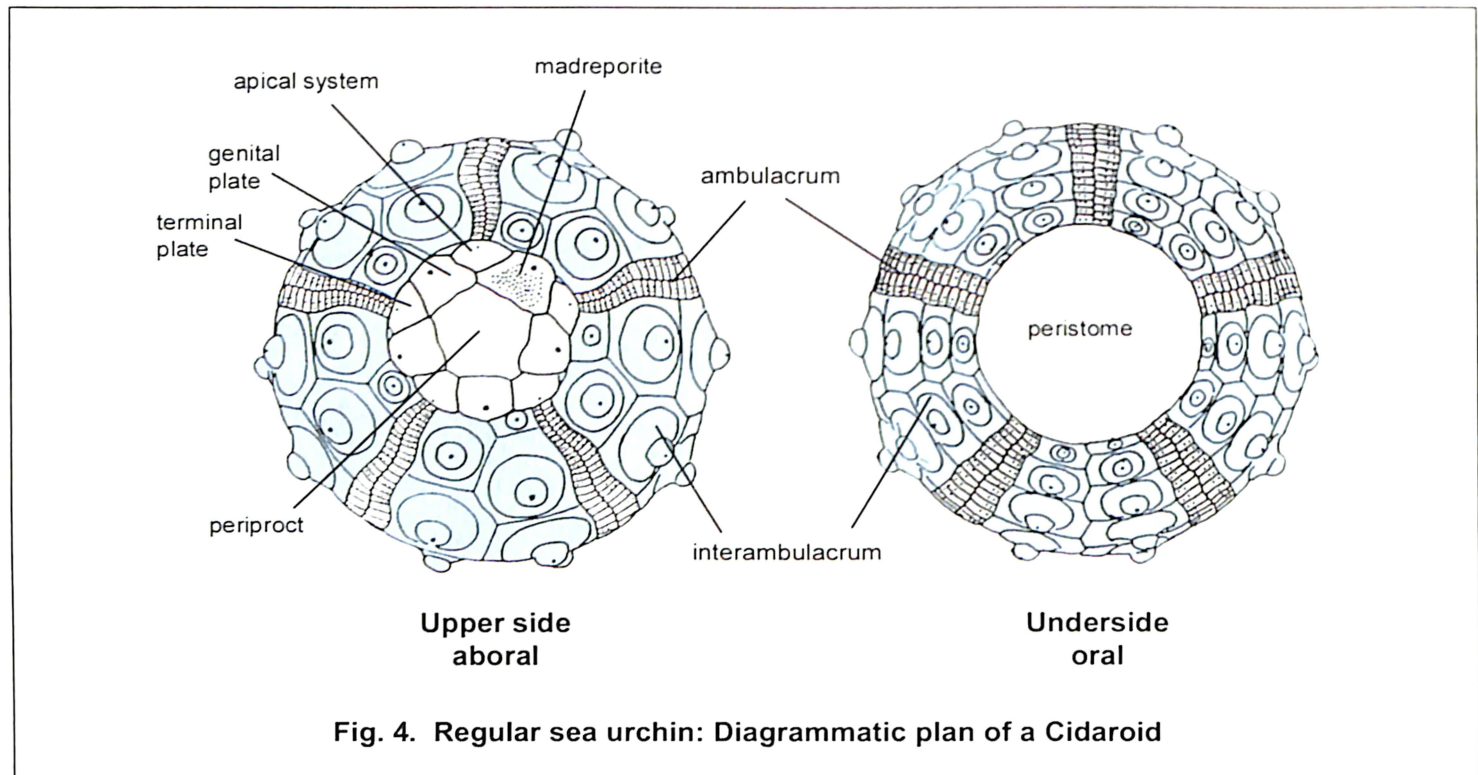


Fig. 2.
Regular sea urchin with pentamerall symmetry.



Fig. 3.
Irregular sea urchin with bilateral symmetry.

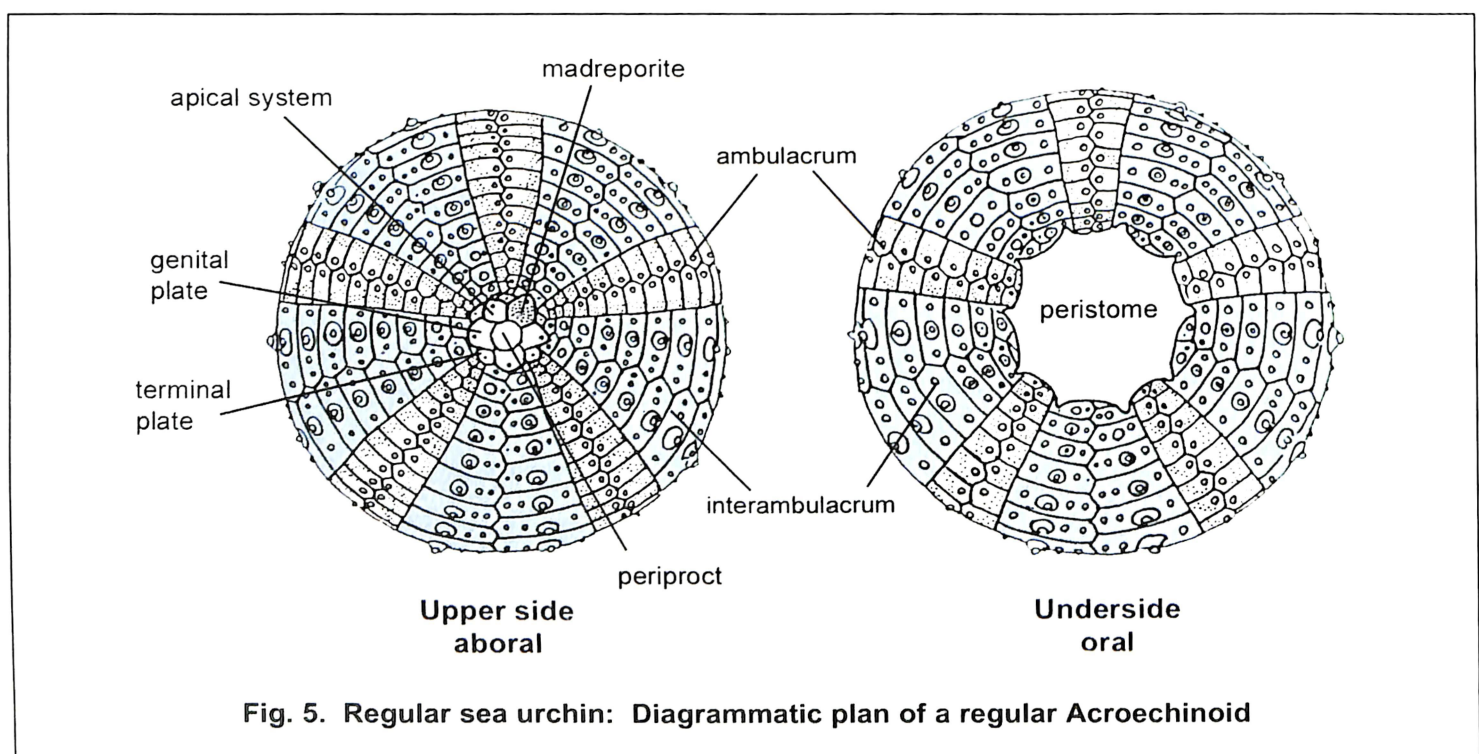
Body Plans of major groups of sea urchins

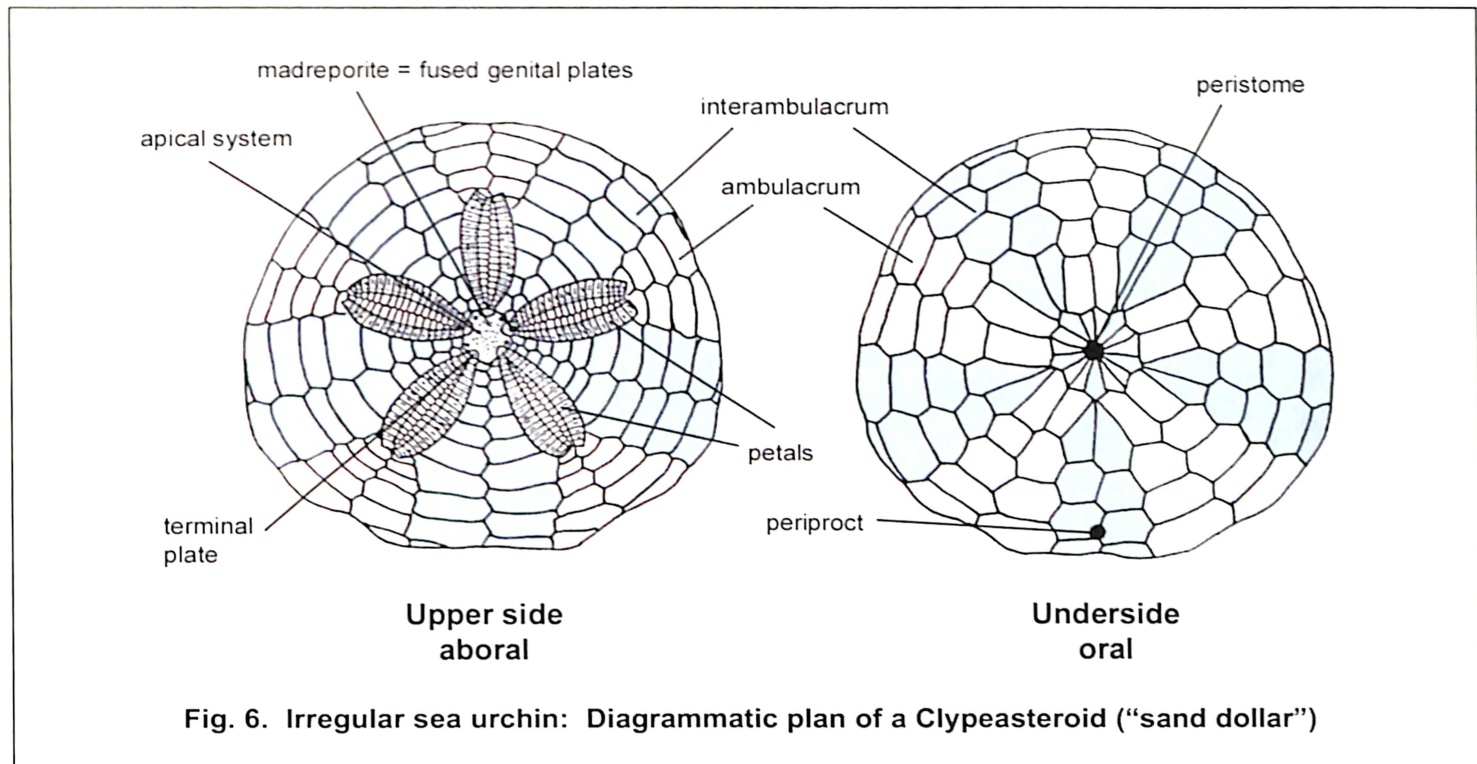


The hollow shell of the sea urchin (**test** or **corona**) is built of ten double columns of plates: five in the **ambulacra**, perforated by one or more pairs of pores or single ones; and five in the **interambulacra**. Each plate is equipped with one or more tubercles of various size, which carry spines or other specialized structures.

The apical system is on the upper (**aboral**) side. It is composed of ten or fewer plates, two to five genital plates, penetrated by **gonopores**, and five **terminal** (or **ocular**) **plates**. One genital plate is a more or less densely perforated sieve plate (**madreporite**), and the terminal plates have one pore. The anus lies enclosed by the ring of apical plates (**periproct**).

The mouth (**peristome**) is on the underside (**oral**).

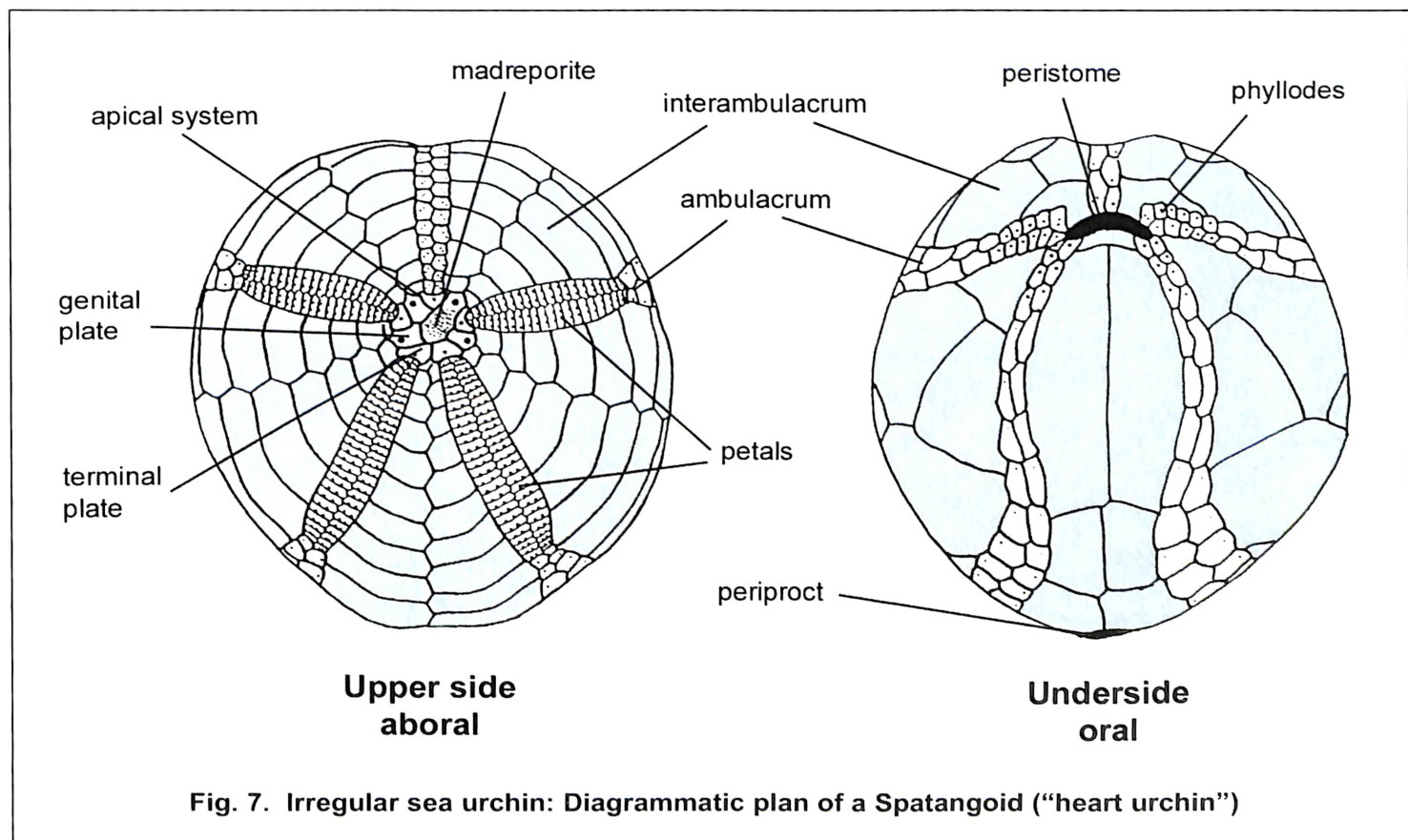




In **regular sea urchins** the double rows of plates are arranged in five virtually identical segments, and the test is pentameral.

In **irregular echinoids** this principal plan is modified and the test is bilaterally symmetrical with two equal sides. The anus has moved from the upper side out of the apical system to the posterior or oral side. On the upper side the ambulacral pores are concentrated in leaf-shaped areas (**petals**), on the oral side they are concentrated 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.



General Morphology:



Fig. 8. Upper side (aboral):
The columns of plates radiate from the apical system.

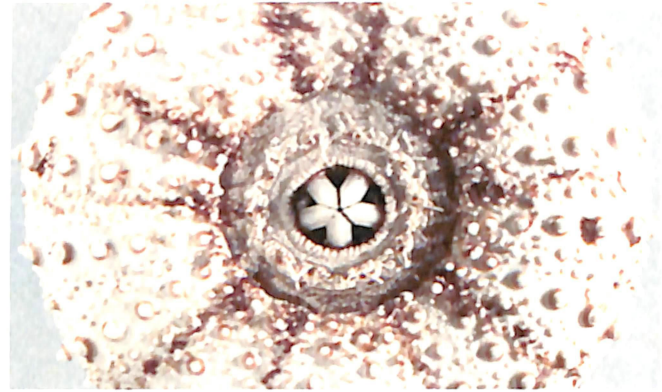


Fig. 9. Underside (oral):
The columns of plates converge at the peristome.

The hollow test, an internal skeleton covered by a skin, is composed of ten double columns of plates: The perforated **ambulacra (A)** are labelled from I to V; the alternating, unperforated **interambulacra (IA)** are labelled from 1 to 5.

The genital plates in the **apical system** are each pierced by a gonopore, from which eggs or sperm are released during spawning. Through the pores of the madreporite the internal **water vascular system** is connected to the exterior. The terminal 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.13).

The **periproct** within the ring of apical plates is in life covered by a flexible membrane, the opening of the anus more or less in the centre. (See figs. 4 – 7)



Fig. 10. External appendages: 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*. Page 279)



Fig. 11. External appendages: **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). See also fig. 34. Scale 5 mm. (*Amphipneustes bifidus*)

In irregular echinoids the number of genital plates varies between two and five according to the group, or there is a single, large star-shaped plate with madrepores.

The anus migrates during development from the apical system, and in adults it is situated at the posterior side or at the underside of the test.

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 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 centre of the peristomial membrane. All regular groups of echinoids have external teeth, which form part of a rather complicated **jaw apparatus**, called "Aristotle's lantern" (or simply "lantern"). 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.

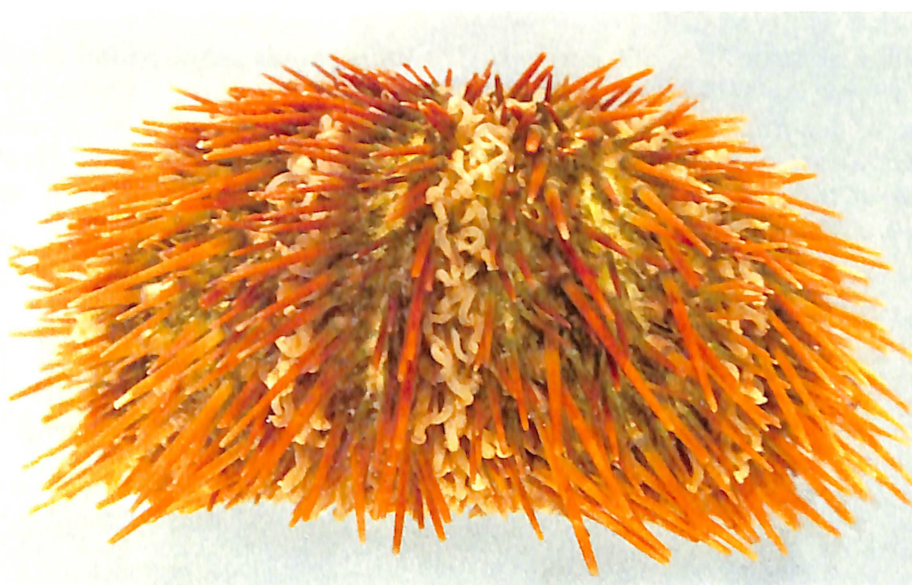


Fig. 12. External appendages: The wormlike **tube feet (podia)** are arranged in two rows in each ambulacrum, protruding from the pore-pairs. Their thin wall function as a surface for gaseous exchange. Their distal end is developed as a sucking disc and contains sensory organs. The tubes of the podia are very extensible. (*Parechinus angulosus*; test diameter with spines 45 mm; Cape Town, South Africa. Page 196).

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. 11 and 12)** 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. 10) are tiny, stalked, pincer-like valves, more or less densely scattered amongst 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.

Internal organs:

The **water vascular system** (fig. 13) consists of a tube connected through the pores of the sieve-plate (**madreporite**) to the exterior. It leads downwards 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 **terminal tentacle**, piercing through the terminal plate in the apical system.

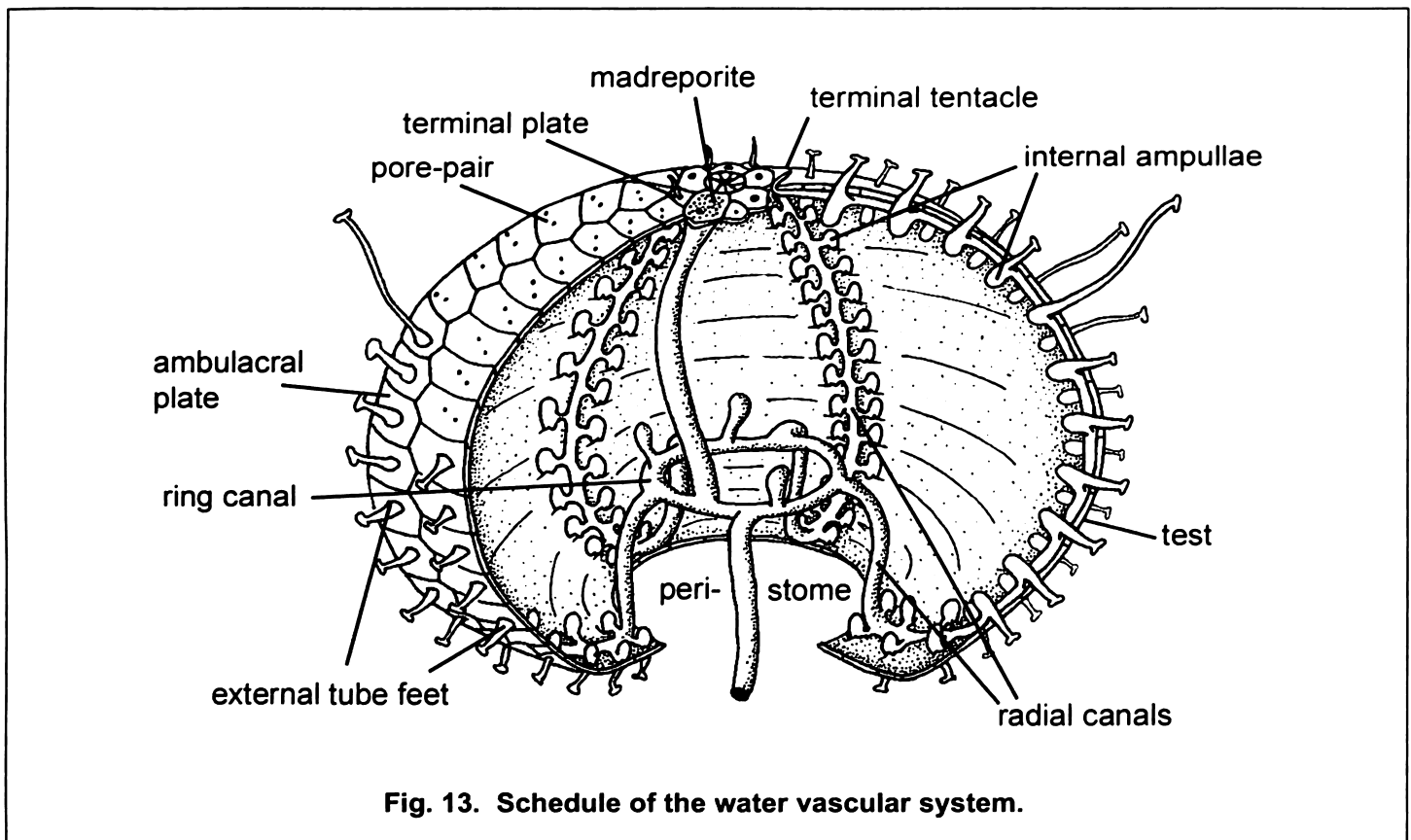
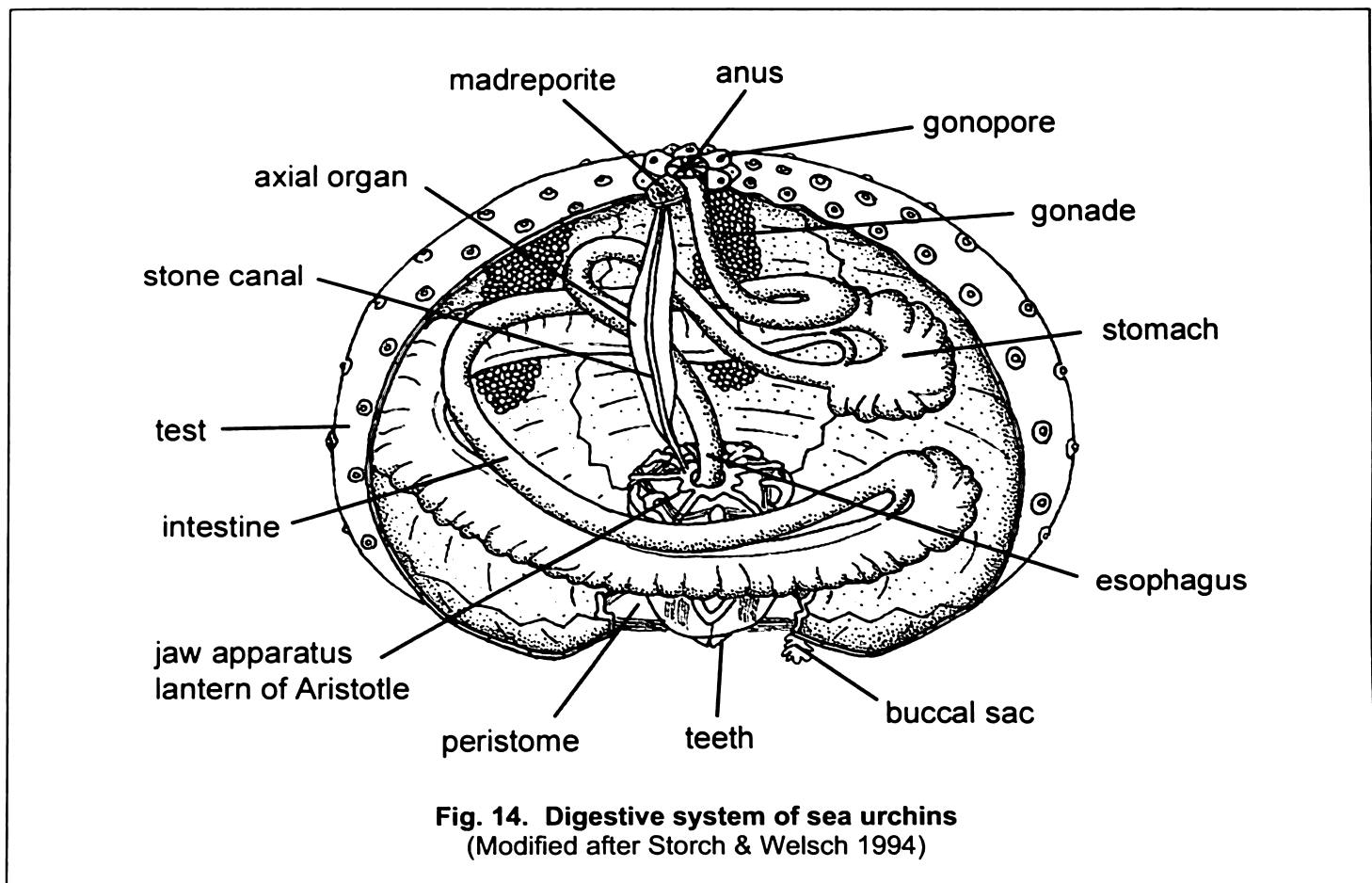


Fig. 13. Schedule of the water vascular system.

The **haemal 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 haemal system, but what precise function it may have is not clear.

Digestive system (fig. 14): 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. This latter ends in the **anus** that exits through the centre of the periproctal membrane.



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 sub-epithelial net of nerves which 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.

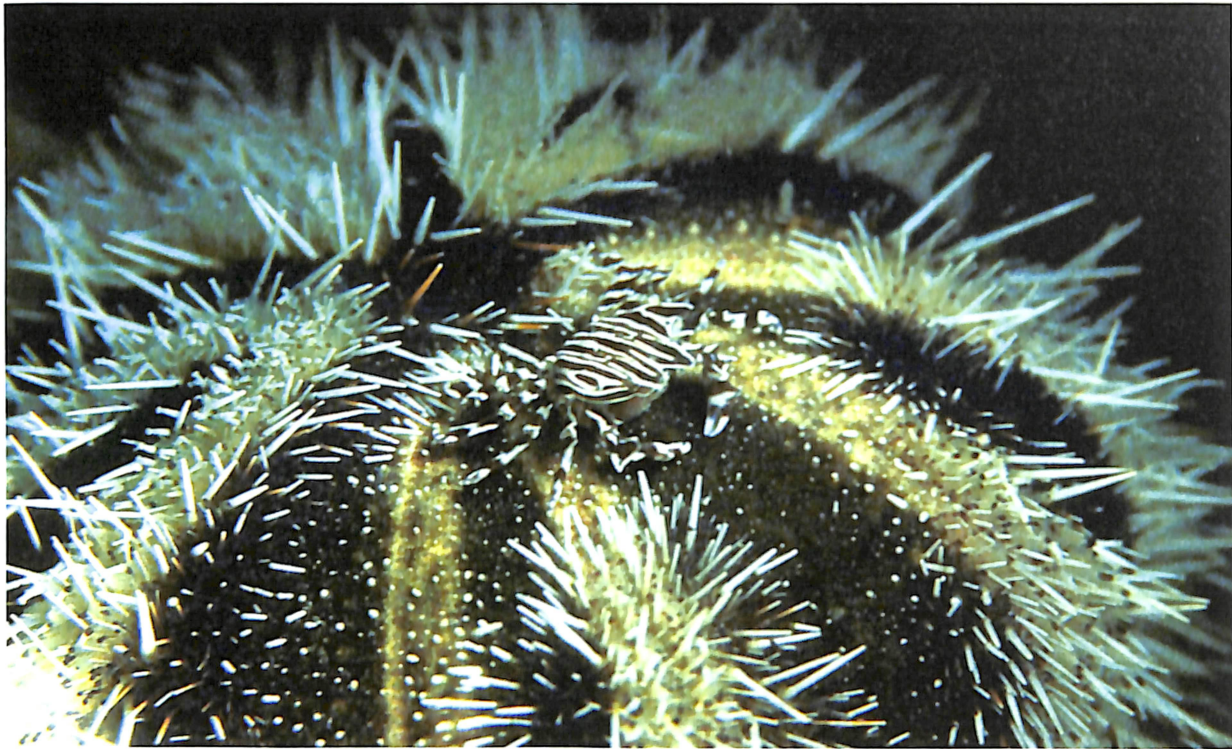


Fig. 15.

A small crab (*Zebrida adamsii*, family Eumedonidae) climbs over the test of the sea urchin. Between the white spines and the black pedicellariae the crab has found a perfect camouflage. Size of crab 15 mm.
(*Tripneustes gratilla*. Lembeh Strait, North Sulawesi, Indonesia. Photo by R. Kraft.)

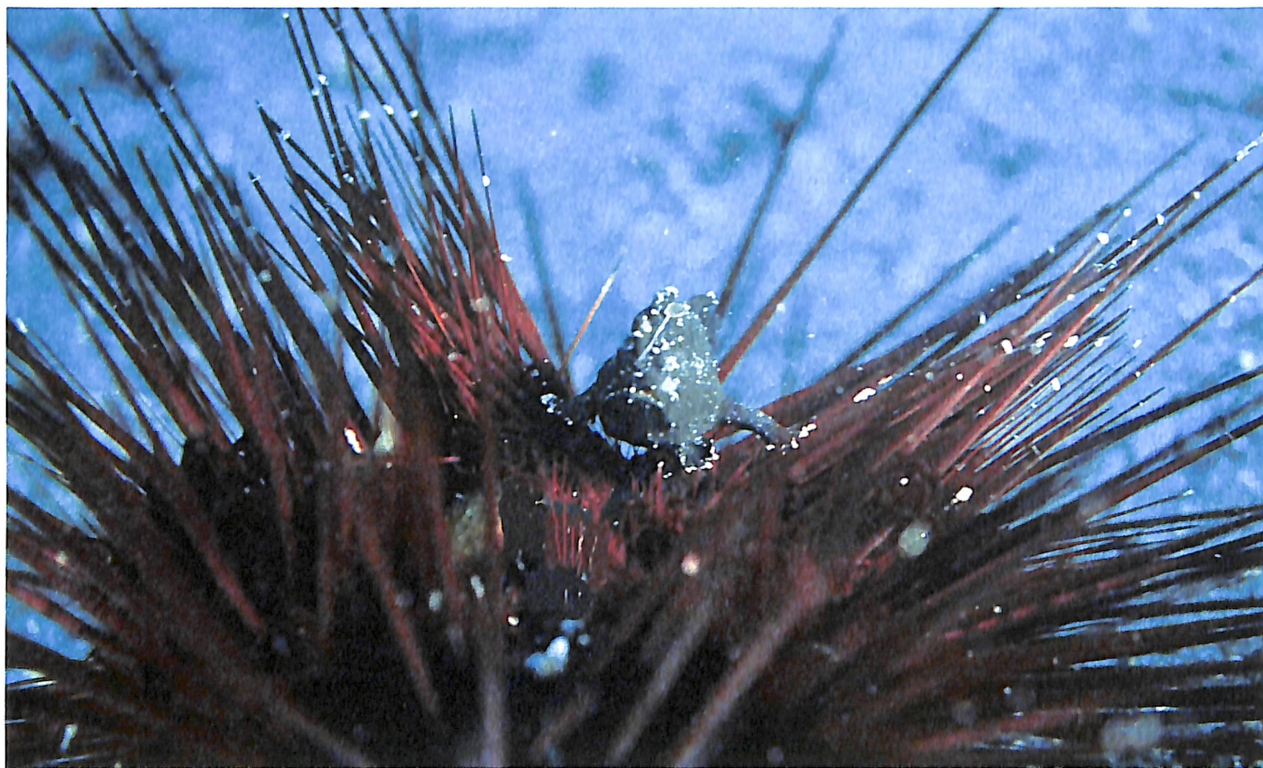


Fig. 16.

The sea urchin has laid its spines to the sides to enable the delicate frog fish (family Atennariidae) to wait for one of the small, black Cardinal-Fishes, which feed between the spines of the echinoid, to come near. Then it catches the prey. Length of the fish ca. 60 mm.
(*Astropyga*. Lembeh Strait, North Sulawesi, Indonesia. Photo by R. Kraft)

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, amongst gravels or in sands or even muds.

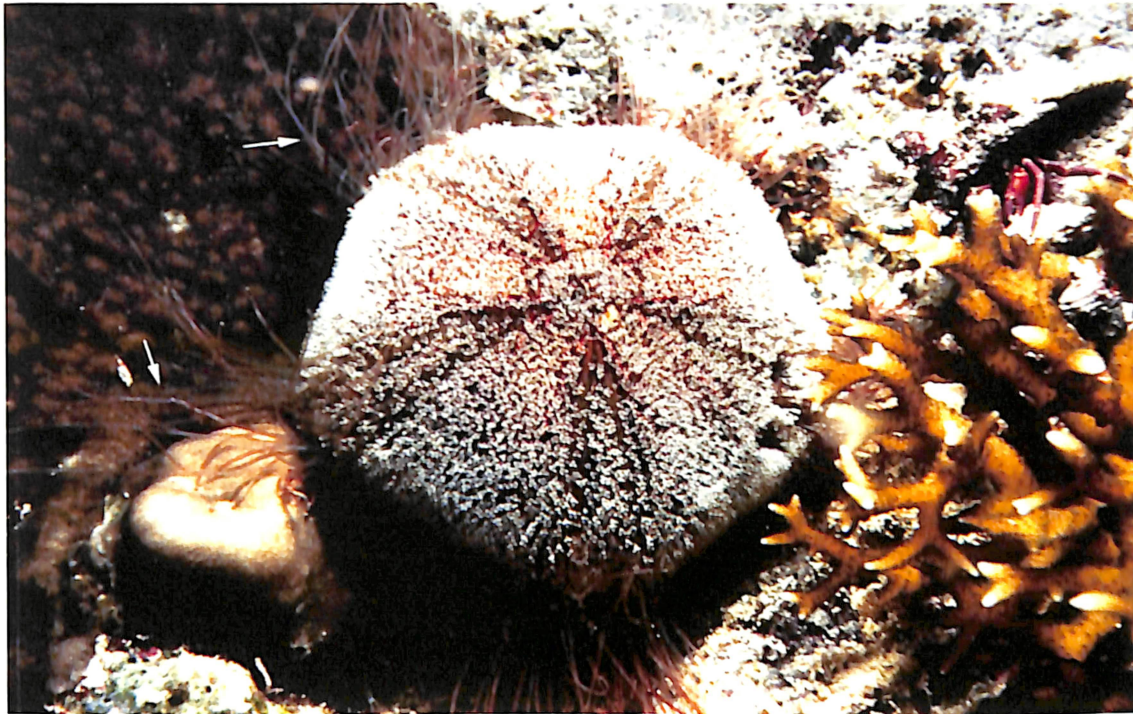


Fig. 17.

The greatly expanded tube feet (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*; Safaga, Egypt, Red Sea. Page 275. Photo H. and I. Rauch)

Locomotion:

Sea urchins generally use their oral spines for locomotion. Regulars move in any direction according to their pentamerous symmetry, while the sensitive, highly extendable tube feet examine the vicinity. 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 help of strong, often spatulate spines they plough or burrow through the sediment. 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.

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 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 abapical 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 faecal material.

Defence, predators and camouflage:

In regular echinoids the dense and spikey spines are used for defence. In cidarids the large interambulacral plates are set with large primary spines. The alternating ambulacra are narrow, 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 several ambulacral plates are fused to provide space for larger secondary spines and therefore better all round defence. The parts of the compound plate each retain their pore-pair, therefore the number of tube feet is not decreased.

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). 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 snails are the main predators of echinoids, the gonads are eaten by humans.

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 defence.



Fig. 18.

In tide pools many sea urchins cover their upper side with organic debris or small gravel particles, which the suckered discs of the tube feet hold tight. In this way the animals camouflage themselves in order to protect their tests against direct light. (*Strongylocentrotus purpuratus*; Mattole Beach, California, USA. Page 250.)

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 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” towards 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 (Fig. 11). They are able to pick up selectively organic particles from the sediment in their burrow. Other penicillate tube-feet, situated at the centre of the upper side, collect food from the surface of the sea bottom, bring it down a vertical funnel and placing 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.

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 aqua-culture of sea urchins has developed in recent years with the trend to rear specimens with more uniform and more attractively coloured gonads.

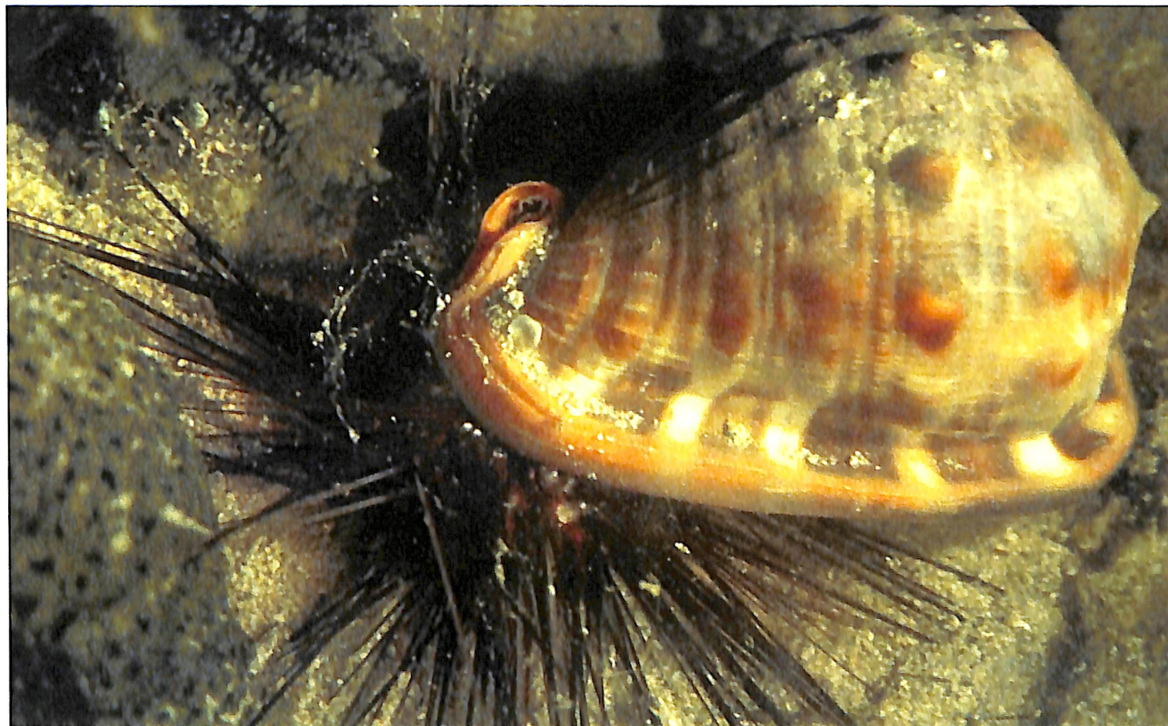


Fig. 19.

A large gastropode preys upon a diademate sea urchin. Length of snail 18 cm. *Cypræcassis rufa* (Linné 1758). Lembeh Strait, North Sulawesi, Indonesia. (Photo by R. Kraft)

Reproduction

In echinoids the sexes are separated. According to the group they have two to five gonades, 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.

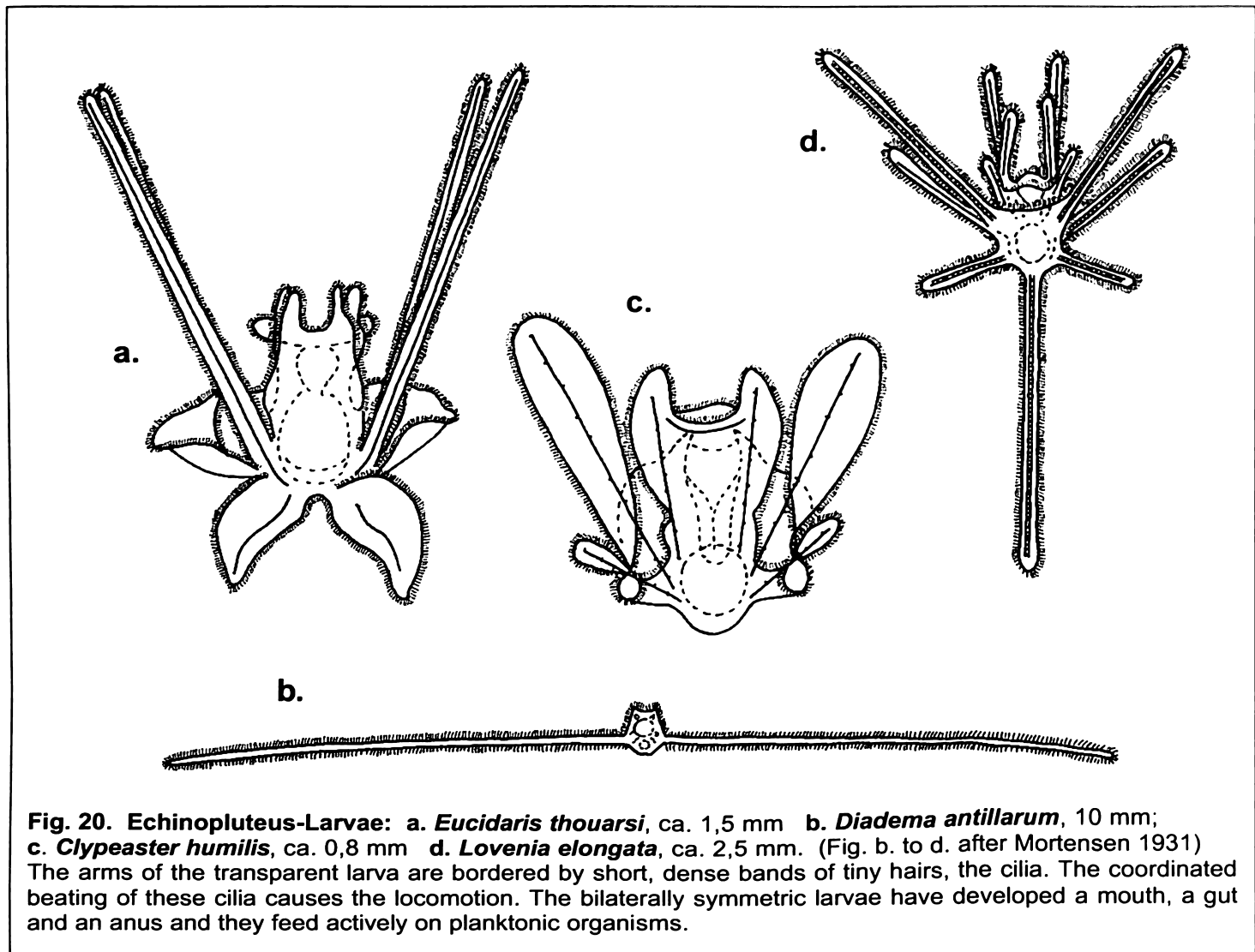


Fig. 20. Echinopluteus-Larvae: a. *Eucidaris thouarsi*, ca. 1,5 mm b. *Diadema antillarum*, 10 mm; c. *Clypeaster humilis*, ca. 0,8 mm d. *Lovenia elongata*, ca. 2,5 mm. (Fig. b. to d. after Mortensen 1931)
The arms of the transparent larva are bordered by short, dense bands of tiny hairs, the cilia. 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.

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. The larva lives in the plankton, actively feeding on micro-organisms (a condition termed "planctotrophic"). 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 pentamer 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 and no 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. The females have distinctly larger gonopores than the male.



Fig. 21. *Fibularia japonica*; Central Japan, Pacific.

Sexual dimorphism: The female (left) has four large gonopores, the male (right) has small gonopores. Length of female 5 mm, length of male 5,5 mm. Page 321.

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 tropic species. In Antarctic schizasterids the young grow very slowly in deep brood pouches (marsupia), living on the yolk from the egg. In the well studied *Abatus cordatus*, endemic to the Kerguelen Islands in the southern Indian Ocean, this stage lasts 8 ½ to 9 months. Then the young are able to feed actively and they leave the female.



Fig. 22. *Amphipneustes marsupialis* (Koehler 1926); 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. Page 447.



Fig. 23. Eggs and embryos of *Amphipneustes marsupialis*;

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.

In brood-protecting cidarids, - the predominant number of them also from Antarctica -, the juveniles are housed on the sunken peristomial membrane on the underside.

Thus there are 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.

Growth

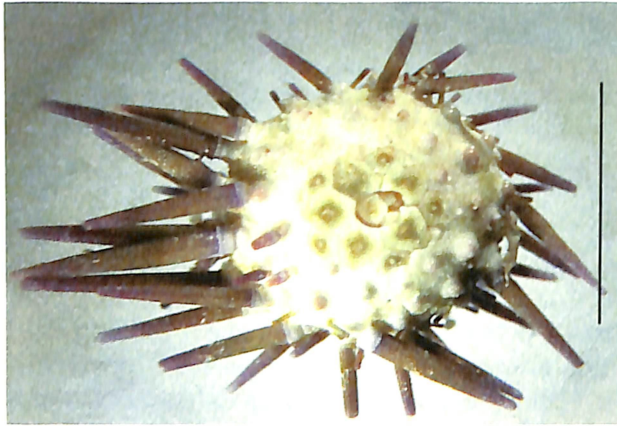
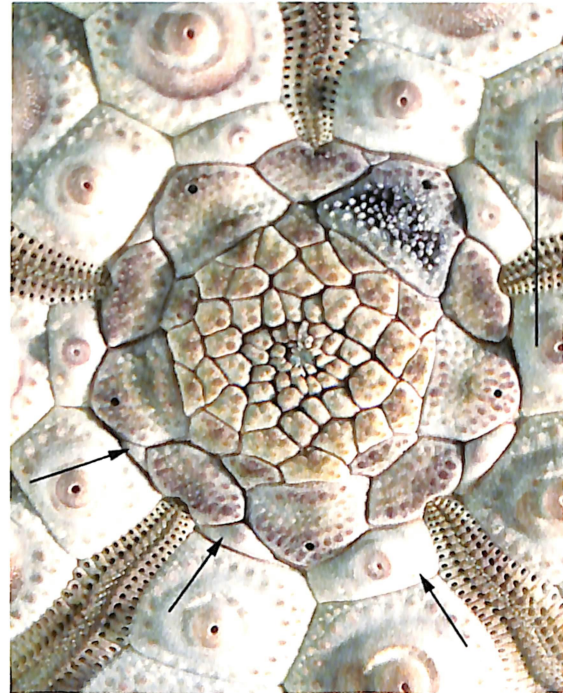


Fig. 24. Growth of echinoids:

(Above) The apical system of the young *Echinometra mathaei* is very large relative to the size of the test. Page 214. Scale 4 mm.

(Right) New plates are created at the outer edge of the terminal plates, the ambulacral plates in the centre 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 a sea urchin grows, new plates are added at the outer edge of the terminal plates. In very young specimens the apical plates cover the whole upper side, but as growth proceeds the apical system becomes smaller relative 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).

Evolution and Phylogeny



Fig. 25. *Hyattechinus pentagonus* Jackson 1912; diameter 49 mm; Lower Carboniferous, Pennsylvania, USA. (Cast of an external mould) (HVT)
Upper side: The broad interambulacra are covered with many columns of imbricating plates. The ambulacra are very narrow.



Fig. 26. *Lepidesthes wortheni* Jackson 1896; diameter 38 mm; Lower Carboniferous, Indiana, USA. (HVT)
Upper side: The ambulacra are broad and set with numerous pore-pairs. There are three columns of plates in each interambulacrum.

Echinoids first appear in the Upper Ordovician, about 450 million years ago. Various forms with flexible, imbricating plates evolved. 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.



Fig. 27. *Paracidaris jeanneti* (Lambert 1924); test diameter 18 mm; Upper Triassic, Hindelang, Germany. (HVT)



Fig 28. *Stereocidaris* sp. diameter 48 mm. Upper Cretaceous, Moen's Klint, Denmark. (JH)

Paracidaris lived 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.

The **cidarids** 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 faeces, released from the periproct on the upper side, are washed away by water currents. – They have principally the same life style as at the start of their evolution, which is restricted by the balance among the five virtually identical sections of the test. 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.

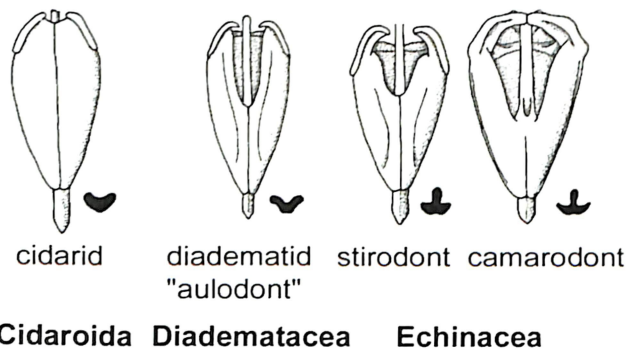
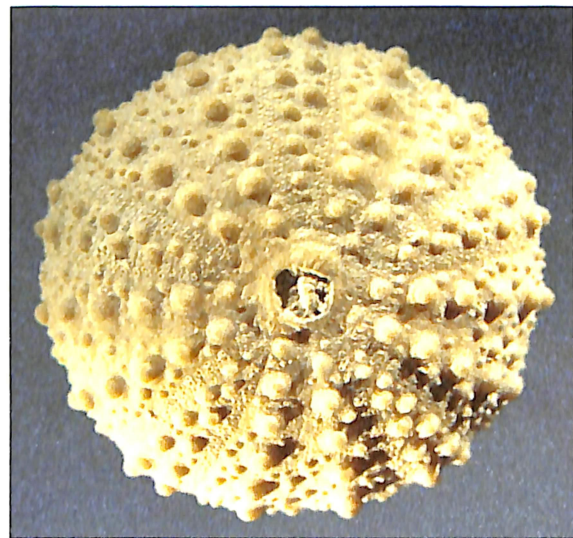


Fig. 29. Evolution of Aristotle's lantern:

Cidarids and diademataceans have teeth with an U-shaped cross section. Stirodont echinaceans evolved mechanically stronger T-shaped (or keeled) teeth evolved. In the camarodont echinaceans 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)

Fig. 30. Acroechinoid regular echinid:
Phymechinus mirabilis L. Agassiz 1846.
Diameter 41 mm. Upper Jurassic, France
(Photo by H. v. Noordenburg)

Below: In ambulacra and interambulacra two series of sub-equal tubercles are developed which in life would have been set with numerous spines for defence.



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 manoevrable lanterns which 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 defence. The number of pore-pairs didn't decrease essentially.

Diademataceans 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. Their “bite” could be harder and they could graze more efficiently on encrusting organisms.

In the Cretaceous the camarodont lantern evolved in the **Temnopleuroidea**, 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 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*. 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 channelled through a depressed anal groove towards the posterior end of the test. The bilateral symmetry, that is 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 Pygasteroidea and the Hololectypoida 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.

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.



Fig. 31. Cassiduloid *Clypeus plotii* Leske 1778, length 102 mm; Middle Jurassic, England. (HM)
Aboral side: With the five narrow ambulacra the test still resembles in appearance that of a regular echinoid. But as the periproct has moved out from the apical system, lying immediately posterior in a deeply depressed groove, the echinoid is bilaterally symmetrical with a clearly defined anterior and posterior.



Fig. 32. Cassiduloid *Hardouinia mortonis* Michelin 1855; length 51 mm; Upper Cretaceous, USA.
Oral side: 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.

The dense uniform spine canopy enabled **cassiduloids** and **disasteroids** to move into finer sediment, 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. Teeth were no 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 Holasteroidea and Spatangoidea in Late Jurassic – Early Cretaceous, both of which inherited this kind of tube foot.



Fig. 33. Holasterid *Hemipneustes striatoradiatus*, (Leske 1778); length 84 mm; Upper Cretaceous, Netherland. (Coll. HvN)

In each petal slit-like pore-pairs are developed, 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.



Fig. 34. 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.

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 which create a current of fresh water over the respiratory podia and the whole surface. The tube feet of the anterior ambulacrum served no longer 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 **holasteroids** lack funnel-building tube feet. Generally, in contrast to the spatangoids, they have never been particularly successful burrowers. 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 two species they have developed the most advanced mode of reproduction, brood-protecting of the young within the body of the female.

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

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 amongst the sand grains. These particles are laid into food grooves to be transported in a mucous string towards the mouth to be crunched by the broadly winged, internal teeth. Obviously this innovation was very efficient, for within 15 to 20 million of years these flat disced sand dollars 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, till the possibilities of the new niches are exhausted.



Fig. 35. Clypeasteroid *Monostychia australis*
Laube 1869; test length 42 mm; Tertiary, Miocene;
South Australia.

Upper side: The ambulacra are broad, each marked by a food groove, which leads round the margin to the central mouth.

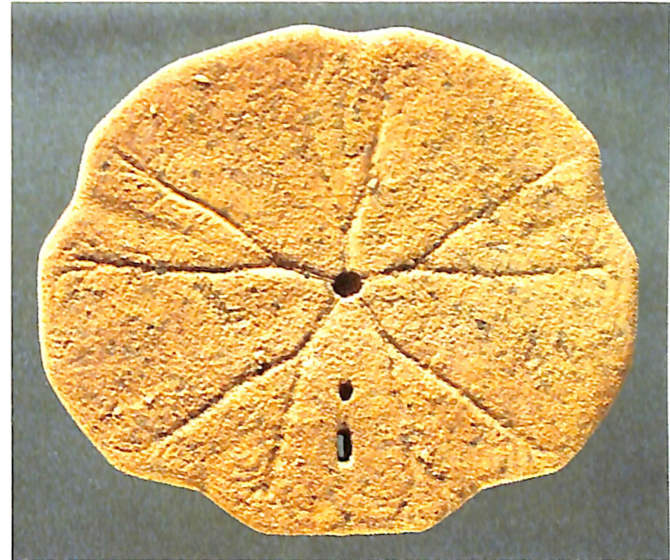


Fig. 36. Clypeasteroid *Monophoraster darwini*
(Desor 1847); test length 58 mm; Tertiary, Miocene,
Argentina.

Oral side: The branched food grooves spread over the surface. The periproct is situated between the peristome and the small anal lunule.

Tribe : Echinodermata

Class: **Echinoidea****SUBCLASS: PERISCHOECHINOIDEA***Lower Silurian - Upper Permian***SUBCLASS: CIDAROIDEA****Order: Cidaroida**

Family: *Miocidaridae*
Psychocidaridae
Histocidaridae
Cidaridae

Lower Permian – Recent
Lower Permian – Recent
Lower Permian – Middle Jurassic
 Lower Jurassic – Recent
 Upper Triassic – Recent
 Upper Triassic - Recent

SUBCLASS: EUECHINOIDEA**INFRACLASS: ECHINOTHURIOIDEA****Order: Echinothurioida**

Family: *Pelanechinidae*
Echinothuriidae
Phormosomidae

Upper Triassic – Recent
 Middle Jurassic – Recent
Middle Jurassic – Recent
Upper Jurassic
 Upper Cretaceous – Recent
 Recent

INFRACLASS: ACROECHINOIDEA**COHORT: DIADEMATACEA****Order: Pedinoida**

Family: *Pedinidae*

Order: Diadematoidea

Family: *Diademataidae*
Aspidodiademataidae
Lissodiademataidae

Order: Micropygoida

Family: *Micropygidae*

Upper Triassic – Recent
Upper Triassic – Recent
 Upper Triassic (Rhaetian) –Recent
Lower Jurassic – Recent
 Lower Jurassic – Recent
 (? Upper Jurassic) – Recent
 Recent
Recent
 Recent

COHORT: ECHINACEA

Family: *Pseudodiademataidae*

Superorder: Stirodonta

Family: *Hemicidaridae*

Order: Phymosomatoida

Family: *Phymosomatidae*
Glyptocidaridae
Stomechinidae
Stomopneustidae
Arbacidae

Order: Salenioida

Family: *Acrosaleniidae*
Saleniidae

Superorder: Camarodonta

Family: *Glyphocyphidae*

Order: Temnopleuroidea

Family: *Temnopleuridae*

Order: Echinoida

Family: *Echinidae*
Parechinidae
Echinometridae
Strongylocentrotidae
Toxopneustidae

Order: Orthopsida

Family: *Orthopsidae*

Upper Triassic – Recent
Upper Triassic –Lower Cretaceous

Lower Jurassic – Upper Cretaceous
Lower Jurassic – Recent
Lower Jurassic – Tertiary (Oligocene)
 Tertiary (Eocene) – Recent
Lower Jurassic – Tertiary (Eocene)
 Tertiary (Miocene) – Recent
 Middle Jurassic – Recent
Lower Jurassic – Recent
Lower Jurassic – Upper Cretaceous
 Upper Jurassic –Recent

Lower Jurassic – Tertiary (Eocene)
Upper Cretaceous – Recent
 Upper Cretaceous – Recent
Tertiary (Paleocene) – Recent
 Tertiary (Miocene) – Recent
 Tertiary Miocene) – Recent
 Tertiary (Paleocene) – Recent
 Tertiary (Miocene) – Recent
 Tertiary (Miocene) – Recent
Lower Jurassic – Upper Cretaceous
Lower Jurassic – Upper Cretaceous

COHORT: IRREGULARIA

Family: *Eodiademataidae*

Superorder: Eognathostomata**Order: Pygasteroida**

Family: *Pygasteridae*

Order: Holectypoida

Suborder: Holectypina

Family: *Holectypidae*
Discoididae
Anorthopygidae

Lower Jurassic

Lower Jurassic – Upper Cretaceous
Lower Jurassic – Upper Cretaceous
Lower Jurassic – Recent
Lower Jurassic – Upper Cretaceous
Lower Jurassic – Upper Cretaceous
 Cretaceous
 Cretaceous

Extinct taxa in italic

Suborder: Echinoneina
 Family: Echinoneidae
Conulidae
Galentidae

Superorder: Microstomata
 Family: *Menopygidae*

Series: Neognathostomata
 Family: *Galeropygidae*

Order: Cassiduloida
 Family: *Clypeidae*
Nucleolitidae
Apatopygidae
Cassidulidae
Archiaciidae
Clypeolampadidae
Piilampadidae
Echinolampadidae
Conoclypidae
Faujasiidae
Neolampadidae

Order: Oligopygoida
 Family: *Oligopygidae*
Togocyamus

Order: Clypeasteroida
Suborder: Clypeasterina
 Family: *Clypeasteridae*
Arachnoididae
Fossulasteridae
Scutellinoididae

Suborder: Laganina
 Family: *Fibulariidae*
Laganidae
Neolaganidae
Rotulidae

Suborder: Scutellina
Proescutella
 Family: *Scutellinidae*
Protoscutellidae
Eoscutellidae
Scutellidae
Echinarachniidae
Abertellidae
Dendrasteridae
Scutasteridae
Astricypeidae
Monophorasteridae
Mellitidae

Series: Atelostomata
Order: Disasteroida
 Family: *Disasteridae*
Collyritidae

Order: Holasteroida
 Family: *Holasteridae*
Stenonasteridae
Corystidae
Urechinidae
Plexechinidae
Pourtalesiidae
Calymnidae

Order: Spatangoida
 Family: *Toxasteridae*

Suborder: Micrasterina
 Family: *Micrasteridae*
Brissidae
Loveniidae
Spatangidae

Suborder: Hemiasterina
 Family: *Hemiasteridae*
Palaeostomatidae
Schizasteridae
Pericosmidae
Aeropsidae

Asterostomatidae

Middle Jurassic – Recent
 Upper Cretaceous- Recent
Middle Jurassic – Tertiary (Eocene)
Upper Jurassic

Middle – Upper Jurassic

Jurassic

Middle Jurassic – Recent

Lower Jurassic – Upper Cretaceous

Middle Jurassic – Upper Cretaceous

Upper Tertiary – Recent

Lower Cretaceous– Recent

Cretaceous

Upper Cretaceous

Upper Cretaceous – Recent

Cretaceous –Recent

Upper Cretaceous – Tertiary (Eocene)

Upper Cretaceous – Tertiary (Eocene)

Tertiary (Eocene) – Recent

Upper Cretaceous – Tertiary (Oligocene)

Upper Cretaceous – Tertiary (Oligocene)

Lower Tertiary (Palaeocene)

Tertiary (Eocene) – Recent

Tertiary (Eocene) – Recent

Upper Eocene – Recent

Tertiary (Oligocene) – Recent

Tertiary (Upper Oligocene to Miocene)

Tertiary (Miocene)

Tertiary (Eocene) – Recent

Tertiary (Eocene) – Recent

Tertiary (Eocene) – Recent

Tertiary, Eocene – Oligocene

Tertiary (Miocene) – Recent

Tertiary (Eocene) – Recent

Tertiary, Eocene – Miocene

Eocene

Middle – Upper Miocene

Middle Eocene – Miocene

Oligocene – Miocene

Oligocene – Recent

Middle Miocene

Upper Miocene – Recent

Oligocene – Miocene

Oligocene – Recent

Miocene

Pliocene – Recent

Lower Jurassic – Lower Cretaceous

Middle Jurassic – Lower Cretaceous

Lower Jurassic – Lower Cretaceous

Cretaceous – Recent

Cretaceous – Tertiary

Upper Cretaceous

Palaeocene - Recent

Miocene ? – Recent

Recent

Recent

Recent

Lower Cretaceous – Recent

Cretaceous

Upper Cretaceous – Recent

Upper Cretaceous – Recent

Upper Cretaceous – Recent

Eocene – Recent

Eocene – Recent

Lower Cretaceous – Recent

Lower Cretaceous – Recent

Upper Cretaceous – Recent

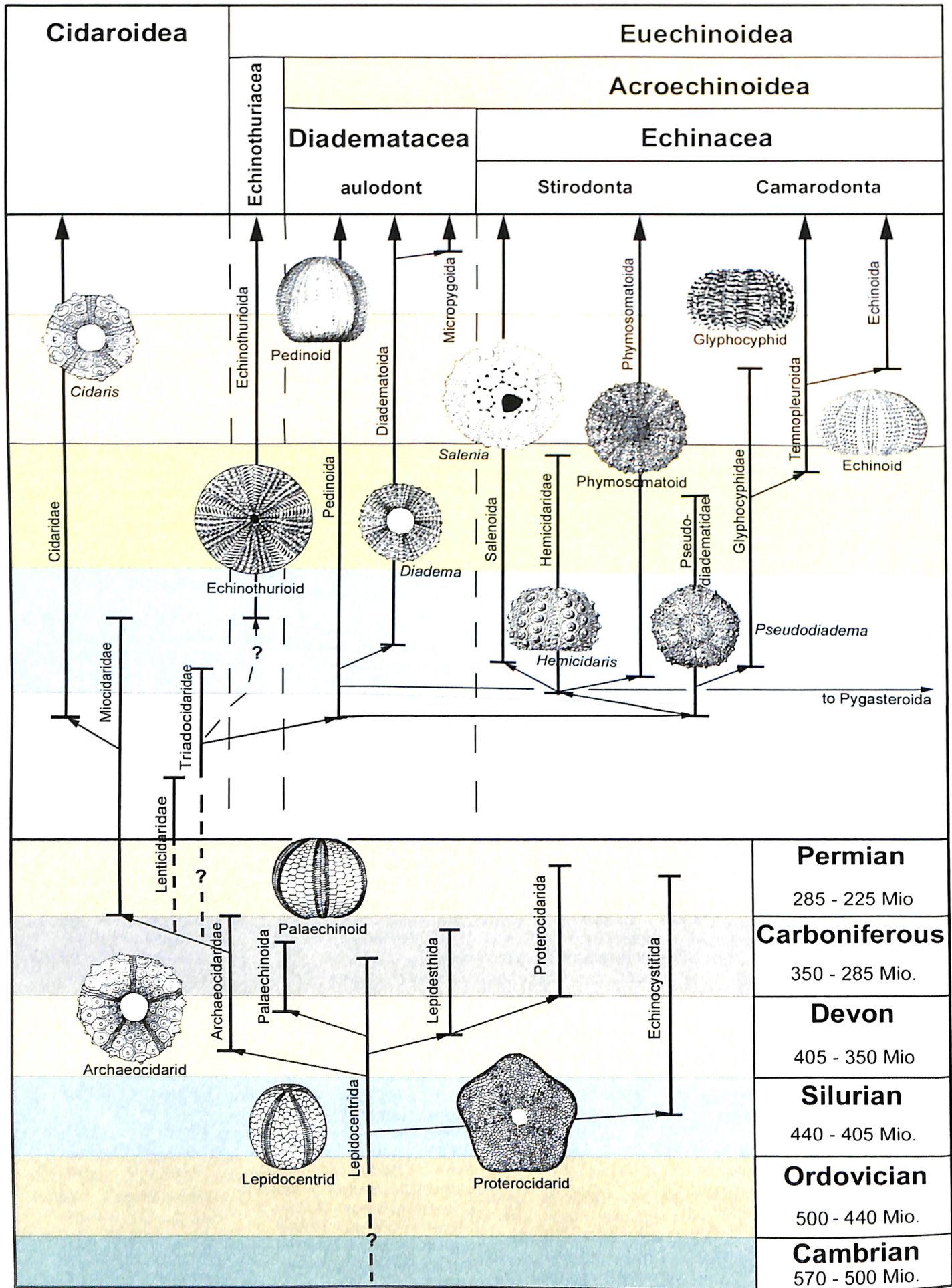
Upper Cretaceous – Recent

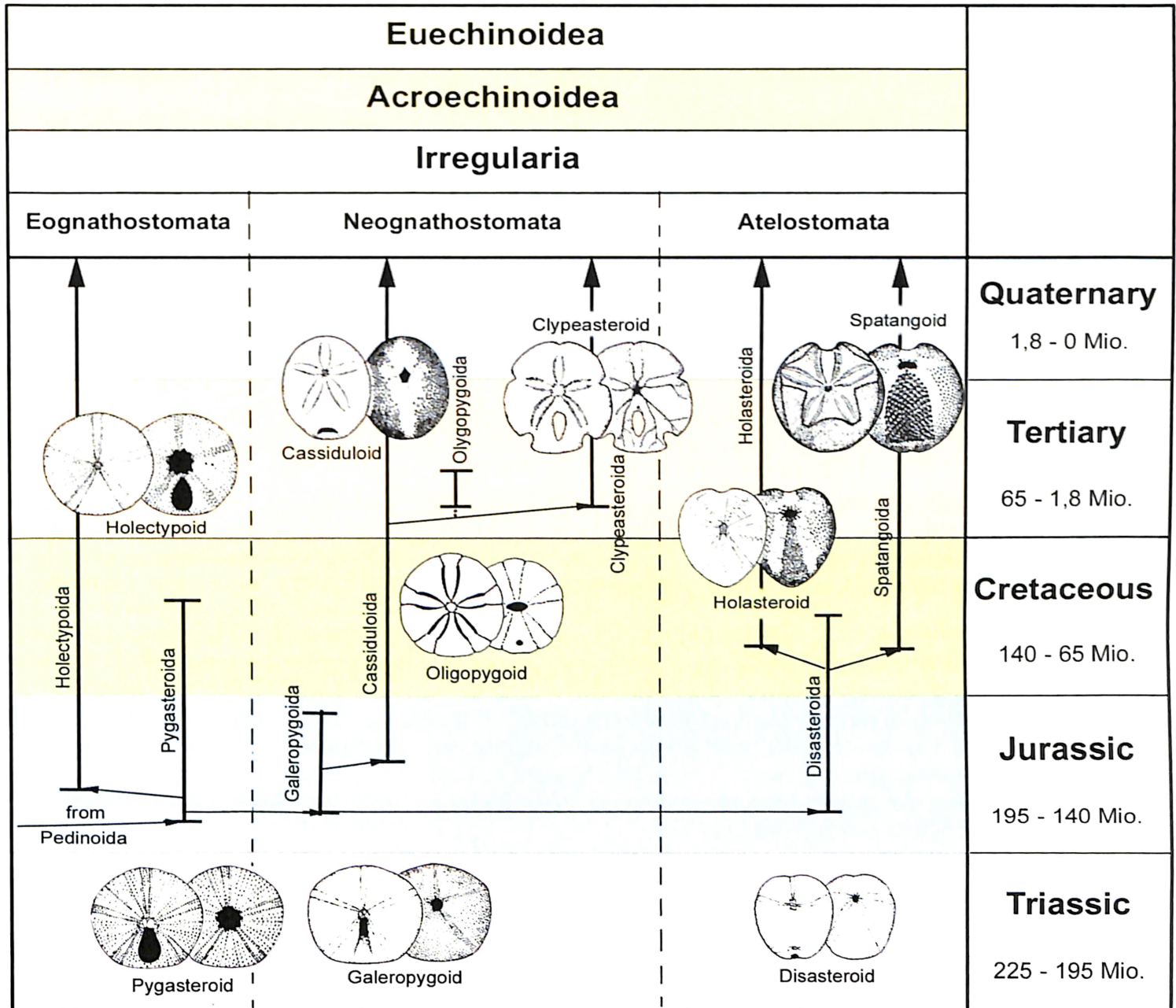
Tertiary (Eocene) – Recent

Recent

Eocene – Recent

(Modified after A.B. Smith 1984) Extinct taxa in italic





Phylogenetic tree and stratigraphical ranges of the Echinoidea

after: A. B. Smith 1984
R. Mooi 1990